Experimental Investigations into the Ecological Functions of Cryptogams in Alpine Plant Communities

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ABSTRACT

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Vegetation scientists and alpinists alike have long noted the impressive collection of cryptogams in alpine plant communities, yet few have endeavored to uncover what ecological roles they may have. I attempted to address the question of whether and how cryptogams affect the higher plants with which they cohabitate, using several manipulative experiments involving the soil-plant-cryptogam matrix. Studies were conducted in the alpine and subalpine zones of mountains in Washington State and Chile. In most experiments, I measured the performance of several alpine plant species in the midst of either abundant or no cryptogam cover, and I coupled this with measurements of the physical and biogeochemical status of the rhizosphere. The results of these experiments cautiously support the view that some cryptogams influence the growth of neighbor plants. Most notable were the reductions in growth of grass-like species seen in plots where fruticose (large-bodied) cryptogams were removed; *Festuca contracta* lost approximately 40% of its initial cover when the lichen *Usnea trachycarpa* was removed from the spaces between plants, and *Carex scirpoidea* lost approximately 10% of its initial cover when the mixture of *Flavocetraria cucullata* and *Cetraria islandica* was removed from its surroundings. These growth reductions coincided with greater leaf temperature swings and some profound

changes in thermal and biogeochemical properties of the rhizosphere. In particular, all of the cryptogams with tissues extending above the soil surface (*U. trachycarpa*, *F. cucullata – C. islandica*, *Polytrichum piliferum*) helped buffer soil temperature extremes, and in some cases buffered leaf temperature extremes and retained soil moisture. Finally, all three cryptogam surfaces studied were associated with higher soil N and C, and both removals and additions of *F. cucullata- C.islandica* were associated with lower NH_4-N. While the mechanisms behind the observed shifts in soil resources are unknown, microclimate data provide sufficient evidence to suspect indirect effects of temperature and moisture on mineralization processes. In summary, I found moderate evidence that cryptogams affect alpine plants, and that this influence might occur through a number of physical and biochemical pathways.

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Chapter 1 – Introduction and Chapter Summary

Section 1.1. Introduction

High altitude landscapes are vital to human welfare in several ways, but perhaps most compelling is their role in the collection and distribution of drinking water. Few can dispute the role of mountains as "water towers" of the world— 65% of the world's population relies on water originating in mountain catchments (World Water Assessment Programme 2012), and nearly 70% of all freshwater is contained in ice or permanent snow cover, much of it in mountains (Shiklomanov 1993). It is in the initial processing of water at the atmosphere-soil interface that mountain vegetation finds its ultimate utility to humans, as mountain plant communities set the biophysical context for headwater catchments. The sediment loads and biogeochemical signatures of mountain waters, as well as the future stability of mountain slopes, are in part a function of the vegetation present (Kopacek et al. 2006, Giguet-Covex et al. 2011, Yang et al. 2012). In this context of "ecosystem services" and against the backdrop of global climate change the study of the alpine gains particular urgency, as our ability to forecast how mountain ecosystems and their associated services will change over the next century depends primarily on how well we understand their current state. A thorough understanding of the determinants of alpine plant community patterns is therefore a problem of considerable scientific merit.

Vegetation scientists and alpinists alike have long noted the impressive collection of cryptogams sharing space with higher plants in alpine regions globally (Cooper 1923, Bliss 1956, Douglas and Bliss 1977, Spence 1981). From temperate latitudes poleward cryptogams become a permanent fixture in the subalpine-alpine landscape. Despite their ubiquity and abundant evidence from arid and polar lands suggesting they are active ecological players (reviewed in Belnap and Lange 2001), few have endeavored to uncover what role they may have in alpine ecosystem functioning.

In the three chapters that follow, I address the question of whether and how cryptogams affect the lives of the higher plants with which they cohabitate. The backbone of this inquiry is composed of several manipulative experiments involving the soil-plant-cryptogam matrix, using both the seed and adult phases of the plant life cycle. In most of the experiments, I measured the performance of several alpine plant species in the midst of either abundant or no cryptogam cover, and in most cases I coupled these measurements with several different indices of the physical and biogeochemical status of the rhizosphere and surface soil environment.

Section 1.2. Descriptions of individual chapters

Section 1.2.a. Cryptogam effects on the rhizosphere in the North Cascades and Fuegian Andes

In Chapter 2, I describe the background and overall structure of the primary experiment of my dissertation, the cryptogam transplant experiment. I begin by outlining the key drivers of alpine plant growth and seed germination and tie this to our current knowledge of cryptogams, making the argument that cryptogams are ideally suited to affect alpine plant growth and seed germination, either positively or negatively. To explain why my expectations were mixed with regard to how cryptogams might influence the near surface alpine soil environment, I highlight some of the conflicting findings in the literature across systems and cryptogam forms. Next, I outline my rationale and methods for study site selection, which involved a combination of vegetation survey data, objective criteria, and opinion. Finally, I describe the rationale and process for conducting the cryptogam transplants. Most notably, the overall experimental structure was not a reciprocal design—in hindsight moving individual plants (in addition to cryptogams) may have offered greater experimental power, but I do not believe such a design would have been permitted by the Washington State Department of Natural Resources. Finally, I outline the range of techniques I used to look at the soil environment from the surface to 5cm depth, the layer of soil in which most roots for our study species were contained.

These datasets suggest that the near surface alpine environment is in part a function of the non-vascular vegetation present and that different cryptogams affect the near-surface alpine environment in different ways. In particular, all of the fruticose cryptogams (*Usnea trachycarpa*, *Flavocetraria cucullata – Cetraria islandica*, *Polytrichum piliferum*) helped buffer near surface soil temperature extremes, and in the cases of *F. cucullata – C. islandica* and *P. piliferum*, retain soil moisture. Next, I draw on other examples from the alpine literature to contextualize the cryptogam effects we observed; from this I can safely assert that the effects cryptogams have on the near-surface soil environment are profound and likely have important biological and biogeochemical consequences

Section 1.2.b The biogeochemical influence of some alpine cryptogams in the North Cascades

. In Chapter 3, I outline current understanding of nitrogen limitation and utilization as it relates to alpine plants. In particular, I acknowledge several factors limiting the efficacy of historical models of N supply and demand in the alpine, namely inadequate indices of inorganic N availability and an insufficiently broad N niche. In spite of this I argue that some assertions can safely be made with regard to abiotic and biotic controls over the alpine N cycle at different scales. I go on to link these to known properties of cryptogams, making the argument that cryptogams are ideally suited to have profound impacts on the alpine N cycle. Finally, I describe the different methods we used to estimate the impact of cryptogams on different indices of soil nutrient availability on Snowshoe Mountain.

Overall, I found background levels of inorganic N, total N, total C, and the C:N ratios to be in line with values reported from other major mountain ranges globally. Next, my experimental data offer modest support to the view that cryptogams play some role in nutrient cycling in the alpine. All three cryptogam surfaces studied were associated with higher soil N and C, and both removals and additions of *F. cucullata- C.islandica* were associated with lower NH_4-N. While the mechanisms behind the shifts in soil resources we observed are unknown, the microclimate data in Chapter 3 provide sufficient evidence to suspect cryptogams affect mineralization processes indirectly by influencing soil temperature and moisture.

Section 1.2.c. The effects of cryptogams on alpine plants in the North Cascades and Fuegian Andes

In Chapter 4, I review in greater detail the environmental factors critical to plant growth in the alpine and link this to current understanding of how cryptogams influence the near-surface soil environment in a range of ecosystems. I provide an overview of the cryptogam transplant experiment introduced in Chapter 2, but here I focus on my choice of analysis techniques, specifically detailing the process for image-based cover analysis. To the best of my knowledge this is the first attempt to use image-based data for plot-scale analysis in plant community ecology. I then go on to describe a laboratory-based seed germination experiment using eight different alpine plant species and nine different surfaces (eight cryptogams and bare soil).

The results of the cryptogam transplant experiment offer cautious support to the view that some cryptogams do influence the growth of neighbor plants. Notably, I found statistically significant reductions in percent cover in treatments relative to controls in several communities. And while there were some potential problems with experimental relicts, the reductions in growth seen in plots where fruticose (large-bodied) cryptogams were removed are particularly noteworthy given the relative lack of disturbance to the plants in these plots. The growth reductions in these treatment plots also coincided with wider amplitude leaf temperature swings and some profound changes in soil thermal and biogeochemical properties (soil effects discussed in later chapters). Finally, I found ample evidence to suggest that different alpine plants germinate preferentially under different cryptogams.

In summary, I found moderate evidence that cryptogams affect alpine plants at seed and adult life stages, and that this influence might occur through a number of physical and biochemical pathways. While some of my results are marred by potential disturbance-related experimental relicts, the findings from the fruticose lichens on Snowshoe Mountain and Cara de Indio are particularly noteworthy; these large-bodied cryptogams insulate the near-surface soil layers from diurnal temperature extremes and maintain soil moisture following precipitation events. Their removal led to more extreme diurnal leaf temperature swings, lower NH_4-N, and lower growth on a relatively short time scale (1-2 years).

Section 1.3. Conclusions

As the globe warms, glaciers retreat, snowfields shrink in extent and duration, and new substrates are revealed in the alpine. Many scientists and citizens have asked which species will move into these new spaces, as well as what will become of the current alpine belt. I believe such questions can only be answered with a thorough understanding of current alpine community dynamics, and here I have presented moderate evidence that cryptogams should be included in such efforts. Fewer yet have asked alpine vegetation questions in the context of whether the future alpine will continue to function as a low-cost source of clean water. To the extent that such ecosystem services are reliant on groundcover and the colonization processes and community dynamics therein, again I propose that cryptogams must be included in future attempts to understand alpine plant communities.

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Chapter 2 – Manipulations of cryptogam cover and their effects on the near-surface alpine microclimate in the North Cascades and Fuegian Andes

Section 2.1. Introduction

By any measure, the alpine climate is strikingly harsh. Extreme temperature swings, unrelenting wind, and intense ultraviolet radiation are just a few of the challenges facing alpine life. It is unsurprising then, that in trying to explain the relative success of certain plants in the alpine, ecologists have focused almost exclusively on plant responses to this extraordinary suite of climatic elements. Literature dating from the mid-20th century details individual and community responses to the physical environment in alpine communities (Bliss 1971, Billings 1974, Walker et al. 1994, Körner 2003). However, a growing body of evidence suggests that the environment alpine plants actually experience is influenced enormously by microsite factors, including neighboring plants (Callaway et al. 2002, Kikvidze et al. 2005, Cavieres et al. 2007, Scherrer and Körner 2010). This highlights the need for a more holistic assessment of species interactions in alpine ecosystems and the mechanisms behind them.

Alpine landscapes in the Pacific Northwest are mosaics of ice, plants, bare ground, and a thin layer of lichens and bryophytes, sometimes referred to in the biological literature as a biological soil "crust" (Gold et al. 2001). Structurally similar crusts are well-studied in arid and arctic ecosystems worldwide; crusts alter soil temperature, fix nitrogen, stabilize soils, and serve as a reservoir for soil moisture (Evans and Johansen 1999, Belnap and Lange 2001). Despite their abundance in alpine ecosystems, their ecological functions in the alpine remain mostly unexplored (Belnap and Lange 2001, Gold et al. 2001). In this chapter I report the results of manipulative experiments designed to determine if soil cryptogams affect the climate that alpine plants experience. For context, I review the literature surrounding two critical questions, (1) what are the environmental factors most important for alpine plant growth?, and (2) how do crusts affect these environmental factors in systems where they are well-studied?

Section 2.1.a. Moisture

Near-surface soil moisture is a critical driver of biological and biogeochemical processes in the alpine. At the community level, above- and belowground patterns in C and N cycling reflect to a large extent patterns in soil moisture (Scott and Billings 1964, Kuramoto and Bliss 1970, Fisk et al. 1998, Baumann et al. 2009). Likewise, at smaller spatial scales and shorter time scales, alpine plant growth is highly sensitive to inter- (Walker et al. 1994, Walker et al. 1995) and intra-annual fluctuations in soil moisture (Billings and Bliss 1959). Soil moisture also effects alpine plant germination (Chambers and Macmahon 1994, Chacon and Cavieres 2008) and flowering patterns (Gimenez-Benavides et al. 2007). The critical role soil moisture plays in alpine plant productivity and biogeochemical cycling highlights its value as a variable worthy of consideration.

Growing season soil moisture in non-monsoonal alpine landscapes is related to the amount of snow received, the timing and duration of snowmelt, soil texture, and slope position. From a plant's perspective, much of the surface area of alpine landscapes in western North America experiences periodic summer drought (Ehleringer and Miller 1975). This is the common explanation for the correlations between discrete vegetation boundaries and steep moisture gradients that are typical throughout the mountainous parts of western North America (Mooney et al. 1965). High-elevation summer drought can be traced directly to high evapotranspiration resulting from thin soils with low total organic matter and high radiation loads (Taylor and Seastedt 1994). The driest conditions in alpine soils are found in surface layers, which can be particularly problematic for germinating seeds, seedlings, and/or shallow-rooted species (Chambers and Macmahon 1994, Körner 2003). Periodic summer drought and the importance of soil moisture to alpine primary production and biogeochemical cycling highlight the potential importance of factors affecting soil moisture in the alpine.

Biological soil crusts are known to affect soil moisture relations in temperate and polar arid systems. Gold and Bliss (1995) noted improved moisture retention under biological soil crusts in the arctic, while George et al. (2003) reported similar findings in the arid Southwest. Eldridge(1993) and Li (2008) have found that soil crusts can also redistribute precipitation by altering infiltration patterns, with associated changes to moisture levels and biogeochemical cycles. In alpine environments, particularly in the more xeric habitats, I might expect similar effects on infiltration and soil moisture associated with cryptogam-covered soils. In the first and only test of this hypothesis to date, Gold et al. (2001) found significantly higher soil water content under lichen crusts than on non-crusted sites, though this was not proven to be solely due to the presence of crusts. Regardless, changes in soil moisture associated with crust presence could be expected to have profound consequences for alpine plant growth, seed germination, and biogeochemical cycles.

Section 2.1.b. Temperature

The temperature of near surface soils in the alpine presents enormous challenges to plants throughout their life cycles. In the broadest sense, alpine plant growth is limited by prevailing low root-zone temperatures (Bliss 1956, 1966). For example, soil temperatures measured at 10 cm depth across alpine environments in Europe suggest that monthly averages rarely exceed 0° C, and often are well below freezing during the winter months (Körner 2003). At the Niwot Ridge Long-Term Ecological Research site (3500m asl) in the Colorado Front Range, the mean *summer* soil temperature at 10 cm depth during 1992-1993 was 2.6° C (calculated using data from: http://culter.colorado.edu/exec/.extracttoolA?soiltemp.ss). Thus for much of an alpine plant's life its roots are forced to operate near the freezing point of water, with consequences for aboveground shoot elongation (see discussion in Körner 2003). This is in stark contrast to aboveground conditions, where midsummer bare soil surface temperatures have been observed as high as 80°C (Körner 2003), and my own experience suggests 60°C is commonplace at temperate latitudes. Such temperatures are potentially lethal to plant tissues (Buchner and Neuner 2003), particularly an emerging seedling whose structure is confined to this near-surface environment. On the other hand, low soil surface temperatures are also known to inhibit germination in alpine species (Sayers and Ward 1966). Alpine plants thus face severe and complex temperature-related challenges in their near-surface confines.

Views on soil temperature controls in alpine systems have undergone some revision in recent years. Globally, reduced atmospheric pressure at higher altitudes drives a general trend towards cooler temperatures, yet solar radiation loads generally increase (Körner 2003). At regional scales these global trends can be subordinate to regional weather patterns; for example in the mountains of Scotland and Japan no increase in radiation occurs with elevation due to increased cloudiness with altitude (Körner 2003). At the landscape and community level, topography is the primary factor driving variability in soil temperature (Loeffler et al. 2006, Scherrer and Körner 2010, Wundram et al. 2010). Historically, ecologists have focused on this community-level, topography-driven temperature variation because this corresponds to the shifts in plant community composition and productivity that are often of interest (Billings and Bliss 1959, Bliss 1966, Komarkova and Webber 1978). More recently, ecologists have shifted some attention to climate controls at even finer spatial scales; in particular, it is now recognized that individual plants can wield considerable influence over their own physical surroundings, with consequences for the growth and survival of neighboring plants (Callaway et al. 2002, Cavieres et al. 2007, Haussmann et al. 2009). While this literature has yielded valuable insights into alpine plant community dynamics, to date the scope of these investigations have been limited to vascular plants.

The contrast between root zone and soil surface temperatures and the degree to which local factors can influence a plant's temperature regime highlight the incredible variety of influences a cryptogam could have on associated plants. Both increases and decreases in near-surface soil temperature associated with the presence of crustose forms (crust-like, thallus tissue appressed to the soil surface, Figure 2.1) have been found (Gold 1998, George et al. 2003, Breen and Levesque 2008). For fruticose forms (bushy, with thallus tissue emerging from the soil, Figure 2.1) dampening of diurnal soil temperature fluctuations has been reported (Kershaw 1977, Gold et al. 2001). Little evidence exists on either side of this question for alpine cryptogams, though Gold et al. (2001) reported cooler temperatures for surface and subsurface soils for a crusted versus non-crusted site in the Olympic Mountains. Illustrating the additional complexity of interacting environmental factors, Gold and Bliss (1995) found in the Arctic that in spite of higher overall temperatures, dark crusts retained more soil surface moisture than non-crusted surfaces, in this case driving higher seed germination and establishment rates (Gold and Bliss 1995, Gold 1998a). This body of evidence suggests that soil temperature responses to cryptogam presence may be complex and depend on the growth form of the cryptogams involved.

Given the evidence I have outlined, I suspect that cryptogams have a number of effects on their physical surroundings in alpine ecosystems. From the literature in temperate and arctic systems it is logical to expect that cryptogams change the moisture content and temperature regime of near surface alpine soils. As a step towards further revealing the role of cryptogams in alpine systems, I proposed to investigate whether cryptogams influence the soil moisture and soil temperature regimes experienced by associated plants in an alpine landscape.

Section 2.3. Site Description

Section 2.3.a. Snowshoe Mountain, North Cascades, Washington State

Field experiments were conducted at two sites. The first site, Snowshoe Mountain (N 48° 59', W 119° 50', sites between 2250-2400m elevation) was located at the eastern limit of the North Cascade Range in the Loomis Natural Resources Conservation Area, Washington State (Figure 2.2). Although the closest reliable weather data comes from the Salmon Meadows SNOTEL site 728, about 1000m lower and 30 km south of Snowshoe Mountain, the data from this site are sufficient to determine that the local climate is particularly continental for the Cascade Range. The mean annual temperature at Salmon Meadows is approximately 3°C and annual precipitation is 540 mm (estimated from NRCS SNOTEL Site 728 at N 48°39', W 119°50', 1359m elevation). Soils on Snowshoe Mountain have been coarsely modeled by the Natural Resources Conservation Service as “rock outcrop- rubble land complex” (Soil Survey Staff 2003), but in my experience often have well-developed A and B horizons, and vary considerably in texture and organic matter content (Appendix 2.1). All of the soils I worked with had sufficient amounts of volcanic ash to qualify as Andisols (Soil Survey Staff 2003), and based on extrapolations from the closest SNOTEL site with year-round soil temperature data (NRCS SNOTEL Site 515 at N 48°43', W 120°40', 1978m elevation) and my own soil temperature data, all are situated within a cryic temperature regime. No previous vegetation research has been conducted on Snowshoe Mountain, though Douglas surveyed several adjacent peaks (Arnold, Chopaka, Snowy) as part of his dissertation work on the vegetation of the North Cascades (Douglas and Bliss 1977).

In 2006 I performed an initial survey of the vegetation on Snowshoe Mountain. In 110 randomly-placed 0.25m^2 square quadrats above treeline, I visually estimated the vertical projection of percent cover of all vascular plant species, cryptogam species, and bare substrate. I used an ordination of these data with non-metric multidimensional scaling (Kent and Coker 1992, and R 2.15.0, vegan package) (Figure 2.3) as an initial step in highlighting species groupings. I then used the following criteria to identify communities suitable for experimentation: (1) either complete or no cryptogam cover between plants, (2) homogeneity in plant and cryptogam community composition over an area large enough for replicates, and (3) modest slope (≤10%). From this survey and general reconnaissance, I identified five suitable communities. These were: 1) the crustose lichen snowbank, 2) the fruticose lichen meadow, 3) the fellfield, 4) the moss snowbank, and 5) the dry sedge meadow communities. All were between 2250-2400m in elevation, near the crest of the northeast-trending ridgeline that defines Snowshoe Mountain (Figure 2.4). The "dry sedge meadow" and "fellfield" communities had very little (< 5%) natural cryptogam cover between vascular plants, while each of the other three communities contained continuous cryptogams in between plants, comprising at least 50% of total vegetative cover (Appendices 1 and 2). Each community's cryptogam assemblage was unique. The interplant spaces at the "crustose lichen snowbank" site were dominated by a near monoculture of *Lepraria neglecta*, a white crustose lichen whose entire thallus (lichen body) is directly appressed to the soil surface. At the "fruticose lichen meadow" site interplant spaces were dominated by a 3-5cm thick mat composed of a mixture of the fruticose lichens

Flavocetraria cucullata and *Cetraria islandica.* Interplant spaces at the "moss snowbank" were covered with a continuous, turf-like mat of the moss *Polytrichum piliferum.*

Section 2.3.b. Cara de Indio, Navarino Island, XII Region, Chile

The second field site was located on Cara de Indio (S 54° 59', W 67° 34'), a peak on Navarino Island, Republic of Chile, in the UNESCO Cape Horn Biosphere Reserve, at the southern limit of the Andean Cordillera (Figure 2.2). The local climate is maritime sub-polar with cool summers (mean 9° C) and mild winters (mean 2° C), with modest precipitation (annual total ≈ 470mm) (Tuhkanen 1992). Vegetation on Cara de Indio is alpine feldmark (Moore 1983) with extensive areas of talus, intermittent dense fruticose lichen cover (almost entirely *Usnea trachycarpa*), and sparse vascular plants (Appendices 2.1 and 2.2). Soils on Cara de Indio have not been classified, nor did I attempt classification, but meet the general requirements for Lithosols (FAO 1974 classification scheme) or Entisols (Soil Survey Staff 2003) with extensive stone polygons reflecting the frost heave characteristic of the subpolar temperature regime and alpine setting. As with Snowshoe Mountain , to my knowledge no previous research of any kind has been conducted on Cara de Indio.

I used the same criteria I used on Snowshoe to select four communities on Cara de Indio in which to conduct experiments. The four communities were within 200 m of each other, between 775 – 800m elevation at the crest of the north-south trending ridgeline that forms Cara de Indio (Figure 2.5), and with a mostly flat (≤ 10%) slope. Due to time constraints, cover and topographic data were not collected at this site. However, all four communities had sparse vascular vegetation (<25% cover). These communities also contained very similar plant assemblages and soils (thus "community" is used for consistency with the Snowshoe sites, but these do not necessarily constitute different "communities" in the classic vegetation ecology sense of the word), but they did differ greatly in the amount of natural *U. trachycarpa* cover (Appendices 1 and 2). The two communities with extensive *U. trachycarpa* cover were approximately 20 meters apart with slightly different aspects (Table 2.1), and the communities lacking *U. trachycarpa* cover were about 100 meters north and 20 meters lower in elevation.

Section 2.4. Methods

Section 2.4.a. Cryptogam Transplant Experiment

To examine the effects of cryptogams on alpine plant growth, I performed a cryptogam transplant experiment. In each community (five on Snowshoe Mountain, three on Cara de Indio), I located pairs of $400cm^2$ plots having nearly identical topography, vegetation, and substrate that were within one meter of each other, and had at least three individuals or ramets of my study species. In four of the five communities on Snowshoe Mountain and in all four communities on Cara de Indio, I established twelve pairs of plots. Because I could not locate another naturally cryptogam free-community on Snowshoe Mountain, in the dry sedge meadow community I established twenty-four pairs of plots. On Snowshoe Mountain I established 72 total pairs, and on Cara de Indio I established 48 pairs.

Within each pair I randomly assigned one plot to retain its natural substrate (cryptogam or bare soil, depending on the natural cover at the site) and one plot to have cryptogam cover removed or added to all interplant spaces, depending on the natural cover in the community (Appendices 2.1 and 2.2). Within each community, the same cryptogam species was always used for addition replicates. In the dry sedge meadow community (Snowshoe Mountain), where there were twenty-four pairs, twelve pairs were used for *L. neglecta* additions and twelve for *P. piliferum* additions. After the end of the growing season in 2007 (late September), all cryptogam material was carefully removed from removal plots. For plots with *F. cucullata* and *Cetraria* *islandica*, this involved simply lifting loose lichen tissue out of the plots. For plots with *L. neglecta* or *P. piliferum*, the two cryptogams directly attached to soil, the cryptogam tissue was cut out of the plot using a knife and a bucket trowel. As much soil was removed from the base of the cryptogams as possible without breaking the pieces apart. In some cases this resulted in a cryptogam-soil layer 2 cm thick, but generally this layer was ≈ 1 cm thick. In all cases, this represented a removal or addition of > 60% (see Appendices 2.1 and 2.2 for plot cover before treatment) of the total ground cover. Following the removals, this cryptogam tissue, along with additional tissue harvested nearby, was used to cover all bare ground in the addition plots.

Section 2.4.b. Soil Temperature and Moisture

To determine the effects of cryptogams on the temperature and moisture regimes experienced by alpine plants, in 2009 I measured soil temperature and moisture in a subset of the paired experimental plots on Snowshoe Mountain. I used two techniques to examine soil temperature. First, to measure subsurface temperature I inserted Campbell Scientific 105-T soil temperature probes (Campbell Scientific, Logan, UT) horizontally into treatment and control plots at 1cm and 5cm depths. All soil probes were set to the nearest 1mm using a 0.1mm caliper. Prior experience in 2008 (see Appendix 2.3) suggested that achieving the precise depth was enormously important— depth variations of just a few millimeters had surprisingly large effects on the data set. Because of the limited supply of sensors and loggers available, with one exception I was only able to simultaneously monitor one pair per community, with one sensor per plot per depth. In the fruticose lichen meadow community on Snowshoe Mountain and an *U. trachycarpa* addition community on Cara de Indio, I used a signal multiplexer (AM25T, Campbell Scientific, Logan, UT) to maintain four replicates at each sensor depth in each treatment.

Next, to gain a more nuanced understanding of the surface temperature dynamics on Snowshoe Mountain, I captured infrared images of my experimental plots using a FLIR Systems S45 NTSC infrared camera (FLIR Systems, Boston, MA). Images were taken between 0900h and 1600h PDT on a clear day (August 15, 2008). To enable me to use the experimental pairings in my analysis of the infrared images I randomized the order images were taken within pairs, and, in all cases, images of both pair members were captured within 30 seconds of each other. Because of the time difference in image capture among communities, I do not consider comparisons between communities valid. On average, the 0.2m * 0.2m experimental plots (144 in total) were represented by approximately 32,000 pixels, with each pixel represented by a single temperature estimate. Images were analyzed with ThermaCam Researcher Professional 2.8; for each image I used only the mean temperature in the analysis.

To estimate soil moisture I inserted EC-5 time-domain reflectometry (TDR) probes (Decagon Devices, Pullman, WA) horizontally into treatment and control plots at 1 cm depth, and in two cases 5 cm (*F.cucullata+C. islandica* removals and *P. piliferum* additions). Because the EC-5 probes integrate their estimate of soil moisture over the length of the probe ((8.9 cm), inserting horizontally was intended to ensure that moisture estimates were isolated to the soil depth of interest. However, on Cara de Indio moisture probes were inserted vertically, thus moisture data from Cara de Indio are an estimate of moisture content from approximately 1 to 10cm depth. I had similar constraints on sensor and logger availability as with the temperature measurements, thus with two exceptions I was only able to monitor moisture levels in one pair per community, with one sensor per plot. Again, in the fruticose lichen meadow on Snowshoe and the *U. trachycarpa* addition site on Cara de Indio, I was able to use a multiplexer to maintain four replicates at each sensor depth in each treatment. All values were recorded on CR10 dataloggers (Campbell Scientific, Logan, UT). Because of the difficulty in accessing the study sites and the fact that I was more interested in the comparative moisture levels among treatments than absolute values, probes were not calibrated to the study sites' soils. However, because my sensors consistently reported negative soil water content values, I performed a post-hoc calibration in the lab (Appendix 2.4). Values are reported as the output from the default calibration curve equation for mineral soil plus a correction factor(λ), where Volumetric Water Content ≈ 0.00119 * datalogger output (mV) $-0.4 + \lambda$ (Decagon Devices, Pullman, WA).

Finally, to broadly compare the climates of Snowshoe Mountain and Cara de Indio, I used two unique data sources. First, I received air temperature data for a weather station installed near treeline on Snowshoe Mountain (~1980 m asl) during the summer of 2009 (Weintraub 2009). These data cover the entire summer (June 25 – September 29, 2009). Second, I received air temperature data for a weather station installed in the alpine on Bandera Mountain (~780m asl), the neighboring peak to Cara de Indio. These data were more limited (December 17, 2008 – January 17, 2009), but nonetheless represent the peak of the austral summer.

Section 2.4.c. Data Analysis

Soil temperature and moisture data were summarized as the mean daily maximum, minimum, and mean. I did not use statistical models with these data due to the lack of replication and autocorrelation characterizing them. Because the infrared images were captured on all plots, I used the mean plot temperatures in a mixed model ANCOVA with pair as a random effect, treatment as a fixed effect, and time taken as a covariate. This analysis was performed in SPSS 19. The temperature time series figure was produced in SPSS. The kernel density plots and soil moisture time series were produced in R 2.15. The kernel density plots represent the relative frequency of different surface temperature values among treatment and control plots; in R these were produced by fitting a polygon onto a density object (polygon(density(data)).

Section 2.5. Results

Based on the patterns observed, I organized the results according to the two broad growth forms of cryptogams studied, fruticose (*U. trachycarpa* and *F. cucullata – C. islandica*) and prostrate (*P. piliferum* and *L. neglecta*). In each section, the results for surface (infrared) and near surface (-1 and -5 cm) soil temperature and soil moisture are described including, except for the infrared results, data from both Snowshoe Mountain and Cara de Indio.

Section 2.5.a. Fruticose lichens

Section 2.5.a.1. Site Comparison

Broad temperature trends differed considerably between the two sites. For example, in 2009 the average daily mean, maximum, and minimum air temperatures on Snowshoe Mountain were 10.7° C, 16.8° C, and 5.4° C (calculated from unpublished data collected by M. Weintraub, University of Washington), respectively, whereas on a neighboring peak to Cara de Indio the average daily mean, maximum, and minimum air temperatures were 4.4° C, 10.4° C, and 0.3° C (calculated from unpublished data collected by L. Sancho, Universidad Complutense de Madrid). Not surprisingly, summer soil temperature trends were also very different at the two sites where the fruticose cryptogam covers, *F. cucullata – C. islandica* and *U. trachycarpa*, were studied. In the fruticose lichen meadow community on Snowshoe Mountain the average diurnal soil temperature oscillation at 1 cm depth was approximately 25° C, whereas for all of the experimental communities on Cara de Indio (all of which were fellfield) temperatures remained in approximately a 13° C range (Figure 2.6). Broad patterns of soil moisture were also very different between the two field sites (Figure 2.7). On Snowshoe Mountain, the seasonal pattern was typically continental, with several extended periods of rapid drying following snowmelt, punctuated by infrequent precipitation events. On Cara de Indio, moisture levels were relatively stable, with small but frequent precipitation events scattered evenly throughout the summer.

Section 2.5.a.1. Cryptogam Transplants

Section 2.5.a.1.a. Surface Temperature

The presence of fruticose lichen cover as the *F. cucullata – C. islandica* mix and the *U. trachycarpa* monoculture had, in most cases, enormous consequences for the near surface temperature regimes in their respective locations. In the fruticose lichen meadow community on Snowshoe Mountain, infrared imaging revealed that the upper surfaces of plots dominated by the *F. cucullata – C. islandica* mix were thermally similar to the surfaces of adjacent removal plots dominated by bare, highly organic meadow soil. In removals and controls, whole-plot mean surface temperatures were approximately 38°C (Table 2.1 and Figure 2.7), and fully sun-exposed surfaces of both lichen and bare soil heated to 45°C or greater (Appendix 2.5). In contrast, in the fellfield community on Snowshoe Mountain the surfaces of control plots (dominated by bare, lighter-hued, gravelly soil) remained approximately 6°C cooler than those of adjacent plots dominated by the added *F. cucullata – C. islandica* mix (Table 2.1 and Figures 2.7 and 2.8). In this setting, fully sun-exposed surfaces of *F. cucullata – C. islandica* heated to 50°C or greater, while the fully sun-exposed gravelly soil in control plots heated to 35-40°C (Appendix 2.5).

Section 2.5.a.1.b. Subsurface: Temperature

With regard to subsurface temperature, in both the fruticose lichen meadow and fellfield communities the *F. cucullata – C. islandica* mix demonstrated substantial insulating properties. Although no formal statistical testing was done on these data, in the fruticose lichen meadow, the average daily maximum temperature at 1 cm depth tended to be cooler (-4.9°C)and the average daily minimum warmer (+1.1°C) under intact *F. cucullata – C. islandica* than under the bare meadow soil (Figure 2.4). Similarly, in the fellfield under the added *F. cucullata – C. islandica* mix the daily maximum temperature at 1 cm depth was generally cooler (-5.3°C) and the average daily minimum warmer (+1.8°C) than under the bare gravelly fellfield soil (Table 2.2). These tentative trends were maintained in both communities down to 5 cm depth, though the buffering observed was approximately 50% of that found at 1 cm (Table 2.2).

It appears that *Usnea trachycarpa* demonstrated analogous insulating properties in the subpolar climate on Cara de Indio (Figure 2.6). In the fellfield community where *U. trachycarpa* was added to previously bare fellfield soil composed mostly of fine gravel, under *U. trachycarpa* the daily maximum temperature at 1 cm depth tended to be cooler (-4.6° C) and the daily minimum warmer (+1.1° C) than under bare fellfield soil (Table 2.2). Similarly, in the communities where *U. trachycarpa* was removed, under intact *U. trachycarpa* there was a trend for the daily maximum temperature at 1 cm depth to be cooler (-4.6° C) and the mean daily minimum warmer (+1.1° C) than under bare soil (Table 2.2). Temperature buffering effects seem to also be apparent down to 5 cm depth, but the buffering seems to be less than that found at 1 cm (Table 2.2); the daily maximum with *U. trachycarpa* was about 1° C less and the daily minimum about 0.5° C higher than without.

Section 2.5.a.1.c. Subsurface: Moisture

In both the fellfield and fruticose lichen meadow communities on Snowshoe Mountain, the presence of *F. cucullata – C. islandica* cover affected soil moisture levels noticeably following snowmelt and precipitation events, when moisture levels in bare soil declined more rapidly than under *F. cucullata – C. islandica* (Figure 2.9), and appeared to stay at approximately

50% lower levels until precipitation events. Although I have a significant data gap in the *F. cucullata* – *C. islandica* removal time series, there was just one minor precipitation event during this time period (see the *F. cucullata* – *C. islandica* addition time series in Figure 2.9, July 24). Based on the post-data gap patterns, I have no reason to suspect this trend reversed during that time period. This more rapid drying was absent at 5cm depth. On Cara de Indio, soil moisture was lower overall in bare ground versus plots covered with *U. trachycarpa.* However, it was difficult to compare moisture retention, a more valid index of cryptogam effects, for two reasons. First, mean soil moisture among bare ground and cryptogam-covered plots never reached similar levels, making it impossible to compared drying rates in a meaningful way. Second, moisture levels remained much more consistent for the length of the summer (Figure 2.9), allowing for fewer periods of rapid drying like those seen in the continental climate on Snowshoe Mountain. During the one long drying event (mid-January to February) that provided an opportunity to compare the drawdown rates, moisture levels declined at similar rates between bare soil and plots covered with *U. trachycarpa*.

Section 2.5.b. Prostrate Cryptogams

Section 2.5.b.1. Surface: Temperature

The two prostrate cryptogams studied, *P. piliferum* (moss) and *L. neglecta* (crustose lichen), had different effects on the near-surface temperature regimes. Also, for both prostrate cryptogams their “effect” depended on the underlying soils involved in the comparison. In the dry sedge meadow, where additions of both prostrate species were performed, and which contained light-colored, sandy soils, infrared imaging revealed that the surfaces of plots with *P. piliferum* added reached higher temperatures than plots dominated by bare soil (Table 2.1, Figure 2.7), whereas plots with *L. neglecta* added were statistically inseparable from bare soil. *P.*

piliferum tissues appeared to heat somewhat more than *L. neglecta*, with fully exposed surfaces often reaching well above 50° C, whereas fully exposed surfaces of *L. neglecta* generally peaked just below 50°C (Appendix 2.5). In the moss snowbank community where removals of *P. piliferum* were performed, the surfaces of plots with intact *P. piliferum* were very similar thermally to the surfaces of removal plots now dominated by the dark-colored, highly organic native soil (Table 2.1, Figure 2.7, Appendix 2.5). In contrast, in the crustose lichen snowbank where removals of *L. neglecta* were performed, the surfaces of plots dominated by intact *L. neglecta* remained, on average, 2.5°C cooler than plots now dominated by the dark, organic-rich native soil (Table 2.1, Figure 2.7, Appendix 2.5). This indicates that *L. neglecta* is perhaps a slightly "cooler" surface than *P. piliferum.*

Section 2.5.b.2. Subsurface: Temperature

Subsurface temperature patterns tended to be different under the two prostrate cryptogams, though again the reference soil was critical in interpretation. In the moss snowbank community, under intact *P. piliferum* there was a tendency for the daily maximum at 1 cm depth to be cooler (-4.3° C) and the daily minimum warmer (+1.1° C) than under the dark bare soil of removal plots (Table 2.2). In contrast, in the crustose lichen snowbank community temperatures at 1 cm depth under intact *L. neglecta* did not appear to be different from those under the dark bare soil of removal plots (Table 2.2).

I directly compared the subsurface temperatures under the two prostrate cryptogams with data from the dry sedge meadow, where additions of both were performed, and which had a light-colored, sandy soil. The temperatures under added *P. piliferum* tended to be nearly identical to those under bare soil, but under added *L. neglecta* there was a trend for the daily maximum be warmer (+4.9°C) and the daily minimum cooler (-0.9°C) than under bare soil

(Table 2.2). For both cryptogams these trends seemed to disappear at 5cm depth, though for unknown reasons the daily maximum under *P. piliferum* was 1.9° C warmer than under bare soil.

Section 2.5.b.3. Subsurface: Moisture

Overall, soil moisture patterns in the prostrate cryptogam removal and addition communities were similar to those in the fruticose lichen addition and removal communities on Snowshoe Mountain. These patterns were characterized by an initial drying after snowmelt followed by several more drying phases punctuated with irregular precipitation events (Figure 2.9). In the moss snowbank community, soil moisture under *P. piliferum* behaved as expected given the subsurface temperature results— after precipitation events, moisture levels 1 cm under intact *P. piliferum* declined more slowly than under bare native soil, whereas moisture levels 1cm and 5cm under added *P. piliferum* behaved very similarly to those under the dry sedge meadow soil (Figure 2.9). The behavior of soil moisture under *L. neglecta* was somewhat counterintuitive. In the crustose lichen snowbank community (*L. neglecta* removal site) moisture levels 1 cm under intact *L. neglecta* declined more rapidly than under the bare local soil whereas, as with added *P. piliferum*, moisture levels under added *L. neglecta* remained nearly identical to those under the lighter-colored, sandier soil of the dry sedge meadow community (Figure 2.9).

Section 2.6. Discussion

My results suggest that the near surface alpine environment is in part a function of the non-vascular vegetation present and that different cryptogams affect the near-surface alpine environment in different ways. In addition, the type of soil on which these cryptograms grow impacts the cryptogam “effect,” as light-colored soils have substantially different microclimatic characteristics than dark-colored soils in close proximity. My strongest results came from the cryptogams with tissue extending vertically aboveground (*U. trachycarpa, F. cucullata – C.*

islandica, *P. piliferum*). These cryptogams appear to buffer near-surface soil temperature extremes (Figure 2.6, Table 2.2) at 1cm depth and, in the case of *F. cucullata – C. islandica* and *P. piliferum,* retain soil moisture (Figure 9). The precise mechanisms behind these ameliorative effects are unknown, but it seems likely some combination of reduced direct radiation and wind at the soil-air interface are responsible. To put these apparent effects into a broadly meaningful ecological context would be complicated and involve the consideration of many species across multiple trophic levels. Although in another chapter I will attempt to directly address one facet of this, the effects of cryptogams on alpine plants, here I will begin to highlight the intersections between these apparent cryptogam microclimate effects and some properties of alpine plants and alpine plant communities.

First, the tendency for cryptogams with tissue extending vertically aboveground (*U. trachycarpa, F. cucullata – C. islandica, P. piliferum*) to buffer near-surface soil temperature extremes to the level observed finds some interesting parallels in temperature trends across larger spatial scales at other alpine sites. For example, I found that plots with these cryptogams tended to have roughly 5° C lower daily maximum temperature readings at 1 cm depth. While few perfectly comparable studies exist, both the precise depth and magnitude of this apparent effect find some interesting parallels in results from other alpine sites. For example, this is slightly larger than the difference Wundram et al. (2010) found in maximum soil temperature at 1 cm depth between north and south aspects of a peak in Central Norway (~1450m asl), aspects which bear different plant communities. The difference I found is similar to the difference Takahashi (2005) found in maximum soil temperature at 5 cm depth between an “upper windy ridge” and a “lower leeward slope” on Mount Shogigashira, central Japan (~2675m asl), where the temperature difference between the sites has been linked to the vastly different stature of *Pinus* *pumila* at both locations. In the central Andes, cushion plants have been found to exhibit similar temperature buffering behavior for the soils under their canopy, in some cases reducing daily maxima by 10°C relative to bare soil, which has been linked with improved seedling survival (Cavieres et al. 2007). The 5°C daily maximum difference I found is also similar to the difference in soil temperatures between the inside and outside of warming chambers used in the global International Tundra Experiment (Marion et al. 1997, Walker et al. 1999); the amount of warming caused by these chambers was intended to simulate global climate change and has been linked to profound changes in species composition, community productivity, and nitrogen cycling in tundra communities worldwide (Walker et al. 2006, Borner et al. 2008). This assortment of evidence provides context for considering the broader community-level consequences of having abundant cryptogam cover throughout a landscape, and supports the assertion that the apparent effects of cryptogams on soil temperature (Table 2, Figure 6) are profound and likely of considerable biological consequence.

At the species level the effects cryptogams appear to have on near-surface soil temperature are particularly relevant when considered in tandem with some unique aspects of alpine plant structure and physiology. First, it is clear from the literature that for many alpine species more root biomass is contained in the top 5 centimeters of soil than any other layer (Webber and May 1977, Hitz et al. 2001, Yang et al. 2009, Li et al. 2011). Given the resolution of our soil temperature data and the rapid dissipation of cryptogam effects with depth, it would be helpful to compare root density among the 1cm and 5cm layers, but to the best of my knowledge no authors have partitioned root data this precisely in the alpine. However, much is still known about alpine plant responsiveness to soil temperature, and it is possible the dissipation of cryptogam effects with depth was due to small treatment areas (20cm x 20cm).

Root respiration (Cooper 2004), root growth (Björk et al. 2007), nutrient uptake rates, and uptake preferences (Raab et al. 1996, Warren 2009) in alpine and subalpine species have been shown to be highly sensitive to soil temperature. Root respiration and root growth, in particular, are sensitive to soil temperature changes on the same scale as those seemingly induced by the presence of fruticose cryptogams(Cooper 2004, Björk et al. 2007). Finally, in some tundra species photosynthesis and stomatal conductance have also been shown to be sensitive to soil temperature changes on this scale, independent of air temperature (Starr et al. 2004). Together these related findings suggest that the soil temperature effects I observed are likely relevant to associated plants to the degree that roots are concentrated in the most superficial soil layers and particular species' above- and below-ground physiology are sensitive to soil temperature changes on the scale discussed.

On Snowshoe Mountain, *F. cucullata – C. islandica* and *P. piliferum* also retained more soil moisture following precipitation events than bare soil surfaces (Figure 9). In particular, when the *F. cucullata – C. islandica* mixture was removed from plots, near-surface soil moisture seemed to decline faster and remain lower until the next precipitation event than with the cryptogam cover intact. This improved moisture retention seemed to dissipate at 5cm depth, though again this could be a function of plot size. I do not know the overall implications of the soil moisture–enhancing properties of these cryptogams, nor did I explicitly investigate this. However, the literature regarding alpine community- and species-level sensitivity to soil moisture can offer some clues, particularly if I consider the actual soil moisture differences I observed.

Community-level relationships with soil moisture offer a glimpse into the moisture-related impacts large areas of cryptogam cover may have. For example, during extended dry periods there seemed to be a trend for plots with intact *F. cucullata – C. islandica* to maintain near surface soil moisture approximately twice as high (~10% VWC versus 5%) as bare soil plots, although this trend was interrupted with precipitation events and data gaps. A 5% VWC difference is similar to the largest differences found between aspects on Niwot Ridge (Litaor et al. 2008) and in the Italian Alps (Penna et al. 2009). On Niwot Ridge soil moisture variability on this scale has been directly linked to species richness in plant communities (Litaor et al. 2008). In Antarctica an experimental snow retention fence led to soil moisture differences of similar scale and subsequent shifts in soil fauna (Ayres et al. 2010). Berdanier and Klein (2011) offer perhaps the most applicable community-level dataset and analysis; we can use their regression of aboveground net primary production against soil moisture from Niwot Ridge with the 5% VWC difference induced by removing *F. cucullata – C. islandica* and come up with an increase of 0.13 grams of biomass per day spent with cryptogam cover during extended dry spells. Albeit rough and narrowly focused on soil moisture, this provides some ecological context for extrapolating the results of our plot-scale experiments to whole communities with significant cryptogam cover.

At the individual level the tendency for some cryptogams to retain near-surface soil moisture overlaps with some characteristics of belowground alpine plant structure and physiology. First, it is recognized that photosynthesis (Johnson and Caldwell 1975), respiration (Kuramoto and Bliss 1970, Johnson and Caldwell 1975), conductance (Oberbauer and Billings 1981), and hydraulic architecture (von Arx et al. 2012) in alpine plants are sensitive to soil moisture levels. Unfortunately, in many cases different moisture estimation techniques or different time scales limit my ability to place my findings more precisely against the backdrop of other alpine studies. However, one of the more relevant is Theodose and Bowman's (1997) work with *Kobresia myosuroides* and *Deschampsia caespitosa*, where they attributed (but did not explicitly prove) higher root biomass and higher root:shoot ratio of *D. caespitosa* in the absence of *Kobresia myosuroides* to increases in soil moisture on a scale comparable to that I found in the presence of fruticose cryptogams. To the contrary, outside of the alpine literature, it has been found that many non-cultivated plant species increase root growth and relative allocation to roots in response to lower soil moisture (for example, see Reader et al. 1993, Padilla et al. 2007, Dhief et al. 2011), which seems likely related to the finding that moderate water stress can stimulate root growth via unique root cell responses to decreased turgor pressure (Triboulot et al. 1995). While these findings are at odds, together they can be taken to suggest that altered moisture conditions on the scale we found should influence rooting behavior and biomass allocation patterns in associated plants.

Also of particular interest are the microclimate phenomena associated with the moss *Polytrichum piliferum*. The global distribution of this particular moss (Merrill 1993), its relatively high productivity in places it occurs (Street et al. 2012), and the growing recognition of mosses more broadly as active ecosystem components (i.e. Beringer et al. 2001, Cornelissen et al. 2007, Douma et al. 2007) highlight the potential importance of physical phenomena associated with its presence. Although *P. piliferum* is a relatively prostrate cryptogam whose visible surface heats to the highest temperatures of any surface I worked with (Table 2.1, Appendix 2.5), the contrast between the infrared and subsurface temperature trends (Figure 2.6 and Figure 2.7) highlight how this 1 cm tall moss has an impressive capacity for dissipating heat energy and thus ameliorating temperatures in the rhizosphere. This capacity for heat dissipation together with the improved moisture retention I observed may help explain the improved seed germination associated with *P. piliferum* that has been observed in other environments with considerable heat and moisture stress (Delach and Kimmerer 2002).

In contrast to the cryptogams with aboveground structures, the one cryptogam studied lacking any prominent aboveground structure, *L. neglecta*, contributes to a subsurface temperature regime similar to bare, highly organic soil, with even more rapid drying following precipitation events despite forming large patches of bright white lichen covered soil. In this case I attribute the more rapid drying associated with the presence of the crustose lichen to more rapid evapotranspirative losses from the live lichen surface than from the bare soil surface, an argument also advanced by Belnap (2001, p. 285). While few published studies have investigated the relationship between crustose lichen cover and near surface soil moisture, Harper and St. Clair (in Tueller 1988) did report lower soil moisture associated with continuous crustose lichen cover.

Section 2.6.a. Conclusions

The broader implications of my findings are several-fold. First, this study suggests a new species- or growth-form specific feedback loop into how climate change might affect alpine tundra at the global scale. Because efforts to forecast tundra plant responses to climate change rely to some degree on local temperature estimates (i.e. Poulter et al. 2010), and the climate tundra plants experience is to some degree moderated or controlled by their non-vascular associates, shifts in both the non-vascular and vascular assemblages must be accounted for in future studies of alpine vegetation. For example, it is reasonable to anticipate a scenario where a particular cryptogam experiences a regional decline or increase in abundance as a result of regional warming (van Herk et al. 2002). If this is a climate-buffering cryptogam such as *P. piliferum,* the *F. cucullata- C. islandica* mix, or *U. trachycarpa,* the areas where the cryptogam declines could prove more or less hospitable to components of their current vascular flora, and community shifts could occur more rapidly or differently than a climate-envelope model (i.e.

Trivedi et al. 2008) might predict when considering only the physiological optima or known ranges of current species.

A logical next step would be to investigate ecological relationships between individual cryptogam and vascular plant species. One direction might be particularly fruitful here. The work of Sedia and Ehrenfeld (2003) in the New Jersey Pine Barrens suggests that *Polytrichum* mosses and *Cladonia* lichens may differentially promote the germination and establishment of vascular plants with different mycorrhizal associations. Similarly, my work demonstrates the physical environments associated with cryptogams of different growth forms are enormously different. A survey of alpine plants and cryptogams at a fine spatial scale in several alpine landscapes could provide some insight into whether either of these forces is influential in driving community spatial structure.

The restoration applications of plant-cryptogam relationships alone merit further investigation for those alpine areas heavily impacted by recreational users, or more broadly, for any restoration site in a harsh environment. For example, by placing cryptogams around seedlings or on seeded areas, could I improve the germination and establishment of plants in places like Sunrise Campground at Mount Rainier National Park? Which plants might benefit the most from cryptogams, and which cryptogams are the most beneficial for establishment? Given recent developments in the functional group literature (i.e. Lavorel and Garnier 2002, Sasaki et al. 2011) and this study's growth form-specific findings, the answers to such questions might be reasonably extrapolated across the alpine from temperate to polar latitudes. As concern heightens over the fate of alpine plant communities and their associated ecosystem services in a warming world, a holistic understanding of all major community processes can be the only foundation for accurately forecasting the fate of the charismatic alpine flora.

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Section 2.8. Figures and Tables

Table 2.1. Mean soil surface temperature in experimental plots measured using infrared imaging. Each infrared image had approximately 32000 temperatures recorded (1 per pixel). For each cryptogam type * treatment, n=12. In this case, to give a better sense of the full range observed, values are reported as mean ± 2 SD. Means in ***bold italics*** indicate significant differences between treatment and controls (ANCOVA, p<0.05, * indicates 0.05< p< 0.1).

	Addition		Removal	
	Crust	NoCrust	Crust	NoCrust
F. cucullata – C. islandica	***41.6 ± 5.9****	***35.4 ± 3.9***	38.8 ± 7.4	38.3 ± 4.4
L. neglecta	40.1 ± 4.9	38.2 ± 10.3	***31.6 ± 4.6***	***34.1 ± 4.0***
P. piliferum	***42.8 ± 7.4***	***38.7 ± 5.4***	40.6 ± 10.5	39.8 ± 6.8

Table 2.2. Soil temperatures for all sites and depths studied arranged by the mean daily maximum, and minimum, and mean. The "Addition" part of the table refers to data from plots in communities where cryptogams have been experimentally added (i.e. the "dry sedge meadow"), and the "Removal" part refers to plots from which cryptogams have been experimentally removed (i.e. the "crustose lichen snowbank"). Means in ***bold italics*** indicate large, though not statistically tested, differences between treatment and control.

Addition Sites

Cryptogam(s) and community (*dates measurements taken*)		1 cm		5 cm	
		Crust	No Crust	Crust	No Crust
F.cucullata – C. islandica "fellfield" (*July 19 – August 15*)	Daily Mean	2.6	3.0	2.7	2.5
	Daily Maximum	***10.1***	***15.4***	6.9	8.4
	Daily Minimum	***-2.1***	***-3.9***	-0.8	-2.0
L. neglecta "dry sedge meadow" (*August 20 – September 27*)	Daily Mean	14.3	13.8	13.6	13.7
	Daily Maximum	***32.1***	***27.2***	22.7	23.4
	Daily Minimum	4.5	5.4	7.2	7.0
P. piliferum "dry sedge meadow" (*August 20 – September 27*)	Daily Mean	13.4	13.4	13.1	13.0
	Daily Maximum	28.9	29.0	23.9	22.0
	Daily Minimum	4.7	4.5	6.4	6.9
U. trachyphylla Navarino Island "fellfield" (*January 9- March 21*)	Daily Mean	4.4	4.9	4.6	4.6
	Daily Maximum	***9.0***	***13.6***	8.2	9.4
	Daily Minimum	1.5	0.4	2.1	1.5

Removal Sites

Cryptogam(s) and community (*dates measurements taken*)		1 cm		5 cm	
		Crust	No Crust	Crust	No Crust
F.cucullata – C. islandica "fruticose lichen meadow" (*August 3 – 15*)	Daily Mean	11.6	12.5	11.6	11.9
	Daily Maximum	***24.1***	***29.0***	17.5	19.5
	Daily Minimum	4.8	3.7	7.8	7.1

L. neglecta “crustose lichen snowbank” (*August 17 – September 28*)	Daily Mean	-1.6	-1.3	-2.1	-2.0
	Daily Maximum	8.6	8.6	2.1	1.9
	Daily Minimum	-7.3	-7.0	-4.9	-5.0
P. piliferum “moss snowbank” (*June 27 – August 29*)	Daily Mean	14.5	15.0	13.3	12.8
	Daily Maximum	***34.3***	***38.6***	24.3	21.7
	Daily Minimum	3.3	2.2	6.0	6.4
Usnea Navarino Island fellfield (*January 9- March 21*)	Daily Mean	5.5	6.1	5.4	5.6
	Daily Maximum	***11.5***	***16.1***	9.5	11.0
	Daily Minimum	1.7	0.6	2.5	2.0

Figure 2.1. Crustose and fruticose cryptogams. A. *Lepraria neglecta*, a crustose lichen. Note the thin white layer of *L. neglecta* tissue appressed to the soil surface. B. *Flavocetraria cucullata*, a fruticose lichen. Note the bushy appearance. C. *L. neglecta* coating the surface of the "crustose lichen snowbank" site between *Antennaria lanata* and *Carex nardina*. D. *F. cucullata* and *Cetraria islandica* forming an understory amidst the leaves of *Solidago multiradiata* and *Carex scirpoidea*.

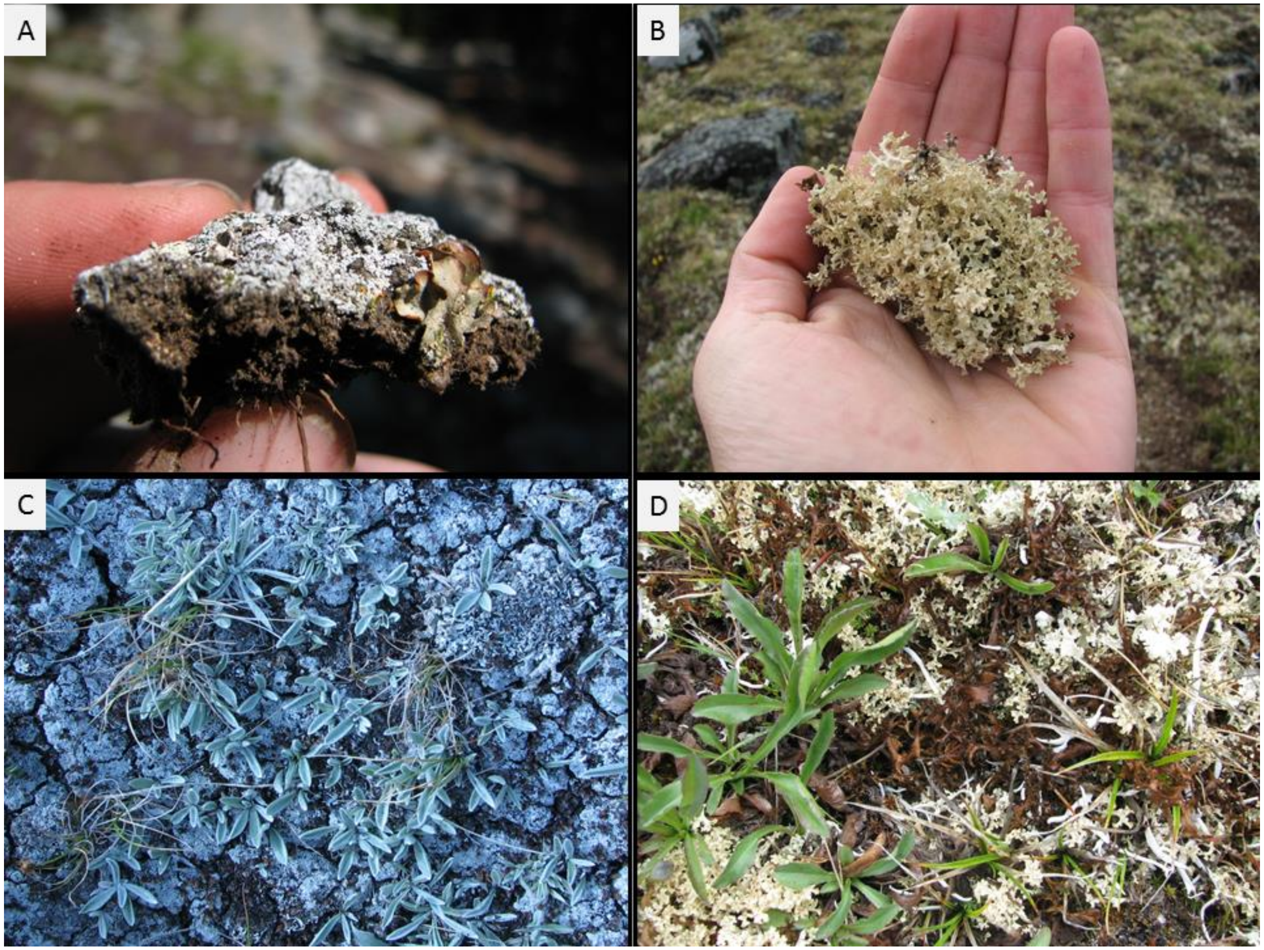


Figure 2.2. Research locations. Inset (top)- Snowshoe Mountain, Washington State, USA, is located approximately at the star, at the eastern limit of the North Cascade Range. Inset (bottom right) – Cara de Indio, XII Magallanes and Antártica Chilena Region, Republic of Chile, is located at the star, in the southernmost Fuegian Andes

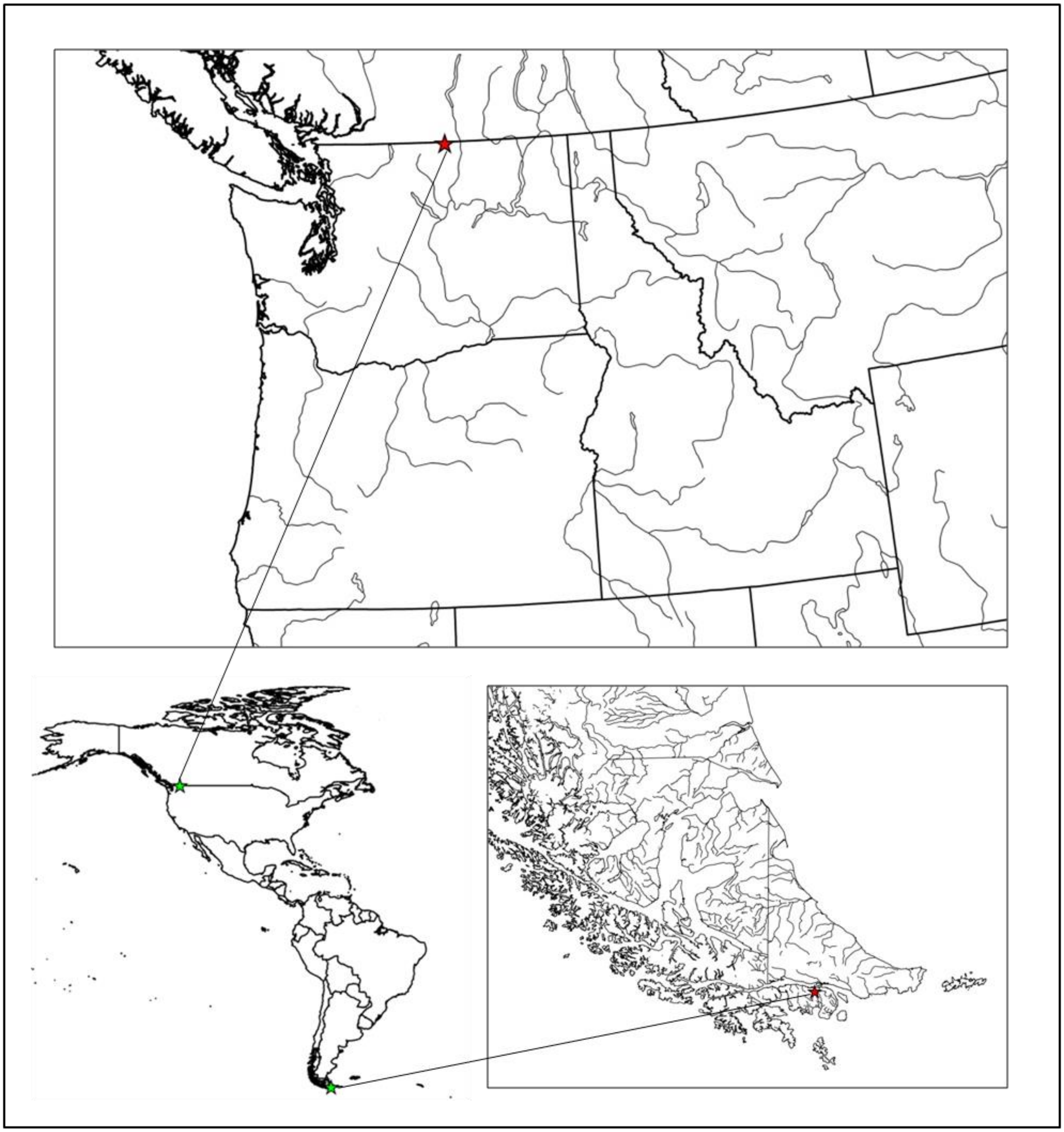


Figure 2.3. NMDS ordination of plant and cryptogam cover data from 110 randomly placed 0.5m x 0.5m square quadrats on Snowshoe Mountain. Shaded areas represent approximate community types used in the cryptogam transplant experiment. *Carex nardina* does not appear here, as our survey data were taken exclusively to the north of the peak and the "crustose lichen snowbank" community, where *C. nardina* occurred, was immediately to the south of the peak. As an "indirect" ordination technique (Kent and Coker 1992), the axes are not directly interpretable (as a particular environmental factor), algorithmically they function simply to maximize the distance between species.

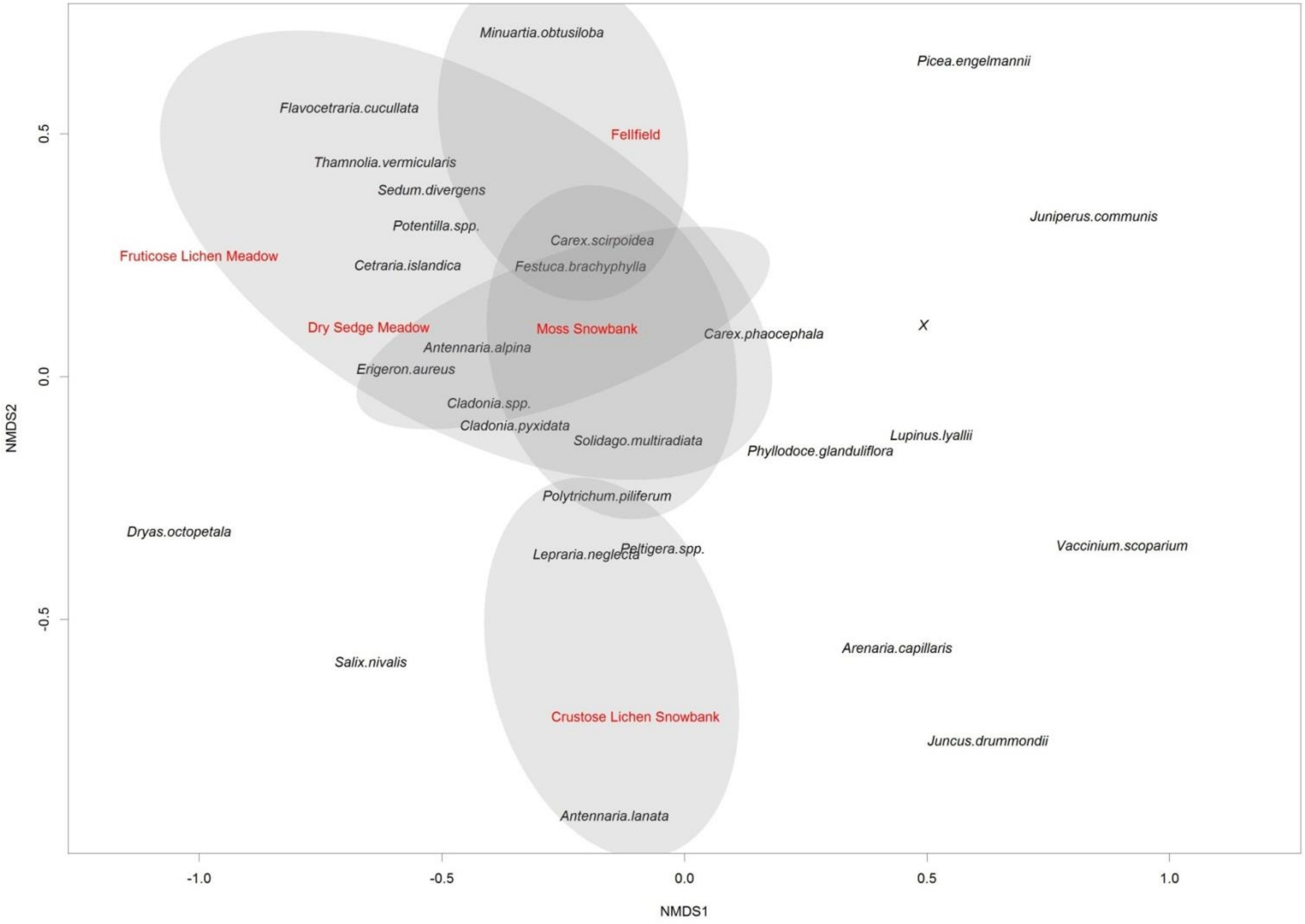


Figure 2.4. Depiction of Snowshoe Mountain, with approximate locations of experimental communities.

Figure 2.5. Depiction of Cara de Indio, with approximate locations of experimental communities.

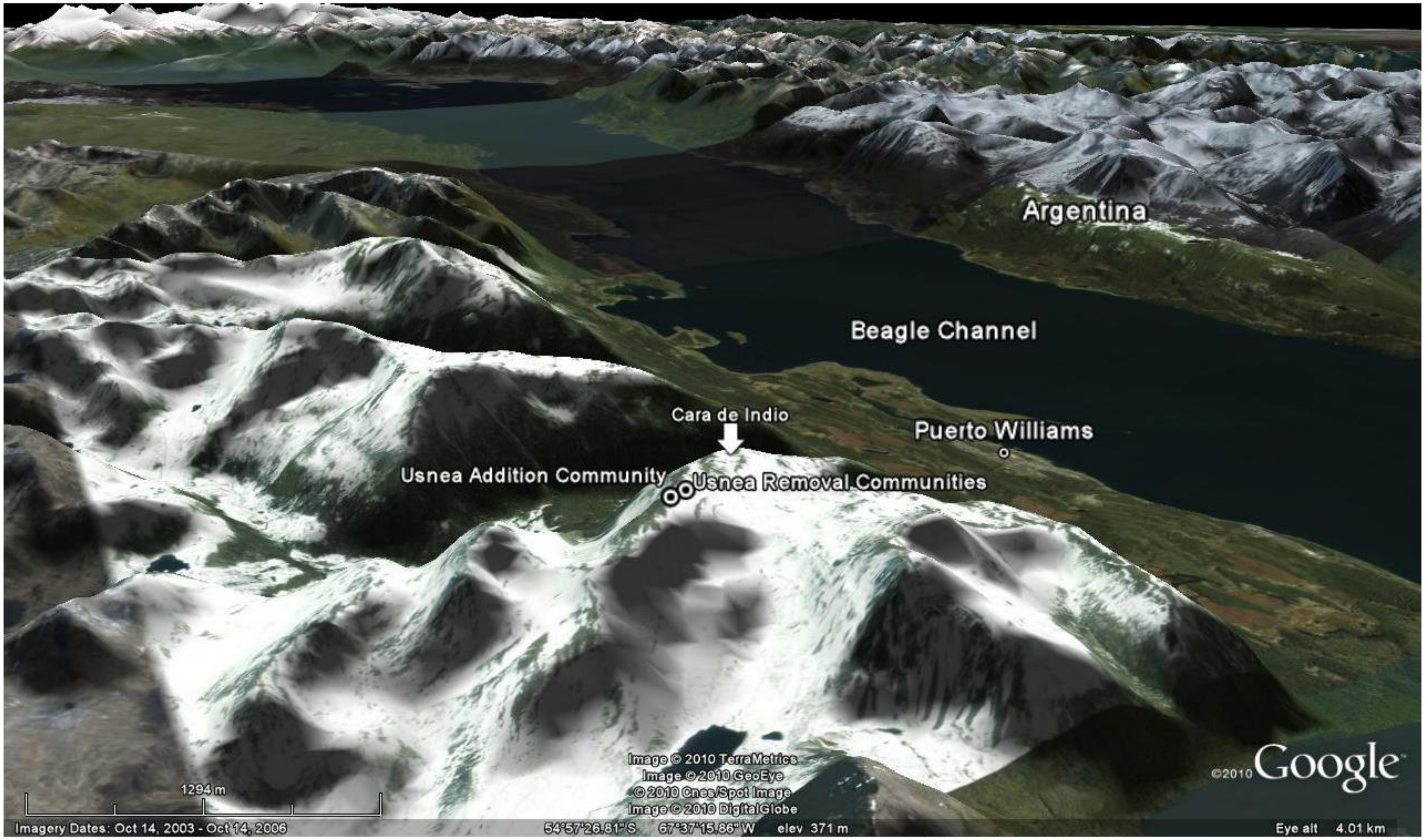


Figure 2.6. Mean daily diurnal temperature time series under different cryptogams and bare soil at 1cm depth. All values are mean (±1SE).

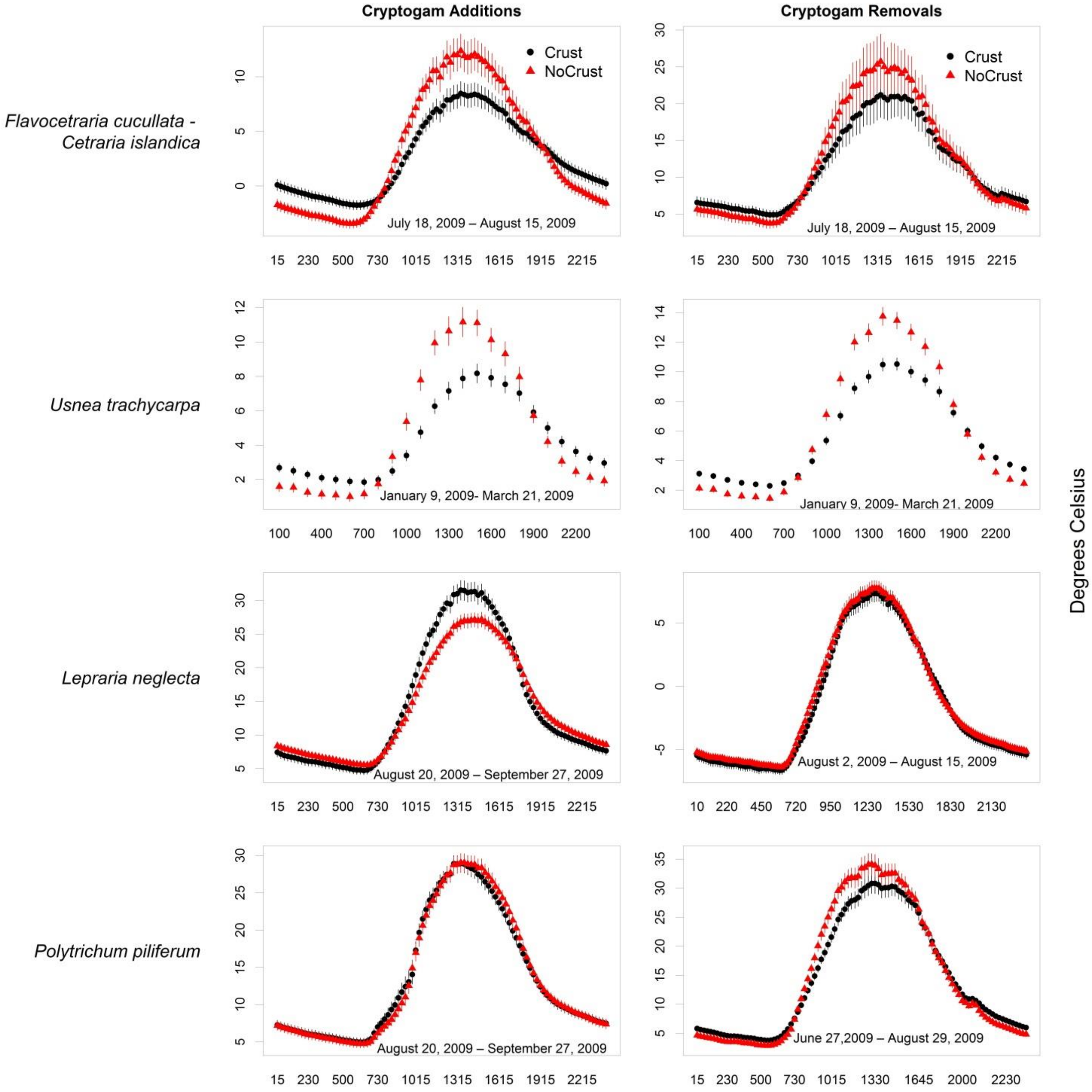
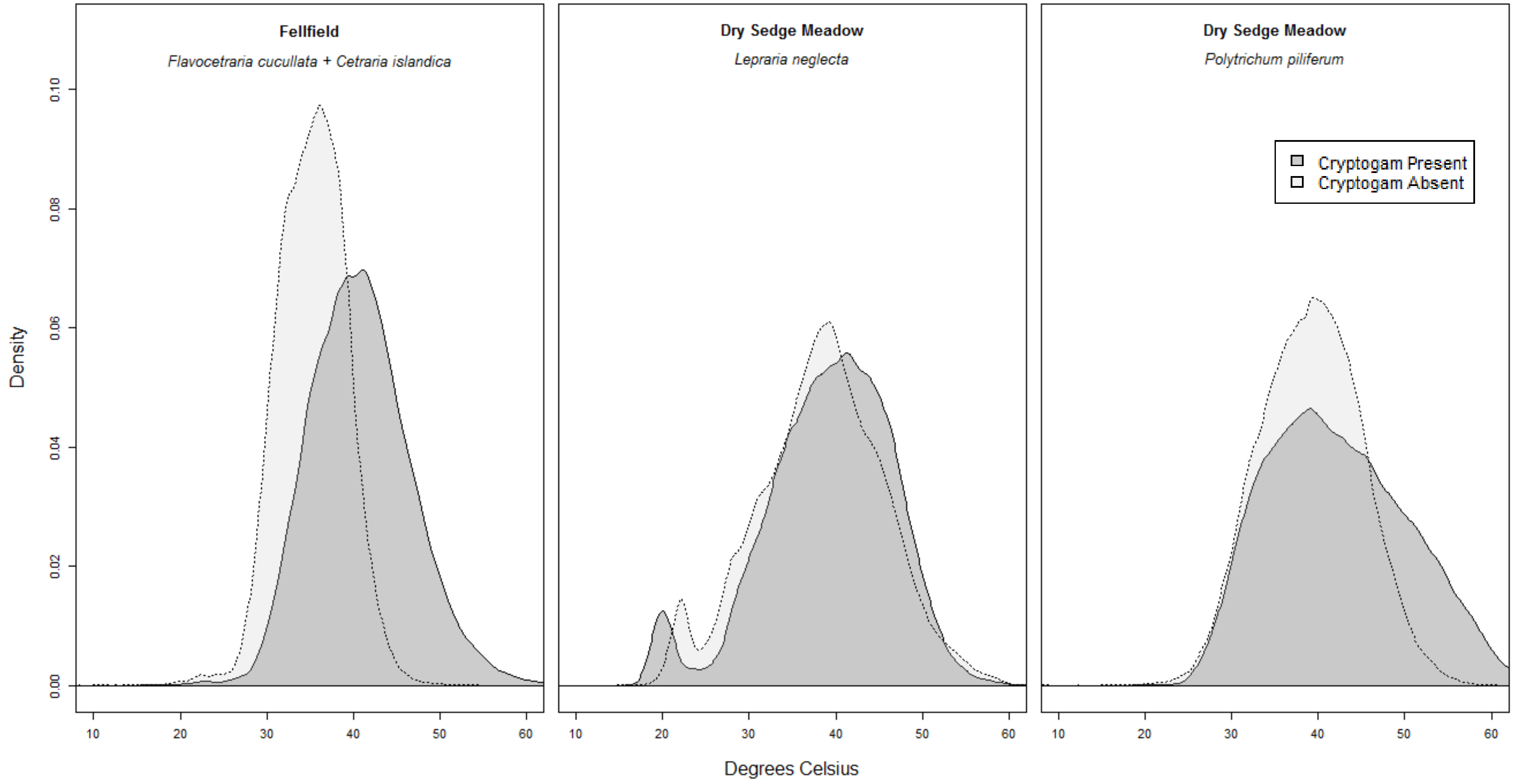


Figure 2.7. Kernel density plots showing the relative frequency of surface temperature values in treatment and control plots.

(A) Three addition sites at Snowshoe Mountain.



(B) Three removal sites on Snowshoe mountain.

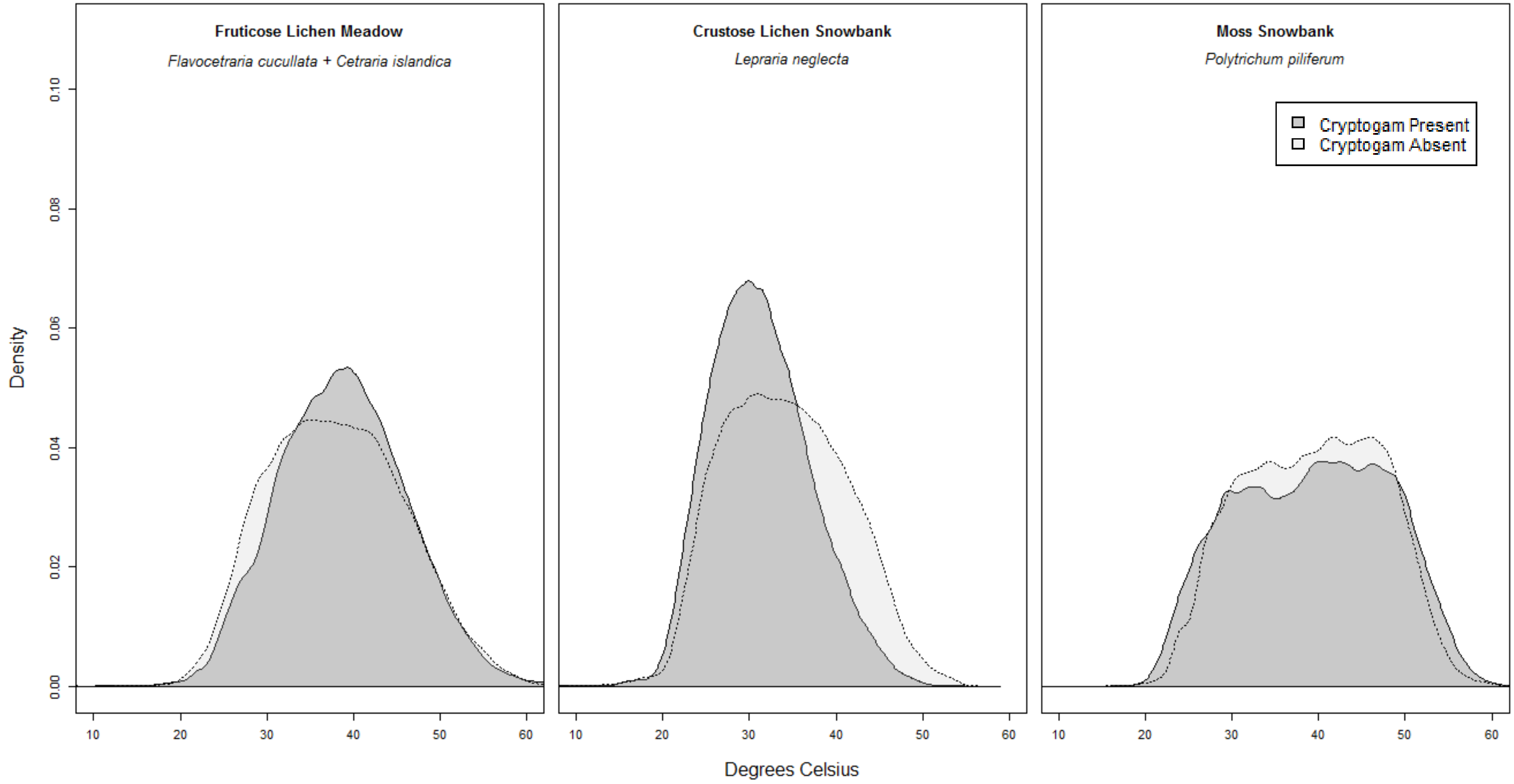


Figure 2.8. Digital RGB and infrared images of treatment and control plots. (a) RGB image of control plot in the “fellfield” community with the natural substrate intact (b) RGB image of addition plot in the “fellfield” community where the *F. cucullata-C. islandica* mix has been added (c) infrared image of the control fellfield plot (d) infrared image of the addition fellfield plot.

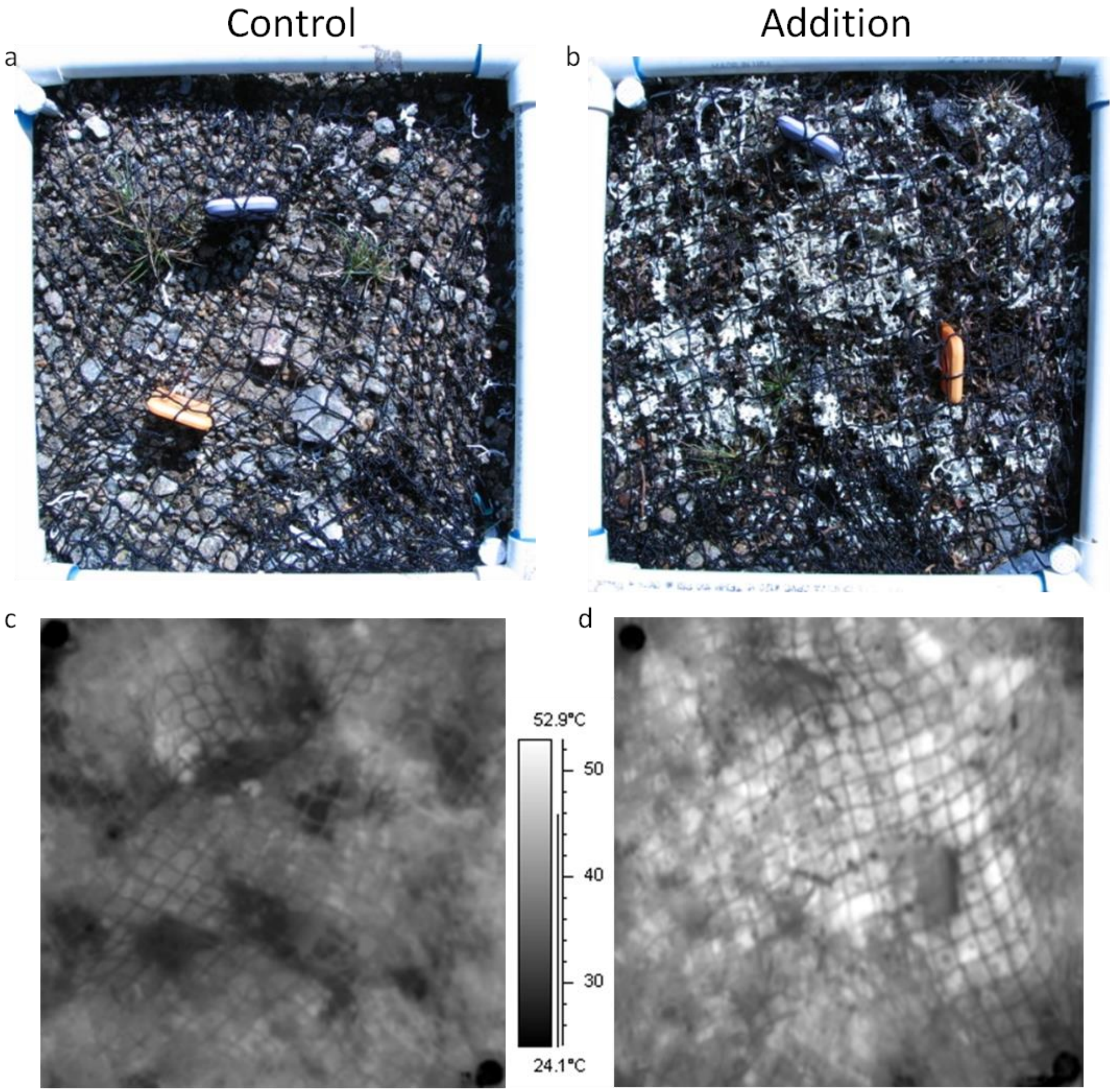
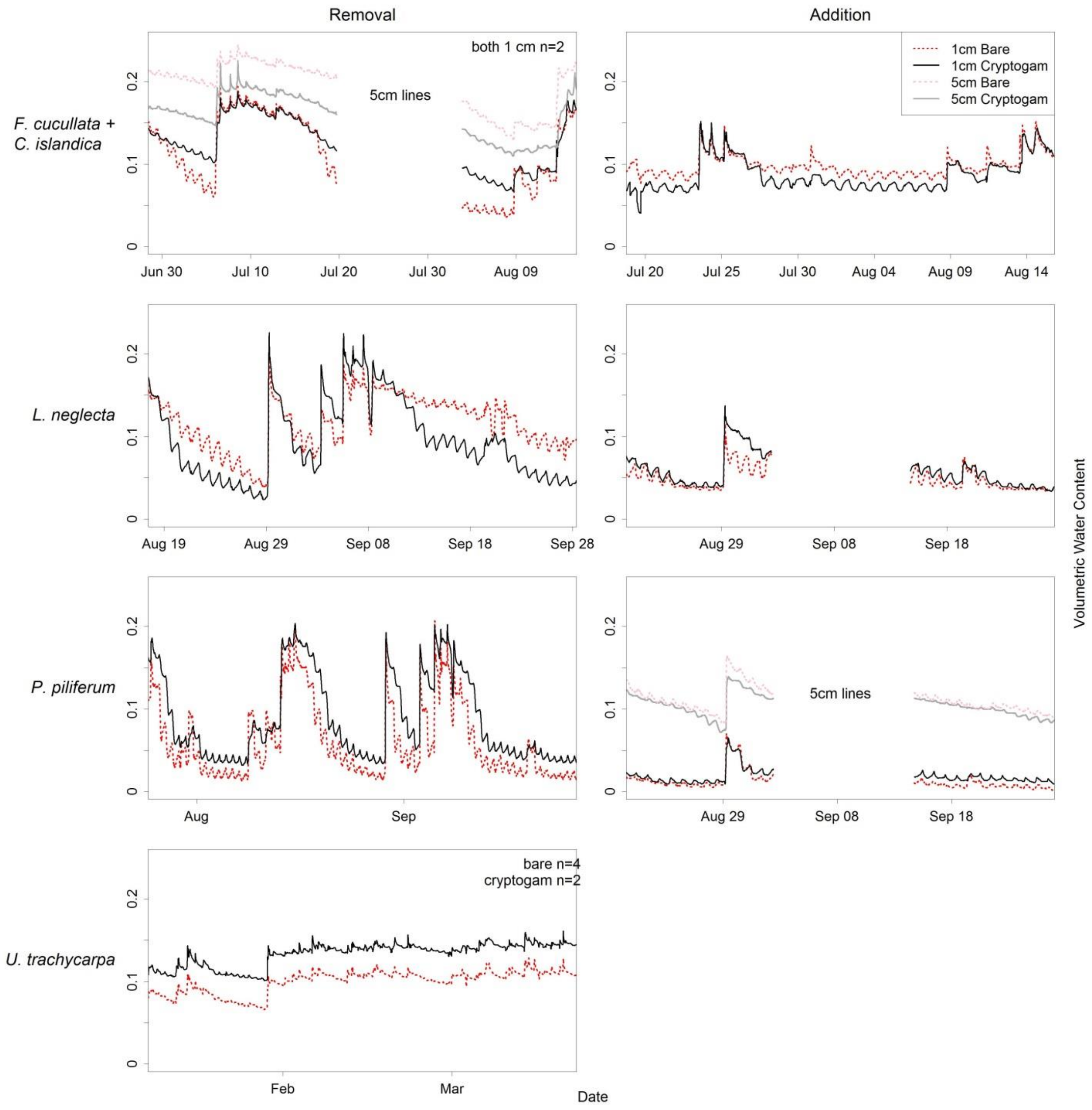


Figure 2.9. Seasonal time series of estimated soil moisture (VWC) at 1cm depth (and 5cm for two cryptogam types) in experimental removal and control plots under all four different cryptogams tested.



Section 2.9. Appendices

Appendix 2.1. Experimental plot composition, topography, and soil characteristics summarized for all experimental communities on Snowshoe Mountain and Cara de Indio.

Site	Community Description
Snowshoe	Dry sedge meadow – *Lepraria neglecta* addition and control plots Elevation: 2270 m Soils: Sandy Cryands

Experimental Plot Topography

	Control	Treatment
Mean Slope	5.8 ± 1	4.9 ± 0.9
Mean Aspect	124.6 ± 32.9	79.8 ± 26.9

Species or soil surface material (* indicates cryptogam)	Mean Cover (% ± 1SE) Control	Mean Cover (% ± 1SE) Treatment
*Lepraria neglecta**	1.3 ± 0.5	1.5 ± 0.6
*Polytrichum piliferum**	1.8 ± 1.6	2.5 ± 1.3
Potentilla diversifolia var. diversifolia	1.5 ± 0.7	1.5 ± 0.7
*Peltigera rufescens**	1.5 ± 1.0	1.2 ± 0.4
Arenaria capillaris	2.3 ± 1.5	4.0 ± 4.2
Carex scirpoidea	7.8 ± 6.1	6.4 ± 3.6
Juncus drummondii	0 ± 0	3.5 ± 0.7
Erigeron aureus	5.2 ± 3.9	5.8 ± 2.8
Unknown bryophyte*	0 ± 0	1.5 ± 0.7
Unknown forb	1.5 ± 0.7	1.3 ± 0.5
Bare Sand	5.9 ± 5.5	5.4 ± 3.2
Bare Gravel	38.0 ± 32.3	31.4 ± 24.2
Mineral Soil	31.1 ± 28.9	29.9 ± 27.7
Bare Rock	7.0 ± 4.2	8.9 ± 3.8
Litter	12.5 ± 6.9	15.6 ± 7.7

Dry sedge meadow – *Polytrichum piliferum* addition and control plots
Elevation: 2270 m
Soils: Sandy Cryands

Experimental Plot Topography

	Control	Treatment
Mean Slope	7.5 ± 1	6 ± 1.2
Mean Aspect	116.4 ± 28.4	114.2 ± 24.9

Species or soil surface material (* indicates cryptogam)	Mean Cover (% ± 1SE) Control	Mean Cover (% ± 1SE) Treatment
*Cetraria islandica**	0 ± 0	1 ± 0
*Lepraria neglecta**	1 ± 0	1.3 ± 0.6
*Polytrichum piliferum**	5.5 ± 12.5	2.6 ± 1.5
*Peltigera rufescens**	2.0 ± 2.2	1 ± 0
Arenaria capillaris	2.2 ± 0.8	2.5 ± 1.3
Carex scirpoidea	8.2 ± 4.1	10 ± 7.1
*Flavocetraria cucullata**	0 ± 0	1 ± 0

Unknown bryophyte*	2.0 ± 1.4	3.0 ± 0.8
Sedum divergens	1.2 ± 0.4	1 ± 0
Erigeron aureus	5.3 ± 2.4	5.3 ± 1.4
Bare Sand	9.4 ± 6.3	9.5 ± 6.8
Bare Gravel	33.5 ± 27.3	30.4 ± 29.6
Mineral Soil	22.0 ± 21.3	28.0 ± 19.5
Bare Rock	9.1 ± 6.1	7.3 ± 5.5
Litter	14.5 ± 7.2	15.7 ± 7.5

Moss snowbank - *Polytrichum piliferum* removal and control plots

Elevation: 2270m
Soils: Highly Organic Cryands

Experimental Plot Topography

	Control	Treatment
Mean Slope	5.5 ± 0.9	5.7 ± 1.1
Mean Aspect	96.9 ± 12.4	88.7 ± 9.8

*Cetraria islandica**	1.8 ± 1.0	1.3 ± 0.5
*Lepraria neglecta**	2.3 ± 1.9	2.2 ± 1.3
*Polytrichum piliferum**	84.7 ± 10.8	87.4 ± 8.1
Erigeron aureus	8.8 ± 4.0	7.2 ± 3.0
Potentilla diversifolia var. diversifolia	1.5 ± 1.0	2.7 ± 1.5
*Peltigera rufescens**	2.9 ± 2.5	4.5 ± 3.4
Arenaria capillaris	4.3 ± 3.0	4.0 ± 2.9
Carex scirpoidea	4.8 ± 3.4	4.9 ± 2.7
Antennaria alpina	1 ± 0	2.5 ± 0.7
Unknown Graminoid	2.3 ± 1.3	1.8 ± 0.5
Unknown forb	3.0 ± 4.6	2.7 ± 1.3
Litter	6.9 ± 4.5	6.7 ± 3.6

Crustose lichen snowbank – *Lepraria neglecta* removal and control plots

Elevation: 2380m
Soils: Highly Organic Cryands

Experimental Plot Topography

	Control	Treatment
Mean Slope	6.9 ± 1.2	7.3 ± 0.7

Antennaria lanata	15.3 ± 5.6	13.3 ± 4.9
Carex nardina	6.9 ± 3.7	5.8 ± 2.9
Cladonia spp.	1.6 ± 1.8	1.4 ± 0.7
*Peltigera canina**	1 ± 0	1 ± 0
*Cetraria islandica**	1.7 ± 1.1	2.0 ± 1.4

Mean Aspect	66.3 ± 14.2	55.8 ± 4.7

*Lepraria neglecta**	60.4 ± 16.3	57.1 ± 16.0
*Polytrichum piliferum**	12.7 ± 7.2	20.3 ± 11.9
*Diploschistes spp. **	2.4 ± 1.5	2.0 ± 0.8
*Peltigera rufescens**	2.1 ± 2.6	3.6 ± 2.3
Carex scirpoidea	2.0 ± 1.2	5.0 ± 3.6
Litter	5.4 ± 2.2	4.6 ± 1.0

Fellfield – *Flavocetraria cucullata / Cetraria islandica* addition and control plots

Elevation: 2284m
Soils: Gravelly Cryands

Experimental Plot Topography

	Control	Treatment
Mean Slope	3.5 ± 0.4	2.8 ± 0.4
Mean Aspect	273.9 ± 20.7	267.4 ± 23.6

*Cetraria islandica**	1.4 ± 0.7	1.4 ± 0.5
*Polytrichum piliferum**	1.4 ± 0.8	1.8 ± 0.8
Carex scirpoidea	1 ± 0	2.5 ± 2.1
Minuartia obtusiloba	1 ± 0	2 ± 1
Festuca brachyphylla	5.8 ± 1.6	5.6 ± 2.5
*Flavocetraria cucullata**	1.3 ± 0.7	1 ± 0
*Thamnolia vermicularis**	1.1 ± 0.3	1 ± 0
Bare Rock	16.5 ± 12.8	21.4 ± 13.9
Bare Sand	3.2 ± 2.8	2.6 ± 1.9
Bare Gravel	74.7 ± 20.4	75.1 ± 17.1
Mineral Soil	2.0 ± 1.1	2.8 ± 2.2
Litter	4.4 ± 2.4	5.1 ± 2.7

Fruticose lichen meadow – *Flavocetraria cucullata / Cetraria islandica* removal and control plots

Elevation: 2283
Soils: Highly Organic Cryands

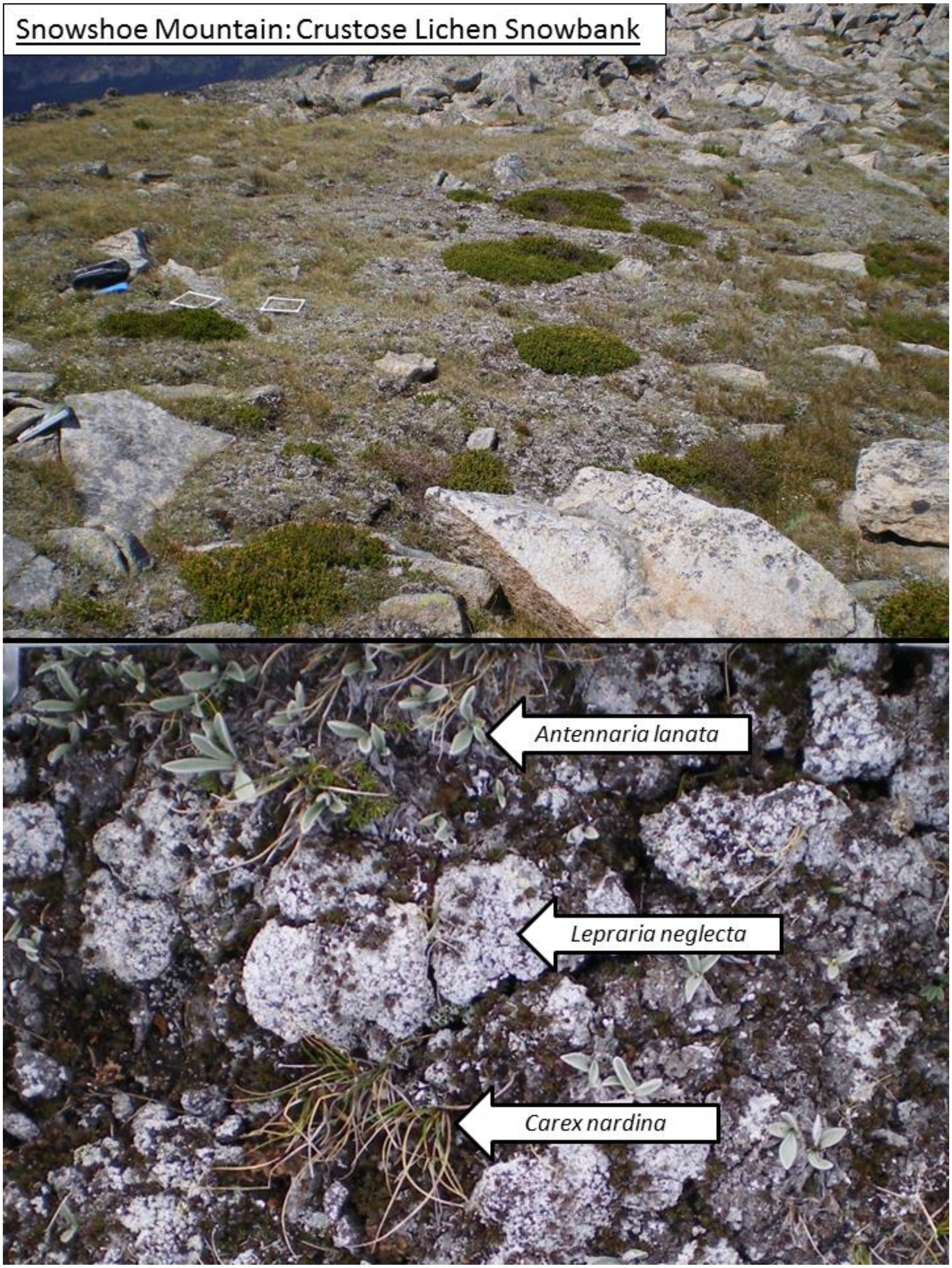
Experimental Plot Topography

	Control	Treatment
Mean Slope	7.8 ± 0.8	8.7 ± 0.8
Mean Aspect	316.8 ± 6.6	313.4 ± 3.8

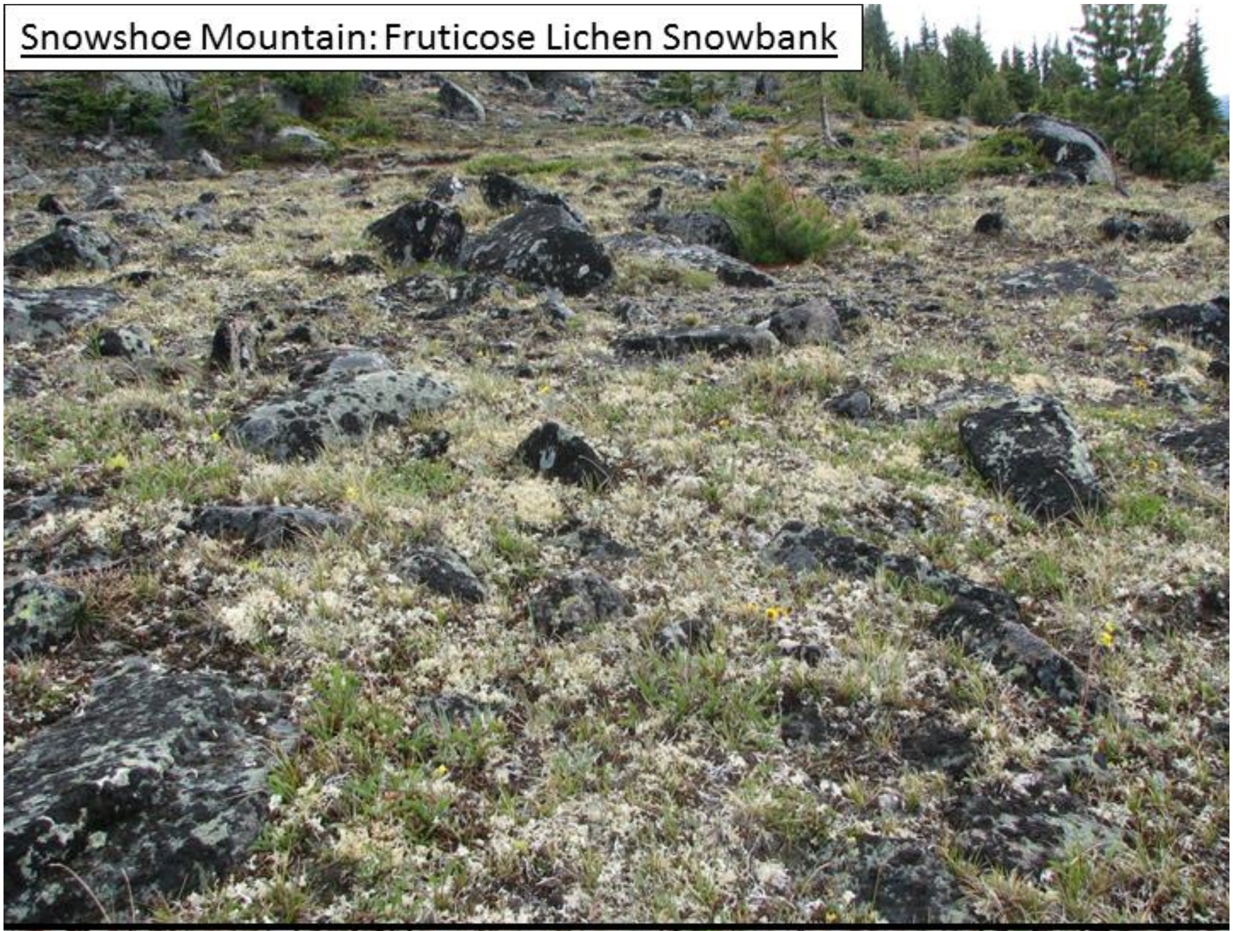
*Cladonia spp. **	1.3 ± 0.5	1.1 ± 0.4
*Cetraria islandica**	17.8 ± 7.3	19.7 ± 8.8
*Polytrichum piliferum**	14.4 ± 9.1	13.5 ± 9.2
Potentilla diversifolia var. diversifolia	1.7 ± 0.7	1.6 ± 0.8
*Peltigera rufescens**	2.1 ± 1.5	2.0 ± 1.2
Carex scirpoidea	5.3 ± 2.1	5.4 ± 2.0
Solidago multiradiata	8.2 ± 5.0	9.7 ± 6.3

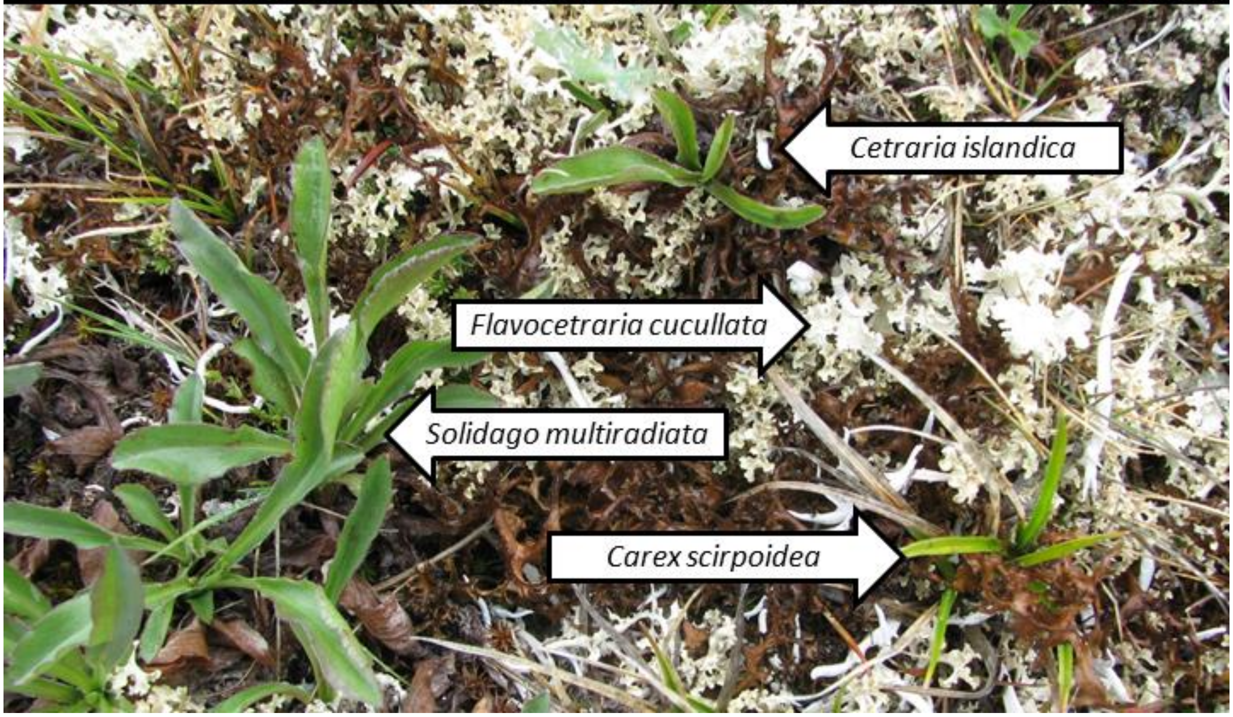
		Minuartia obtusiloba	2.2 ± 1.3	2.4 ± 2.6
		Festuca brachyphylla	2.3 ± 0.8	2.0 ± 0.8
		Antennaria alpine	2.0 ± 1.2	2.0 ± 1.5
		*Flavocetraria cucullata**	45.0 ± 11.5	44.0 ± 13.2
		*Thamnolia vermicularis**	2.3 ± 1.2	2.1 ± 1.0
		Carex phaocephala	2 ± 2	1.8 ± 0.8
		Unknown Graminoid	1.1 ± 0.4	1 ± 0
		Litter	10.1 ± 3.8	9.3 ± 2.9
Cara de Indio	Fellfield – *Usnea trachycarpa* removals around *Festuca contracta* Elevation: 775 – 800m Soils: Lithosols Slope: ≤10% Aspect; East	*Senecio humifusus*	Sparse	Sparse
		Festuca contracta	Moderate	Moderate
		*Usnea trachcarpa**	Abundant	Abundant
	Fellfield – *Usnea trachycarpa* removals around *Senecio humifusus* Elevation: 775 – 800m Soils: Lithosols Slope: ≤10% Aspect; West	*Senecio humifusus*	Sparse	Sparse
		Festuca contracta	Moderate	Moderate
		*Usnea trachcarpa**	Abundant	Abundant
	Fellfield – *Usnea trachycarpa* additions around *Senecio humifusus* Elevation: 775 – 800m Soils: Lithosols Slope: ≤10% Aspect: East	*Senecio humifusus*	Sparse	Sparse
	Fellfield – *Usnea trachycarpa* additions around *Festuca contracta* Elevation: 775 – 800m Soils: Lithosols Slope: ≤10% Aspect: East	Festuca contracta	Sparse	Sparse

Appendix 2.2. Communities and species used in the cryptogam transplant experiments on Snowshoe Mountain and Cara de Indio.

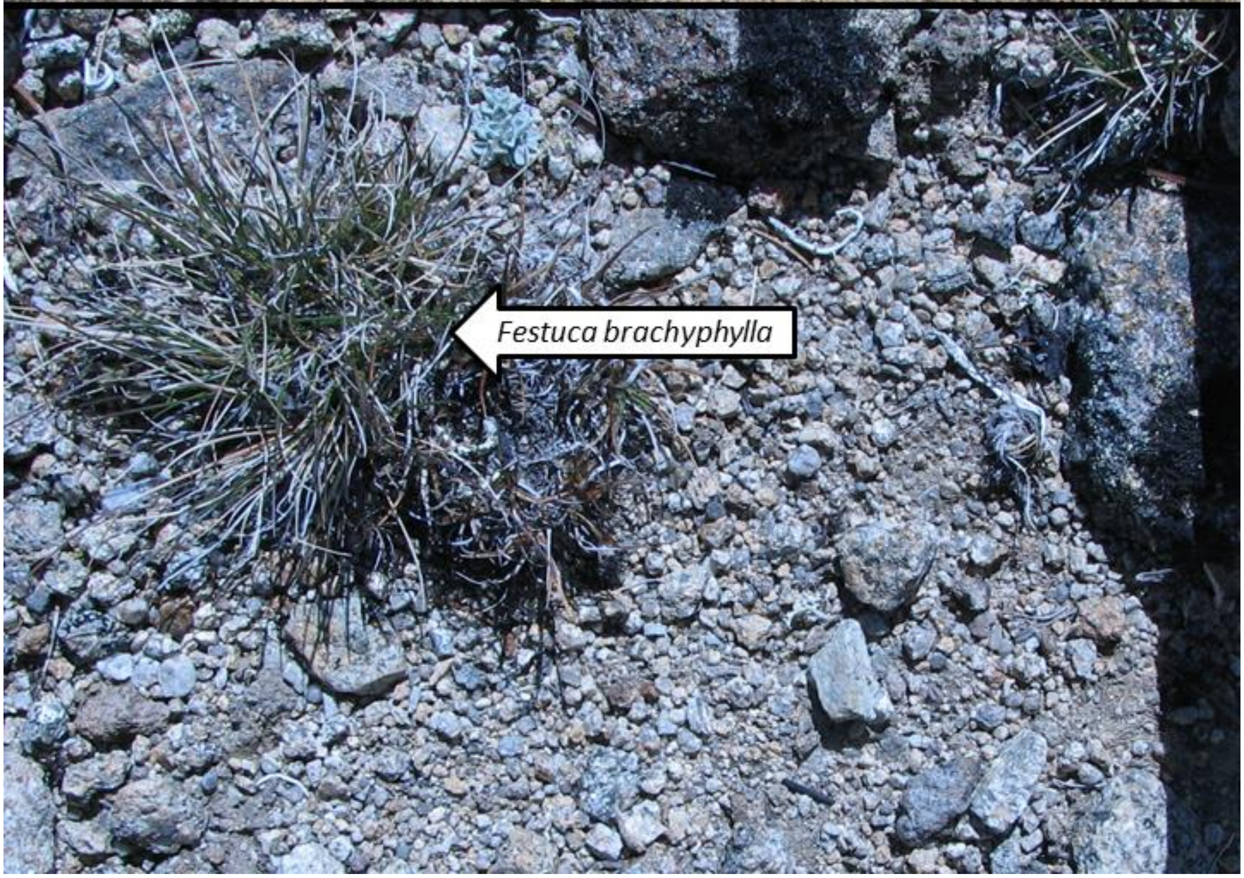


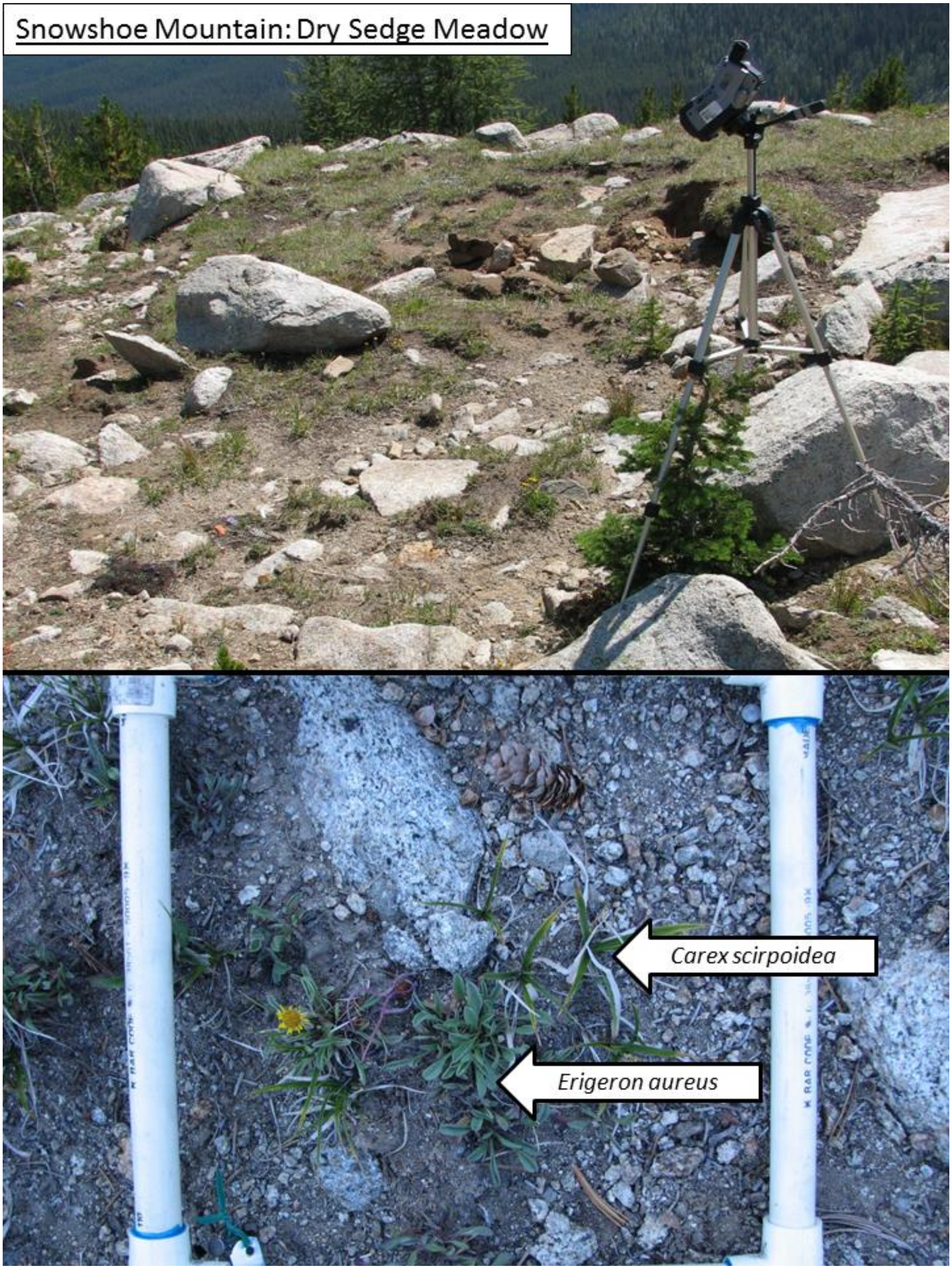
Snowshoe Mountain: Fruticose Lichen Snowbank






Snowshoe Mountain: Fellfield


Festuca brachyphylla



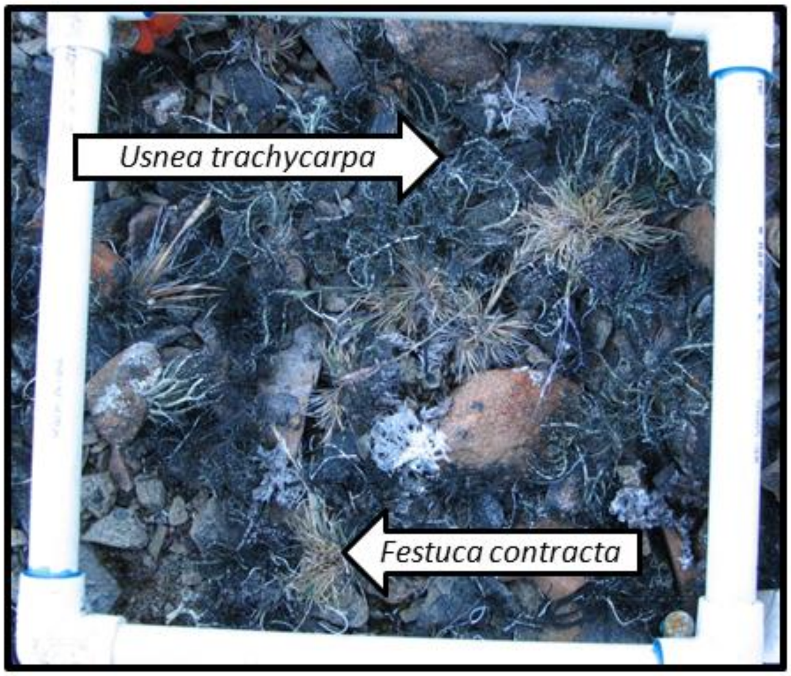
Snowshoe Mountain: Dry Sedge Meadow

Snowshoe Mountain: Moss Snowbank

Cara de Indio Fellfield

Cara de Indio: Usnea trachycarpa removals around *Festuca contracta*

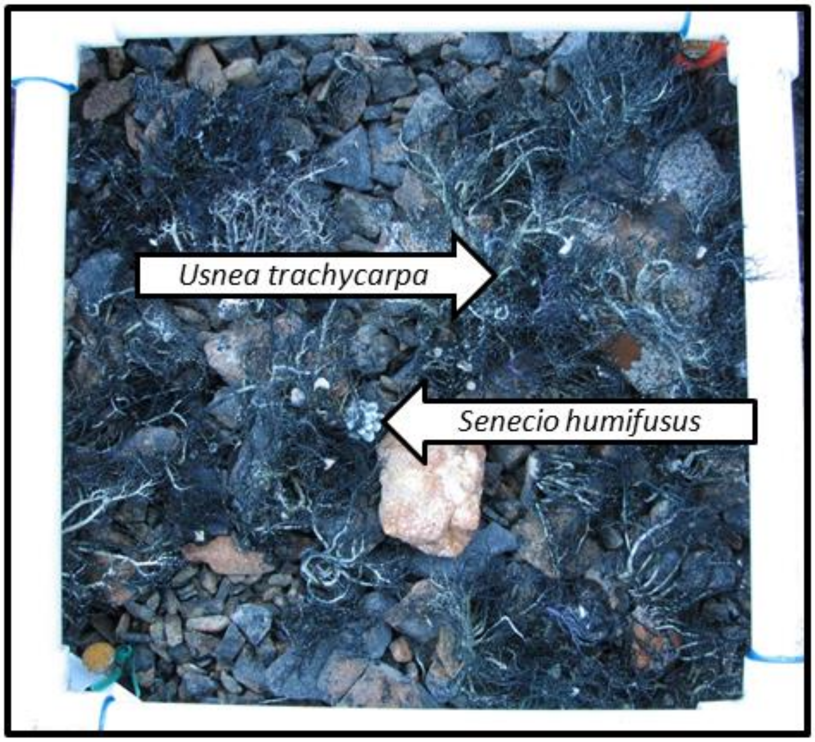
Before



After

Cara de Indio: Usnea trachycarpa removals around *Senecio humifusus*

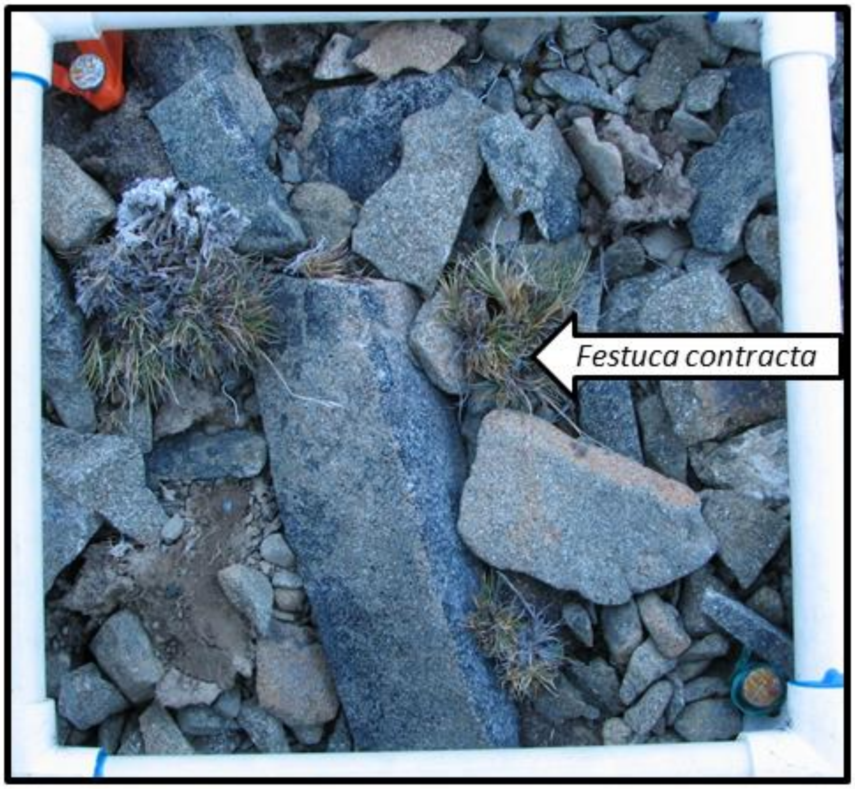
Before



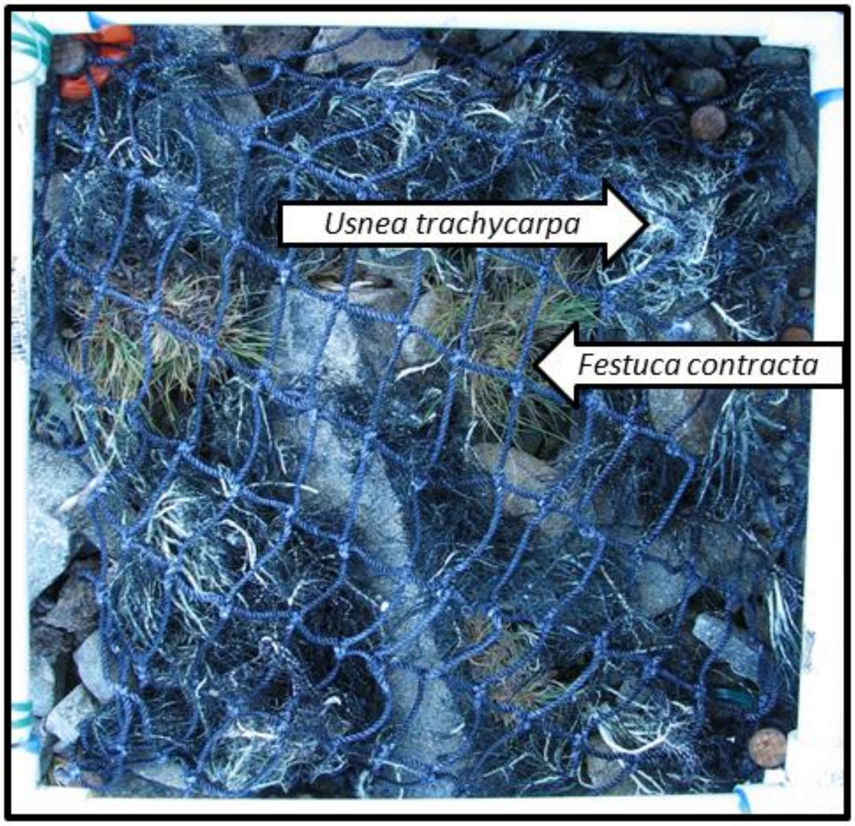
After

Cara de Indio: Usnea trachycarpa additions around *Festuca contracta*

Before

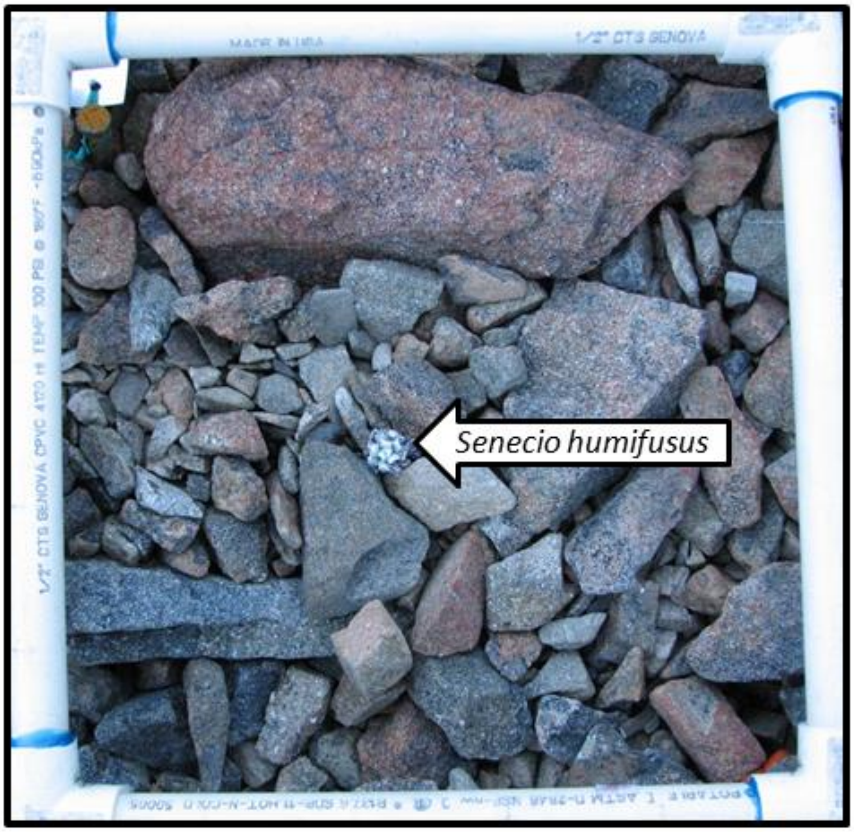


After

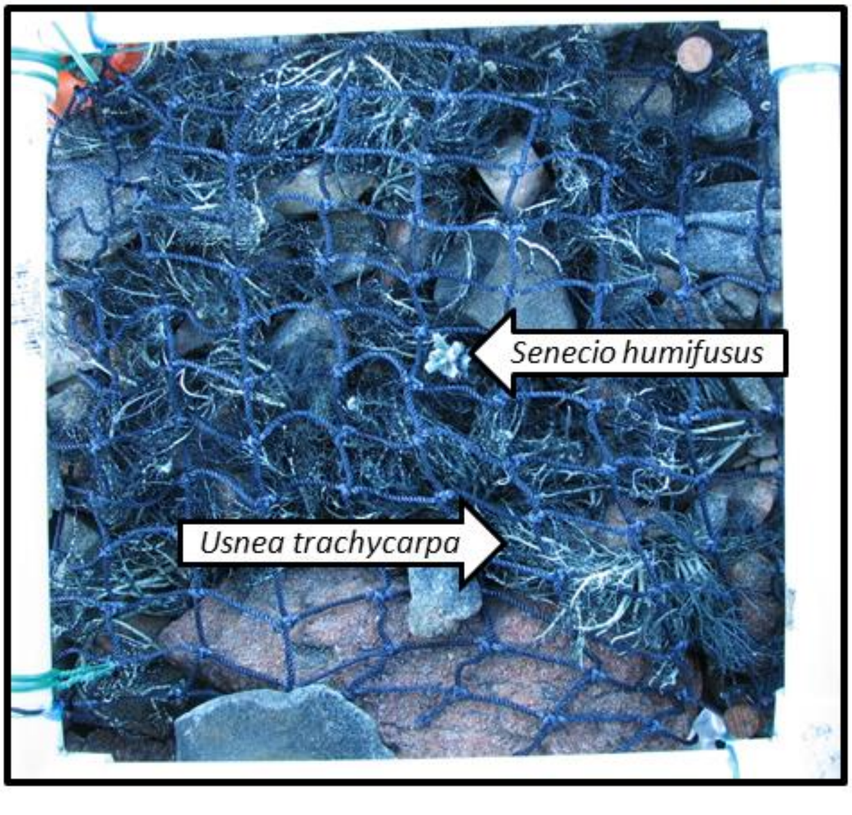


Cara de Indio: Usnea trachycarpa additions around *Senecio humifusus*

Before



After



Appendix 2.3. Additional methods associated with the measurement of temperature

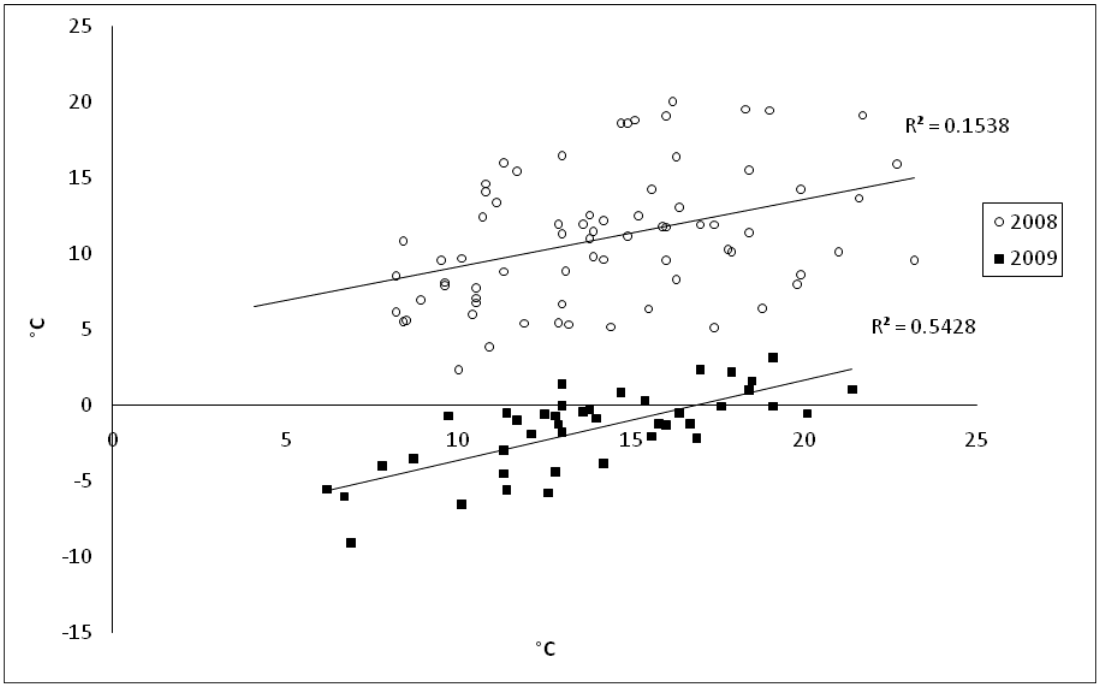
Although post-treatment data were collected in the summers of 2008 and 2009, I used different protocols for collecting the data. I made the decision to change my protocols in 2009 because, after some preliminary analysis of my 2008 data, I considered the temperature data from 2008 to be unreliable. Here I will outline the factors behind that decision, and explain why I consider the 2009 data reliable.

The summer of 2008 was the first growing season after the cryptogam treatments had been installed. To determine the effect the cryptogam treatments had on the temperature and moisture regimes experienced by alpine plants, I measured soil temperature and moisture in a subset of the paired experimental plots. To measure subsurface temperature I inserted Campbell Scientific 105-T soil temperature probes (Campbell Scientific, Logan, UT) into treatment and control plots at 1-3mm and 5cm depth.

The shallow sensor was inserted horizontally, with great effort taken not to disturb the soil surface. Despite this, upon several return trips to Snowshoe Mountain I noted some sensors had become uncovered due to sloughing off of the fragile thin soil layer covering the sensor, often coincident with a precipitation event. These episodes of sensor exposure appeared to cause enormous variability in the data, and further, after reinserting the probes, often the patterns apparent before the uncovering event were less apparent or absent afterwards. Late in the season I began using a caliper to measure the depths of the sensors more precisely, and I discovered that the depth of the manually installed sub surface sensors varied greatly and was between 1-5mm. Although this does not seem a particularly large range, these small differences in depth affected the actual temperature measured and corresponded closely to the noise and variability I was seeing in the data. To examine whether soil temperature data from 2008 were reliable, I examined how closely they correlated (Figure A3-1) to air temperature data from the nearest weather station (Salmon Meadows Snotel site number 728, elevation 1,359 m; 48°39’N, 119°50’W USDA Natural Resources Conservation Service). For each site, average temperatures were calculated and compared for the same day.

In 2009, to avoid sloughing of the near surface layer above the probes, I placed the sensors with a caliper to 1 cm depth. The use of a caliper enabled me to achieve 1mm precision in the depth of the sensor. Due to the more precise probe placement, there was a distinctly stronger correlation between soil temperature data and the Snotel air temperature data in 2009 than in 2008 (Figure A3-1). Because of the enormous difference in the strength of this relationship, I decided not to use the 2008 soil temperature data in my analysis.

Figure A2.3.1. Crustose lichen snowbank daily mean near surface soil temperature vs. daily mean air temperature at the Salmon meadows Snotel site.

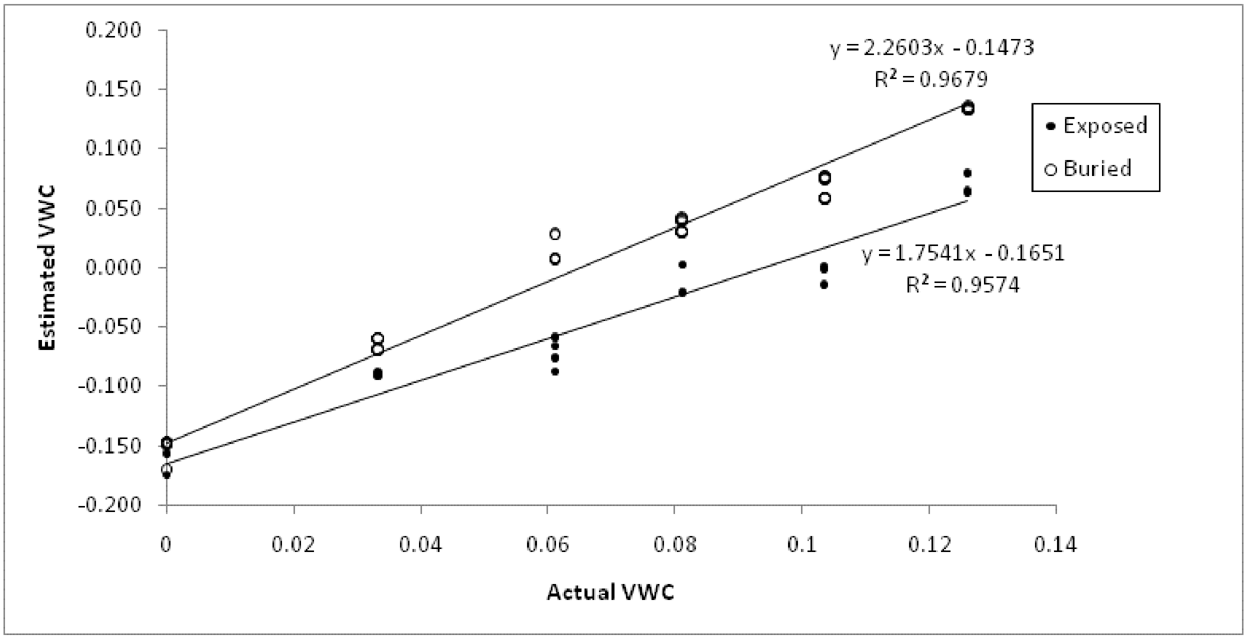


Appendix 2.4. Additional methods associated with the measurement of soil moisture

Because of the difficulty in accessing the study sites and the fact that I was more interested in the comparative moisture levels among treatments than absolute values, probes were not calibrated to site soils. In prior versions of my analysis, values were reported as the output from the default calibration curve equation for mineral soil, where Volumetric Water Content ≈ 0.00119 * datalogger output (mV) – 0.4 (Decagon Devices). However, this resulted in negative water content values for much of the summer in some plots. Decagon Devices technical support staff suggested this underestimation may have been due to the exposed overmolding, where much of the sensor circuitry is located. They further stated that the trends were reliable, as the probe itself was always in the soil, and that I could simply calibrate the probes in a mineral soil with this overmolding exposed, and develop a correction factor.

The protocol for developing the correction factor was as follows. First, I filled a 20 liter bucket with fully compacted, oven-dried potting soil to 15 cm depth. I inserted four probes at 5 cm depth, two with the overmolding exposed, and two with it buried. I set the datalogger to take measurements every ten seconds, and to record the average of these ten second readings every minute for ten minutes. I then wet the soil with a known volume of water and homogenized the moisture levels in the soil by manually turning the soil for five minutes. After this I performed the same measurement protocol, and repeated this for five consecutive additions of water. Because the volume of soil and water in the bucket were known and great efforts were taken to homogenize moisture levels throughout the soil throughout turning, I consider the ratio of water volume/ soil volume to be the true volumetric water content (VWC). These known VWC values are compared with the estimated values in Figure A2.4.1.

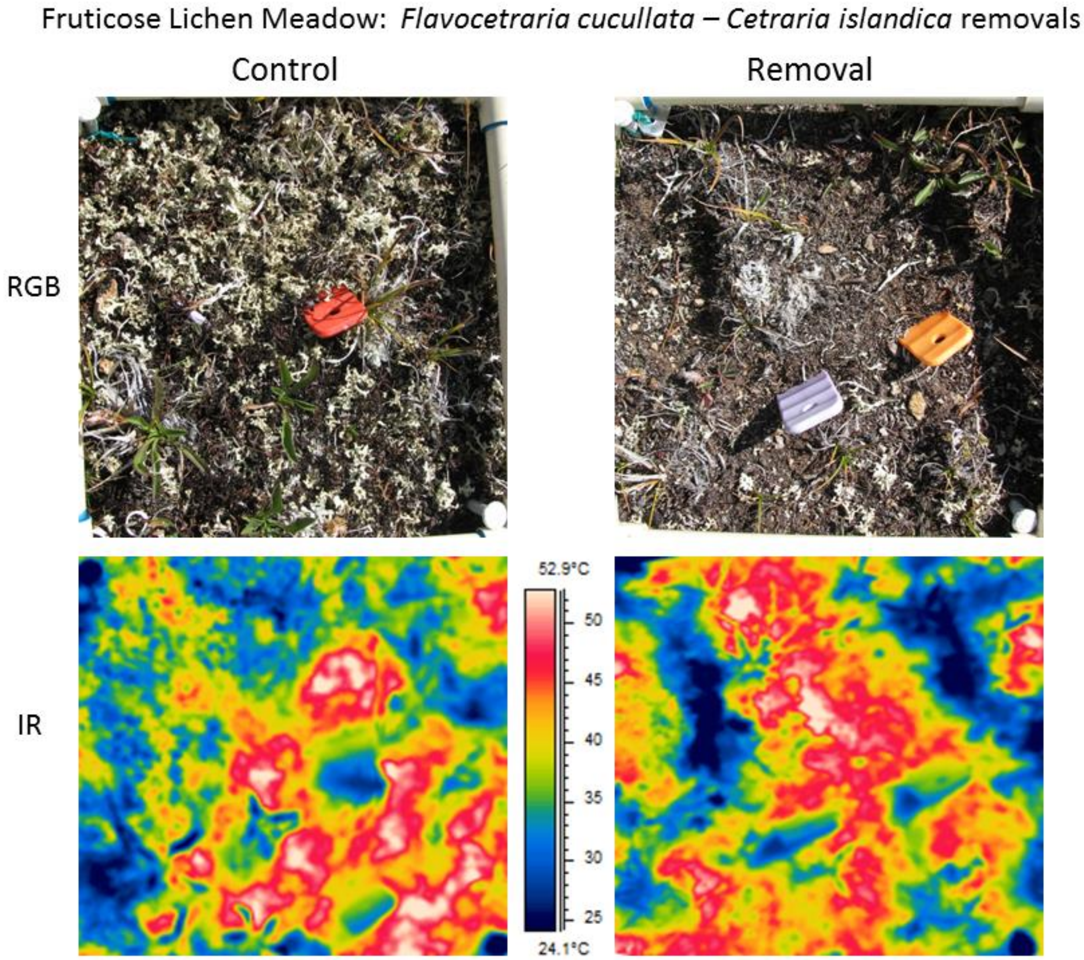
Figure A2.4.1. Estimated soil volumetric water content (VWC) versus actual VWC for six different moisture levels



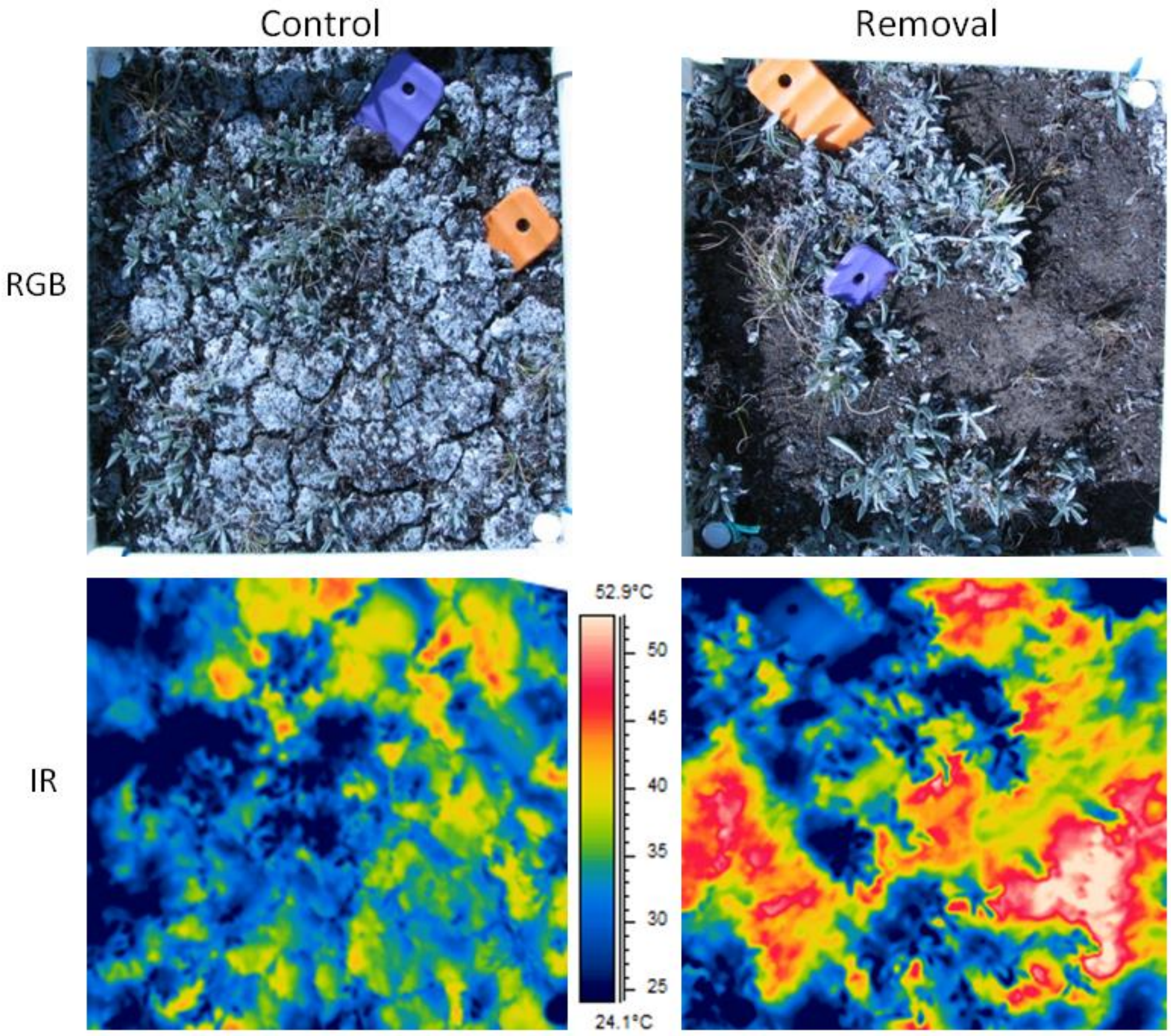
These data demonstrate that probes with overmoldings both buried and exposed all underestimated true VWC. While there was some difference attributable to overmolding exposure, the y-intercepts for the best fit linear models for data from both installation styles suggests that VWC of oven dry soil is underestimated in both cases by approximately 15-16%. This is similar to the most negative values I observed in the field. Because all of the probes were installed with the overmolding exposed, I will simply use the best fit linear model in Figure A2-1 for exposed probes to estimate actual VWC from the recorded values. This equation will be:

Corrected VWC = [Raw Value + 0.1651] / 1.7541

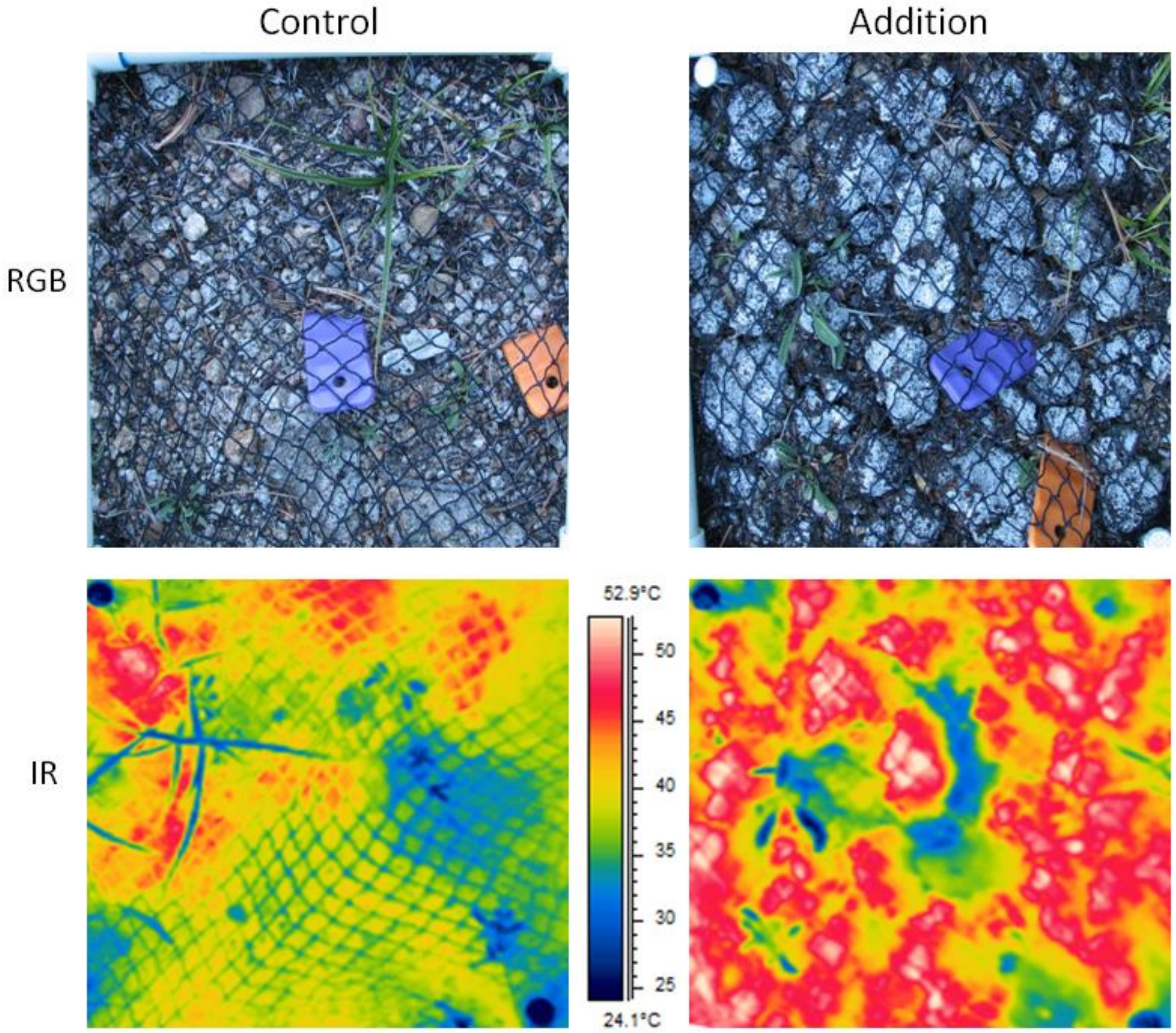
Appendix 2.5: Digital RGB and Infrared Images of treatment and control plots from all experimental communities on Snowshoe Mountain. Community type is noted at the top, treatment is noted above the RGB images, image type is noted to the left, and the infrared color-temperature scale is located between the two infrared images. The same scale was used for all images, though because of the large difference in times among communities, between-community comparisons are not valid.



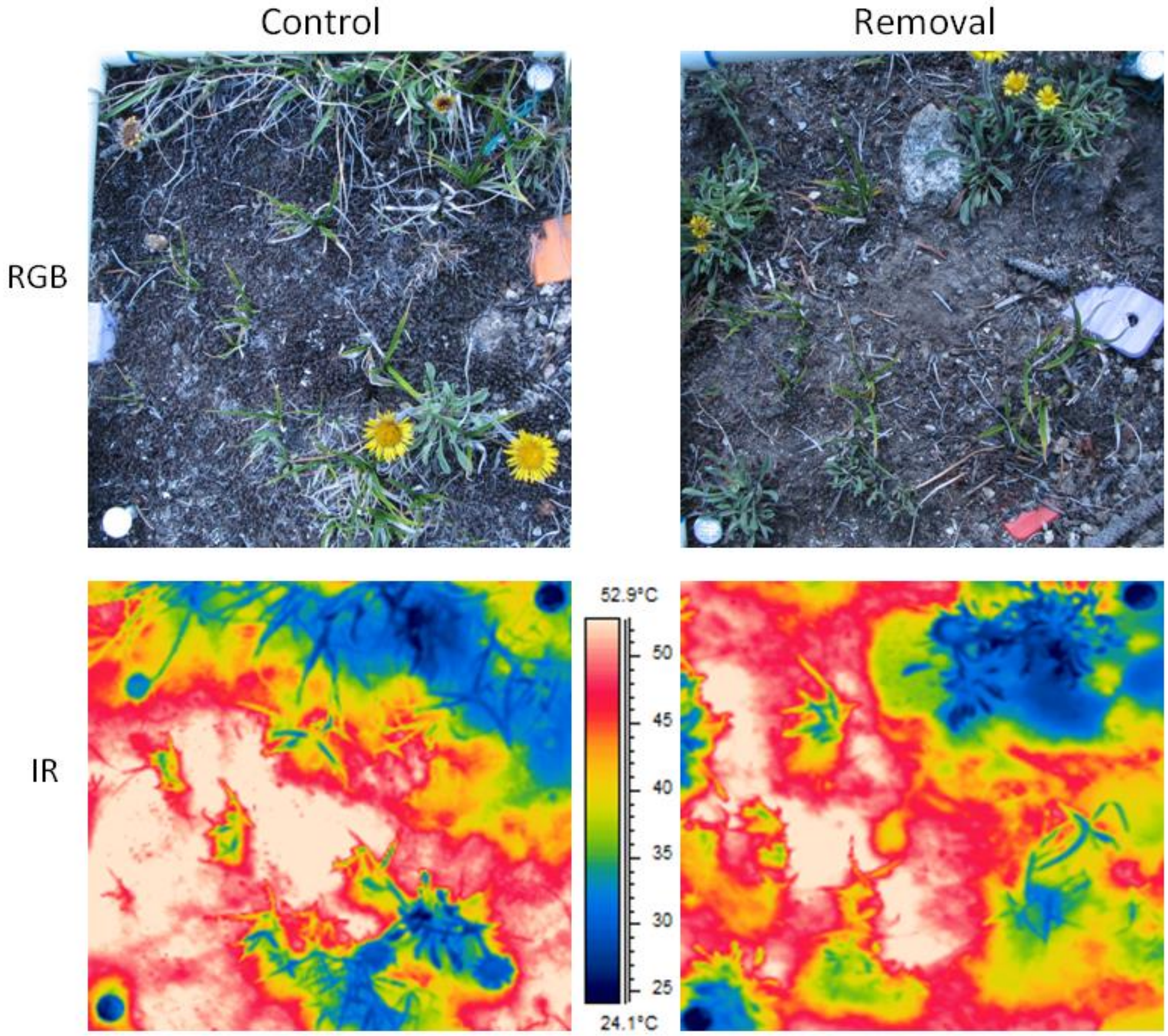
Crustose Lichen Snowbank: *Lepraria neglecta* removals



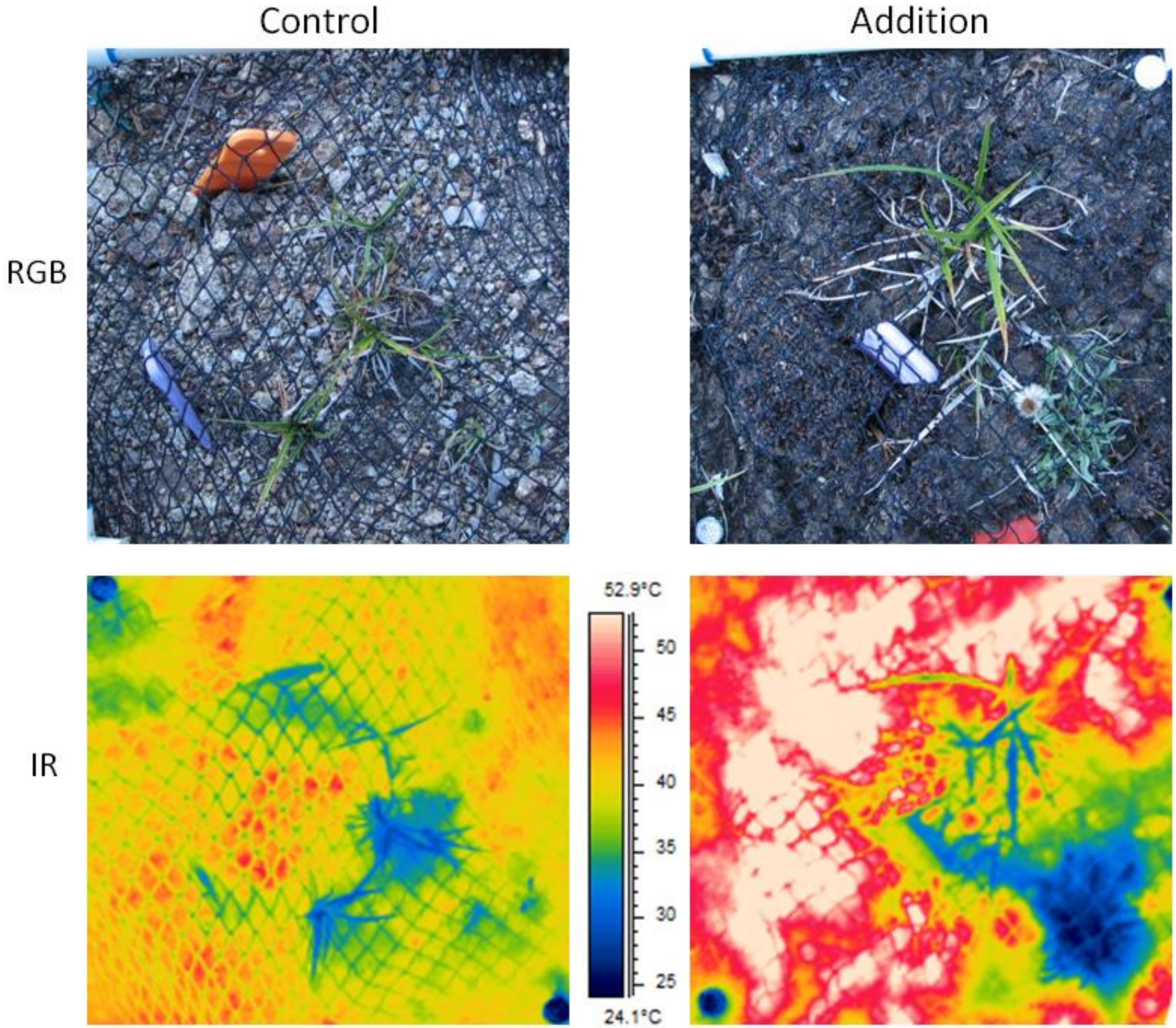
Dry Sedge Meadow: *Lepraria neglecta* additions



Moss Snowbank: *Polytrichum piliferum* removals



Dry Sedge Meadow: *Polytrichum piliferum* additions



Chapter 3: Experimental investigations into the biogeochemical influence of some alpine cryptogams in the North Cascades

Section 3.1. Introduction

The study of biogeochemical cycling in the alpine has a short history relative to most other ecosystems. With the exception of some extensive survey work in the Alps during the 1970’s (Rehder 1976, Gokceoglu and Rehder 1977, Rehder and Schafer 1978), most alpine biogeochemical work has been highly experimental and/or focused on one or more elements of global change (including, but not limited to Bowman et al. 1993, Bowman and Conant 1994, Bowman et al. 1995, Chapin et al. 1995, Arnone 1997, Soudzilovskaia and Onipchenko 2005, Soudzilovskaia et al. 2005, Ashton et al. 2008, Meier and Bowman 2008, Ashton et al. 2010). Because one of the most active alpine biogeochemical research groups in the world work does most of its work in the Colorado Front Range (for example, see work of Bowman, Seastedt, Baron, and others associated with the Niwot Ridge LTER) much of our understanding of alpine nitrogen (N hereafter) cycling has been shaped by the issues facing that region, in particular high inorganic N deposition. Given this, here I discuss current knowledge of N cycling in alpine ecosystems with a bias toward inorganic N. I use this background as context to argue that cryptogams are ideally suited to make substantial, but heretofore unexplored, contributions to the cycling of N in the alpine.

Section 3.1.a. Limitation

Inorganic (often referred to as “plant-available” or “mineral”) N partially limits primary production in alpine plant communities (Bowman et al. 1993, Soudzilovskaia and Onipchenko 2005). In spite of high amounts of organic N in alpine soils, in many alpine systems high C/N ratios, slow mineralization, and acidic conditions all contribute to low inorganic N availability, the traditional metric of soil fertility (Körner 2003). Unsurprisingly, many alpine plants respond rapidly to increases in their inorganic N supply (Bowman and Conant 1994, Munoz et al. 2005, Soudzilovskaia and Onipchenko 2005). A number of fertilization studies have refined our understanding of this limitation as species and life-form specific (Bowman et al. 1995, Suding et al. 2005), and Körner has argued convincingly that because community composition often changes in these N addition experiments, bringing into existence entirely different communities, *current* alpine plant communities cannot be considered N-limited (Körner 2003). However, though it may not be reasonable to consider extant alpine communities N-limited, I can safely assert that based on available evidence, particularly from fertilization studies, some individual species in alpine communities are indeed N-limited (Bowman and Conant 1994, Bowman et al. 1995, Soudzilovskaia and Onipchenko 2005).

Section 3.1.b. Supply, demand, and controls

Theoretically, N limitation in alpine plants must result from the relationship between external N supply and internal N demand. Historically, it was assumed that the primary currency of the alpine nitrogen economy was inorganic N, and that the major source of "new" inorganic N available for uptake by plants was the product of mineralization of soil organic matter (SOM) by microbes. However, estimates of annual inorganic N uptake by alpine vegetation have ranged between 2-7 g m^{-2} yr^{-1} (Fisk et al. 1998, Körner 2003), with most of this uptake thought to occur between snowmelt and peak biomass production (Lipson et al. 1999). This is far below most estimates of total annual demand for biomass production, which vary between 10-22 g m^{-2} yr^{-1} (Rehder and Schafer 1978, Körner 2003). Other potential sources of inorganic N include atmospheric deposition, which in some mountain ranges is thought to be driving changes in supply dynamics (Baron et al. 2000), and N fixation by free-living cyanobacteria or plant-bacterial associations (e.g. legumes), which in rare cases can meet up to half of annual demand (Bowman et al. 1996, Jacot et al. 2000). The gap between annual demand and uptake led to attention being focused on N resorption efficiency and storage, which can run as high as 50% (Körner 2003).

However, recent work has demonstrated that for alpine plants N demand is often distributed amongst inorganic (NO_3-N + NH_4-N) *and* organic (amino acids) forms, with relative proportions depending on the plant species involved and their neighbors (Raab et al. 1999, Xu et al. 2004, Xu et al. 2006, Ashton et al. 2008, 2010). Such plasticity in resource use has been proposed by Ashton and colleagues (2008, 2010) as a mechanism for coexistence in alpine communities. However, henceforth I focus exclusively on inorganic N; at the time of study design this was still considered the dominant form of N required by alpine vegetation and our data reflect this.

Attaining useful estimates of inorganic N available for plant uptake from mineralization assays has proved problematic. For example, Fisk and Schmidt (1998) estimated negative net mineralization (total N mineralized minus total N immobilized by soil microbes) rates in all communities on Niwot Ridge, despite annual N demand for tissue production ranging between 4 and 7 g $m^{-2}yr^{-1}$. Because of examples such as this, net mineralization is not considered an adequate index of the inorganic N supply rate (Cain et al. 1999), and ion-exchange resins are preferred for estimating inorganic N availability (Binkley and Matson 1983).

Regardless of the form, most inorganic N is biologically-derived, thus N availability and cycling in alpine communities are intimately related to parameters governing total biological activity and the processing of soil organic matter (SOM). Thus at the broadest level rates of N and C cycling covary positively with soil temperature and moisture, reflecting landscape-level patterns in topography, slope position, snowpack, and vegetation (Rehder and Schafer 1978, Fisk et al. 1998, Makarov et al. 2003).

As with the alpine climate, ecologists historically studied variability in the alpine nitrogen supply primarily at the community or "mesotopographic" level because of the measureable differences in vegetation structure at this scale (Rehder 1976, Rehder and Schafer 1978, Fisk et al. 1998, Makarov et al. 2003). From this work it is thought that NH_4-N is the dominant inorganic N form in most alpine soils (Makarov et al. 2003, Miller and Bowman 2003, Makarov et al. 2008), with levels of NO_3-N often 50% or more lower (in some cases an order of magnitude). NH_4-N has also been found to be more abundant in arctic wet sedge tundra (Elliott and Henry 2011), boreal forest (Huang and Schoenau 1996, Jerabkova and Prescott 2007), temperate grassland (Kahmen et al. 2008), subtropical moist forest (Mo et al. 2003), temperate coniferous forest (Thiel and Perakis 2009, Johnson et al. 2011), and temperate hardwood forests in Maine (Szillery et al. 2006), whereas NO_3-N has been found to be more abundant in the Chihuahuan desert (Allred and Snyder 2008), the Mojave desert (Drohan et al. 2005), coniferous forests in Maine (Szillery et al. 2006), and Hawaiian *Acacia koa* forests (Idol et al. 2007). In the alpine levels of NH_4-N are often positively correlated with soil moisture within communities (Miller and Bowman 2003) and in many cases across communities (Makarov et al. 2003, Miller and Bowman 2003, Makarov et al. 2008), whereas levels of NO_3-N are often positively correlated with soil temperature in alpine soils, but display variable relationships with soil moisture within and across communities (Miller and Bowman 2003, Makarov et al. 2008).

Recently, attention has turned to biogeochemical diversity at finer spatial scales. For example, it is now recognized that individual plants have the ability wield considerable influence over their biogeochemical surroundings via preferential uptake of different forms of soil N (Ashton et al. 2008), various root exudates (Meier et al. 2009), and unique litter chemistry (Bowman et al. 2004), with consequences for the growth of neighboring plants (Onipchenko et al. 2001, Suding et al. 2004). For reasons to be discussed, cryptogams are an obvious addition to the list of local factors which may hold sway over the alpine biogeochemical setting.

Section 3.1.c. A role for cryptogams

In the alpine, nitrogen originating with cryptogams has received little attention despite the fact that in other systems cryptogams are recognized for their ability to supply fixed nitrogen to the ecosystem (Millbank 1982, Belnap and Lange 2001, Gold et al. 2001, Körner 2003). For example, the cyanolichens (lichens containing N-fixing cyanobacteria) *Stereocaulon paschale, Ochrolechia upsaliensis,* and various *Peltigera* species frequent alpine landscapes in the Pacific Northwest (Glew 1998, Gold et al. 2001). These taxa (among others) and their capacities for N-fixation and photosynthesis were the focus of considerable attention in the 1970's as part of the International Biological Programme (e.g. Schofield et al. 1973, Kallio 1974, Alexander and Kallio 1976). While I provide a small sample of these and other N—fixation estimates here (here I restricted myself to work from systems with a significant cold season; for estimates from a broader range of systems see Table 7.1 in Nash (1996) or Evans and Lange in Belnap and Lange (2001)), they provide a rough outline of the potential N_2-fixing activity of alpine cryptogams. For example, in mixed boreal forest, Kallio (1974) estimated total annual nitrogen fixation of *S. paschale* and *Nephroma arcticum* to be between 10—40 kg ha^{-1} yr^{-1}. During this same time Hussdanell (1977) reported fixation estimates of 10 kg ha^{-1} yr^{-1} for *S. paschale* in dwarf-shrub pine forest in northern Sweden. Aridland estimates (for review see Evans and Lange in Belnap and Lange 2001) usually include contributions from free-living cyanobacteria.

These include the efforts of Rychert and Skujiņš (1974), who estimated N fixation in the Great Basin Desert of between 10-100 kg ha^{-1} yr^{-1}, and the work of Jeffries et al (1992), whose estimates for the Colorado Plateau ranged between 0.7 to 3.6 kg ha^{-1} yr^{-1}. Finally, most lichens are notoriously porous and capable of losing considerable quantities of inorganic N during precipitation events or when otherwise saturated (Pike 1978, Millbank 1982, Crittenden 1983). For example, Alexander and Kallio (1976) reported annual outputs of 2 kg ha^{-1} yr^{-1} for just one *Peltigera* species found in their study area. This combination of active fixation and porosity suggest it is reasonable to expect that cyanolichens, particularly when saturated early in the summer, may directly contribute inorganic nitrogen to alpine plant communities at a time when plants are most actively acquiring nutrients (Lipson et al. 1999). Gold et al. (2001) provide the only estimates of direct inputs thus far of 1.2 kg ha^{-1} day^{-1} in areas with high *Peltigera* cover, but this was under optimum moisture and temperature conditions and therefore cannot be reasonably extrapolated to an annual estimate.

Other pathways for cryptogam influence on alpine nitrogen dynamics, while promising, have received even less attention in other systems. For example, cryptogam leachates or cryptogam-related changes to temperature and moisture regimes could also be expected to indirectly affect inorganic N levels by altering N and C mineralization and immobilization rates (Bowman et al. 1995). Sedia and Ehrenfeld (Sedia and Ehrenfeld 2005) demonstrated such indirect effects of lichen-dominated (*Cladonia spp.*) and moss-dominated (*Polytrichum spp.*) cryptogam mats in the New Jersey Pinelands, where high nutrient soils were generally associated with moss patches whereas low nutrient soils were associated with lichen patches. They attributed this discrepancy to improved organic matter accumulation and NH_4-producing mineralization processes under mosses as opposed to low organic matter accumulation and NO_3-

producing mineralization processes under lichens. Finally, some contemporary boreal work has highlighted the potential for N fixation via symbioses between bryophytes and cyanobacteria in boreal forests (DeLuca et al. 2002, Zackrisson et al. 2004), though it is unknown whether such symbioses exist in the alpine. This small sample of the cryptogam literature illustrates the variety of possible indirect effects of cryptogam presence or absence on nitrogen cycling in the alpine.

The evidence from other ecosystems regarding cryptogam biogeochemical influences has led me to suspect that cryptogams have a number of effects on their biogeochemical surroundings in alpine ecosystems. In places where cyanolichens are abundant, it is logical to expect direct inputs of fixed nitrogen to alpine soils. Further, from the literature in temperate and arctic systems it is logical to expect that cryptogams change the moisture content and temperature regime of near surface alpine soils, thereby altering the rates of mineralization/immobilization processes and their net outcomes. As a step towards uncovering the role of cryptogams in biogeochemical cycling in alpine systems, I proposed to investigate whether cryptogams influence the total C and N content of alpine soils along with the NH_4 and NO_3 supply rates. To accomplish this I used two experiments, the cryptogam transplant experiment outlined in Chapter 2, and a novel sandbox experiment where the dominant cryptogam assemblage from each community type was applied to previously bare sand. In each experiment I estimated the annual inorganic nitrogen supply over two consecutive years following application of the experimental treatments, and at the end of each experiment I estimated total N and C from soil cores. In addition to addressing the experimental questions outlined here, to the best of my knowledge these are the most detailed set of alpine soil data from the Northern Cascades to date.

Section 3.2. Methods

Section 3.2.a. Site Comparison and Transplant Experiment

To determine the effects of cryptogam presence on some aspects of soil carbon and nitrogen cycling, I performed two experiments on Snowshoe Mountain. The first was the cryptogam transplant experiment, which I will describe only briefly here (See Chapter 2 for more details of experimental design). In five different plant communities on Snowshoe Mountain, I located twelve (24 in the dry sedge meadow community) pairs of 400cm^2 plots (144 total) having nearly identical topography, vegetation, and substrate that were within one meter of each other and had at least three individuals or ramets of my study species. Within each pair I randomly assigned one plot to retain its natural cover (cryptogam or bare soil, depending on the natural cover at the site) and one plot to have cryptogam cover removed or added to all interplant spaces (again, depending on the natural cover at the site). In all cases, this represented a removal or addition of > 60% of the total ground cover (see Chapter 2, Appendix 2.1 for plot cover before treatment).

To estimate plant-available inorganic N, in each plot of the cryptogam transplant experiment I buried Plant Root Simulator (PRS™) probes (Western Ag Innovations, Inc., Saskatoon, SK, Canada) to approximately 5 cm depth. Cation and anion-specific probes continually adsorb nitrate (NO_3-N) or ammonium (NH_4-N) to a thin ion-exchange resin membrane throughout the growing season. In theory this should avoid the problems with season-long estimates of inorganic N availability constructed from instantaneous samples—temporal variability in N supply is often high due to shifting temperature or moisture conditions (Western Ag Innovations Inc., 2007). I installed two rounds of probes; the first round was installed in October 2007 after the growing season. I removed the first round for analysis and replaced them following the 2008 growing season (October, 2008) and removed the second round for analysis following the 2009 growing season (October, 2009). Probes were cleaned of soil and rinsed with deionized water in the field, and rinsed a second time in the lab before being sent to Western Ag Innovations Inc. for analysis. Also, at the end of the 2009 growing season I removed three 45cm^3 soil cores to 5 cm depth from each plot in the cryptogam transplant experiment and combined them. Core samples were dried, sieved to 1 mm, homogenized, and subsampled. Subsamples were analyzed for total N and C using a Perkin-Elmer 2400 CHN analyzer.

Section 3.2.b. Sandbox Experiment

Second, to simultaneously compare the biogeochemical influence of all three cryptogams (*P. piliferum, F. cucullata - C. islandica, L. neglecta*) on an identical substrate I set up a "sandbox" experiment. In a flat bare area on the Snowshoe Mountain ridgeline (approximately 20 m^2), I randomly arrayed thirty PVC rings (25 cm diameter X 8.5 cm tall, Figure 3.1). Each ring had porous landscape fabric fastened across the bottom. I then filled each sandbox to 6 cm depth with pure sand (≈ 3 liters) and randomly assigned one of the following four surface treatments to each: *P. piliferum, F. cucullata - C. islandica, L. neglecta,* or control (bare sand). For the cryptogam treatments, the entire sand surface of the sandbox was covered with the cryptogam assigned. As in the experimental plots, in each sandbox I installed two rounds of PRS™ probes. The first round was installed in October 2007 and removed in October 2008. The second round was installed in October 2008 and removed in October 2009. Probes were cleaned and rinsed in the manner previously described. I also collected three 45cm^3 cores from each sandbox to 5 cm depth at the end of the 2009 growing season, homogenized them, and analyzed them using the same technique already described for total N and C.

Section 3.2.c. Analysis

In my analyses I considered total N, total C, as well as the C:N ratio. For the PRS probe data I considered NO_3 and NH_4 separately, as well as the NH_4:NO_3 ratio. Because there were large differences among years in the N supply rate data, I treated each year separately.

For the data from the experimental plots I performed two different analyses. First, using data pooled from the control plots, I used a General Linear Model (GLM) with site as a fixed effect to examine natural variability among my sites for total N, total C, C:N ratio, $NH_{4,}$ NO_3, and NH_4:NO_3. When significant differences were indicated, *post-hoc* mean comparisons were performed using Tukey's honestly significant difference (HSD) test.

Next, to test whether my experimental treatments had any effect on these response variables, I used linear mixed models (procedure lmer in R package lme4) on data from each site (six in total) with treatment as a fixed factor and pair as a random factor.

For the sandbox experiment, I used a GLM with surface type as a fixed effect for total N and C and N supply rate data. I did not analyze the C:N ratio data from the sandbox experiment because the values I obtained were unrealistic, presumably due to differential accumulation rates in a previously sterile substrate. *Post-hoc* mean comparisons were performed using the Tukey honestly significant difference (HSD) test. For all analyses, where data did not conform to the homogeneity of variance and normality assumptions of a linear model, log transformations were applied. All statistical tests were performed in R 2.15.0.

Section 3.3. Results

Section 3.3.a. Landscape level

Based upon all soil core data collected in October, 2009, the mean ± 1 standard error levels of total soil N on Snowshoe Mountain were 0.52% ± 0.03%, while the mean ± 1 SE level of total soil C was 7.9% ± 0.48 (Figure 3.2). From the two years of in-situ PRS ion-exchange resin probe data, the overall mean ± 1 SE levels of NO_3 and NH_4 were 10.4 ± 0.6 μg NO_3 $10cm^{-2}$ $year^{-1}$ and 7.4 ± 0.3 μg NH_4 $10cm^{-2}$ $year^{-1}$, respectively. Both forms were more abundant overall in year one than year two; the mean ± 1 SE level of NO_3 in year one was 13.2 ± 1.0 μg NO_3 $10cm^{-2}$ $year^{-1}$ compared with 7.7 ± 0.4 μg NO_3 $10cm^{-2}$ $year^{-1}$ in year two, whereas for NH_4 the mean level in year one was 9.6 ± 0.5 μg NH_4 $10cm^{-2}$ $year^{-1}$ compared to 5.2 ± 0.3 μg NH_4 $10cm^{-2}$ $year^{-1}$ in year two. The overall distributions of all of these variables were noticeably left-skewed. In the case of total N and C the overall distributions were also somewhat bi-modal—the most common values were either very low ($0 \leq N \leq 0.4\%$, $0 \leq C \leq 5\%$) or moderately high ($0.5 \leq N \leq 1\%$, $7 \leq C \leq 14\%$) (Figure 3.2).

Section 3.3.b. Site comparison

Naturally occurring levels of soil N and C varied considerably among the communities studied (Figure 3.3). The highest levels and variability of both N and C were found in the crustose lichen dominated snowbank community, with the lowest levels and least variability in the fellfield community. Variability among sites in the C:N ratio was low; the C:N ratio remained between 13-16 in all communities studied, and while there was still enough variation among sites to be statistically significant ($p<.001$), this was almost entirely due to the particularly low C:N ratio at the fellfield site.

With regard to inorganic N levels, annual levels of NO_3 and NH_4 as well as the NH_4:NO_3 ratio varied significantly among the communities studied in both years following the cryptogam transplants (Figure 3.4). Particularly high mean levels of NO_3 (22.6 μg NO_3 $10cm^{-2}$ $year^{-1}$) in the dry sedge meadow were responsible for most of the variation in NO_3 in year one; the other sites had statistically indistinguishable mean levels between 7.4-10.7 μg NO_3 10cm^{-2} year^{-1}. Nitrate levels were more homogeneous among sites in year two, though significant differences still developed among sites due to particularly low NO_3 levels at the crustose lichen snowbank and fruticose lichen meadow communities.

Different patterns among sites were found for NH_4 (Figure 3.4). Particularly high levels (16.6 μg NH_4 10cm^{-2} year^{-1}) were found at the moss snowbank site in year one, while low levels (3.9 μg NH_4 10cm^{-2} year^{-1}) were found at the fellfield site. As with NO_3, NH_4 levels were less variable among sites in year two, though significant differences still developed, mostly due to higher levels (7.4 μg NH_4 10cm^{-2} year^{-1}) found again at the moss snowbank site.

As reflected in the NH_4:NO_3 ratios, the relative abundance of the two N forms differed significantly among sites in both years (Figure 3.4). NH_4 tended to be the more abundant form of inorganic N at more sites than was NO_3. In both years NO_3 levels tended to be dominant in only the dry sedge meadow and fellfield communities, the two sites with naturally-occurring bare soil. In year one, relatively high NH_4 in the moss snowbank and NO_3 in the dry sedge meadow, along with unusually low NH_4 in the fellfield were the primary sources of variation driving statistically significant differences among sites in the NH_4:NO_3 ratio. In year two, the primary sources of variation were again the relative abundance of NO_3 versus NH_4 in the dry sedge meadow, but also the relative scarcity of NO_3 in the crustose lichen snowbank.

Section 3.3.c. Transplant Experiment

The patterns I observed in the cryptogam transplant plots were complex. All three cryptogams were associated with higher N and C levels; in all three of the removal experiments removal plots had significantly lower N and C in the two years following treatment (Figure 3.5). Likewise, adding *P. piliferum* or *L. neglecta* raised both N and C after two years.

With regard to the C:N ratio, results were mixed. Statistically meaningful treatment effects appeared in two of the six experimental communities (Figure 3.5). The presence of *P. piliferum* was associated with lower C:N ratios; adding *P. piliferum* tended to lower the C:N ratio (though not in a statistically meaningful way) relative to bare soil, while removing *P. piliferum* raised the C:N ratio relative to undisturbed plots with. While statistically insignificant, there appeared to be a more mixed response in the C:N ratio to *L. neglecta*, with no response to additions and a tendency towards lower C:N following removals. The C:N ratio seemed to respond differently to the mixture of *F. cucullata* and *C. islandica*, with higher C:N ratios following additions and a tendency towards lower C:N ratios in removals relative to undisturbed plots.

Of the two years of post-treatment PRS data collected, NH_4 showed the only statistically meaningful response to the experimental treatments (Figure 3.6). In both the removal *and* addition experiments involving the mixture of *F. cucullata* and *C. islandica*, NH_4 was lower in the "treatment" plots in one of the two years. This treatment effect was somewhat larger in the *F. cucullata - C. islandica* addition experiment. Overall, although no further statistical differences were detected, there did appear to be a tendency towards lower NO_3 and NH_4 in all of the removal experiments. Finally, there also was a tendency in the cryptogam addition plots, particularly noticeable in the *F. cucullata - C. islandica* additions, for lower variability in both NH_4 and NO_3 in the additions than the bare soil controls.

Section 3.3.d. Sandbox Experiment

In the sandbox experiments, both total N and C were influenced by surface type (Figure 3.7). Total N was higher under all cryptogams than sand and highest under *P. piliferum*, but the only statistically significant difference among treatment groups was between *P. piliferum* and bare sand. Similarly, total C was higher under both *P. piliferum* and *L. neglecta* than under the *Flavocetraria-Cetraria* mix and bare sand.

Surface type also explained some of the overall variance in inorganic N levels in both years (Figure 3.8). The highest levels of NO_3 in both years were found under bare sand (though this pattern was notably weaker in year two), and particularly high levels of NH_4 were found under *L. neglecta* in year one. Also of note were the consistently low levels of NH_4 found in year two under all surface types except sand, implying some background level of aerial N deposition.

Section 3.4. Discussion

Section 3.4.a. Broad Patterns

By considering data from other descriptive and experimental alpine studies concurrently with my data, three broad generalizations can be made from this work. First, the levels of total N, total C, and the C:N ratios in soils from Snowshoe Mountain were in line with values reported from other alpine sites (see Körner 2003 for an expanded list), including the Colorado Rockies (Holtmeier and Broll 1992), the Caucasus (Makarov et al. 2003), the Australian Alps (Atkin and Collier 1992), and the Sierra Nevada (Williams et al. 1995). Second, the immense variability in total C and N but relative consistency in C:N found across sites on Snowshoe Mountain echoes landscape-level patterns found in the Caucasus (Makarov et al. 2003), the Colorado Rockies (Neff et al. 1994, Darrouzet-Nardi 2010), and the European Alps (Rehder 1976). Third, taken together this suggests that rates of aboveground primary production and decomposition on Snowshoe Mountain are within the ranges reported from other cryic high elevation sites in North America. This supports the use of Snowshoe Mountain, and more generally the northeastern Cascades, as a site for testing general alpine biogeochemical hypotheses.

With regard to my inorganic N data, unfortunately few easily comparable alpine data sets exist. While ion-exchange resins have been popular in the natural sciences for some time, the per-area basis of PRS data is unique; historically, most resin data have been reported (Martinsen et al. 2012) on a per unit resin weight basis (i.e. Arnone 1997). However, from other recent PRS studies (Table 3.1) I can say that broadly the levels of NH_4 and NO_3 I observed (Figure 3.4) were within the range of values reported from the Colorado Front Range (Litaor et al. 2008, Berdanier and Klein 2011), Mount Saint Helens (Gill et al. 2006), and arctic tundra (Kelley and Epstein 2009, Aerts 2010, Elliott and Henry 2011), but lower than those reported from arctic grassland (McLaren and Turkington 2010) and far lower than those reported from agricultural settings (Adderley et al. 2006). The variability I observed in inorganic N among communities has been reported in the Colorado Front Range (Miller and Bowman 2003, Berdanier and Klein 2011) and the High Arctic (Schmidt et al. 2010). Together this indicates that many of the inorganic N-related phenomena that have been the focus of much effort over the past two decades are likely to find analogs in the northeastern Cascades. For example, different communities should respond very differently to increases in N deposition (Bowman et al. 1993, Makarov et al. 2003), with shifts in dominance depending on the preferences and nitrogen “behavior” of the community dominants (Suding et al. 2004)

Further, NO_3 was dominant at the two natural bare soil sites with the lowest levels of total N and C (Figure 3.4) and what seem to be some of the driest conditions found (Chapter 3,

Figure 3.5). This is echoed by other alpine studies that have shown the relative abundance of NH_4 versus NO_3 in alpine soils to be related to soil temperature, organic matter, acidity, and moisture (Makarov et al. 2003, Miller and Bowman 2003, Makarov et al. 2008). Generally speaking higher moisture and organic matter in alpine soils have been shown to favor increased microbial biomass, higher mineralization and immobilization rates, and higher available NH_4 (Fisk and Schmidt 1996, Fisk et al. 1998, Zhang et al. 2012), whereas warmer and drier conditions temperatures have been shown to favor nitrification and higher available NO_3 (Makarov et al. 2003, Miller and Bowman 2003, Lu et al. 2012).

Finally, although NH_4 was the dominant form of inorganic N at more sites than was NO_3, it was remarkably less dominant than has been found at other alpine sites (Brooks et al. 1996, Mullen et al. 1998, Makarov et al. 2003, Clement et al. 2012). However, due to differences in measurement techniques and time scales, it is difficult to say whether this is a real difference between my data and other alpine data sets. It's possible that despite high organic matter content in many of my soils, higher temperatures in this part of the soil profile favor higher NO_3.

Section 3.4.b. Experimental Patterns

The experimental data suggest that, at a minimum, cryptogams play some role in biogeochemical cycling on Snowshoe Mountain in communities where they are abundant. This is consistent with findings from other ecosystems globally, both tundra and otherwise (Evans and Ehleringer 1993, Sedia and Ehrenfeld 2005, Cornelissen et al. 2007), and supports the view that cryptogams should be considered active participants in future studies of biogeochemical cycling in the alpine.

In particular, all three of the cryptogam types studied were associated with higher soil N and C pools in at least one of the removal or addition experiments (Figure 3.5). Likewise, in the sandbox trials, cryptogam type was an important predictor of both N and C (Figure 3.6). Overall, the treatment effects were small relative to natural variability among sites or those observed in pure N fertilization plots on Niwot Ridge (Neff et al. 2002). However, an appropriate interpretation of my results should consider the treatment effects compounded over a longer history of soil development. For example, if we consider the *L. neglecta* and *P. piliferum* addition plots, the presence of cryptogams was associated with 0.03-0.08% higher N concentrations in near-surface soils two years following treatment, far less than the ten-fold difference in N concentrations I observed across all of my sites. If one assumes a linear increase in N of 0.03-0.08%/ year, about 12-35 years of soil development under cryptogams would be required to increase the soil nitrogen pool from the lowest (fellfield) to the highest levels (crustose lichen snowbank) observed at Snowshoe Mountain. Similarly, total C increased only 0.51 -1.18% in plots with cryptogams added, much less than the 15-fold level of background variability I observed in C concentrations across sites. However, given this accumulation rate of 0.51 – 1.18% /year, again only about 15-30 years of soil development would be required to raise total C from the lowest to highest observed values.

The mechanism behind the shifts I observed in soil N and C pools in the experiments is unknown. Total N and C effects could have been the result of direct inputs through fragmentation and decomposition of cryptogam tissue. However, this line of reasoning is less attractive in explaining the improved N and C under the prostrate cryptogams in the experimental plots with native soil. Existing evidence suggests that of these two cryptogams, only *P. piliferum* is likely to have been enriched in N or C relatively to the underlying soil, and even in that case only slightly so (Allen et al. 1967, Palmqvist et al. 2002, Sedia and Ehrenfeld 2006). It is further possible that the treatment effects I observed were simply due to fragmentation and decomposition of soil attached to the underside of the cryptogams (it was physically impossible to remove all soil from the cryptogams, particularly *L. neglecta* and *P. piliferum*). To avoid such experimental artifacts I restricted my sampling to the original soil underneath the transplanted cryptogam material, but it is unlikely this fully avoided sampling soil imported with these cryptogams. However, it is unclear to what degree one should attempt to distinguish between cryptogam and soil as they are physically inseparable in practice; it could be argued, for instance, that the soil/organic matter appressed to a cryptogam is part of its biogeochemical legacy and therefore represents a legitimate portion of the cryptogam "treatment."

I believe that higher N and C pools in the cryptogam-covered plots were in part an indirect result of their particular soil temperature and moisture regimes (Chapter 2, Figures 2.6 and 2.8), as temperature and moisture are known to regulate biogeochemical transformation rates in alpine systems (Koch et al. 2007). In particular, the more moist conditions associated with *P. piliferum* might well favor improved immobilization, as has been found elsewhere (Fisk et al. 1998), but this offers no explanation for the trends associated with *L. neglecta*. A final possibility stems from the widely observed fact that many cryptogams, primarily lichens, are rich in secondary compounds with antimicrobial properties (Nash 1996) that have been shown to influence N transformation rates (Sedia and Ehrenfeld 2005). Though I have little specific information on the cryptogams I worked with, it's possible that secondary compounds associated with the cryptogams reduced mineralization rates, resulting in increased total N and C.

The experimental inorganic N supply rate results were challenging to interpret. Here I will focus on two results in particular, the first being that both the addition and removal of *F. cucullata- C. islandica* reduced available NH_4-N,. Without further investigation it is impossible to determine why these parallel reductions in available NH_4-N occurred. A scenario that must be considered is that these are not real patterns, and that replicate efforts to quantify the N supply in these plots would not have similar results. However, given their statistical significance, I must consider the possibility that they are real treatment effects. The most likely scenario that could explain both these values involves the physicochemical indirect effects of cryptogam presence. In both cases the treatments changed patterns in soil temperature and moisture, and likely precipitation chemistry as well. In particular, plots with *F. cucullata- C. cucullata* removed had warmer near-surface soil temperatures and more rapid drying of near-surface soils than control plots (See Chapter 2, Figures 2.6 and 2.9). Given that levels of NH_4-N in alpine soils are often positively correlated with soil moisture within and across communities (Makarov et al. 2003, Miller and Bowman 2003, Makarov et al. 2008), whereas levels of NO_3-N are often positively correlated with soil temperature (Miller and Bowman 2003, Makarov et al. 2008), it is likely that these conditions would have favored nitrification and denitrification, and lower NH_4. On the other hand, this offers little explanation for the lower NH_4 in plots with *F. cucullata- C. islandica* added, which had cooler soil near-surface soil temperatures than control plots (See Chapter 2, Figure 2.6 and 2.9). If this is a real trend, I believe the slower decomposition and mineralization that would explain such a trend could either be a byproduct of cooler soils or a case of secondary chemicals depressing activity in the soil microbial community. To the latter, it is unknown the degree to which these particular “cetrarioid” lichens possess and/or exude chemicals allelopathic to the soil microbial community, but *F. cucullata* has been reported to contain usnic acid, with known antifungal properties (Boustie et al. 2011), and *C. islandica* is known to possess several secondary metabolites with bioactive properties (Boustie et al. 2011). Added to a previously bare substrate with a microbial community not adapted to their presence, it is possible the effects of these secondary chemicals simply overrode the effects of soil temperature and moisture changes.

The second finding of interest in these data was the particularly high variability in inorganic N at some sites and not others (e.g., *F. cucullata- C. islandica* additions). Given the consistency of these outliers across forms and across years, it is my opinion that these values are real and represent "hotspots" of inorganic nitrogen availability (Johnson et al. 2010, Darrouzet-Nardi and Bowman 2011, Johnson et al. 2011). Hotpots are thought to result from preferential flow paths between the O and mineral horizons that can establish and remain stable over centuries of soil development (Bundt et al. 2001), and are thought to be the source of the positive skew that often characterizes inorganic N data (Johnson et al. 2010) . As organic matter and moisture levels tend to be higher in the immediate vicinity of these flow paths, microbial biomass, mineralization, and inorganic N levels tend to be much higher as well (Bundt et al. 2001). Finally, as with my experimental plots, the scale on which hotspots occur is often the sub-meter scale—plots less than a meter apart can have vastly different biochemical signatures (Johnson et al. 2011).

Given the shifts I observed in total N and C pools, it was surprising that inorganic N levels in many of the removal and addition experiments were not more responsive to the treatments. In particular, it was reasonable to expect more indirect effects of shifts in moisture and temperature regimes on N availability (Bardgett et al. 2007), similar to those I believe occurred with total N and C. Although my results tentatively support the hypothesis that the annual inorganic N supply is affected by some cryptogams, the question of N supply for alpine plants is also not necessarily best answered on this time scale. Lipson et al. (1999), for example, demonstrated that alpine plants most actively assimilate N during very specific time windows soon after snowmelt. An interesting future study could compare mineralization rates and N availability under different cryptogam covers during this period of heightened demand. Finally, because the presence of all three cryptogams were associated with lower available N levels in the sandbox experiment, it seems likely that these cryptogams are retaining some N deposition, echoing findings from other cryptogam-rich systems (Tye et al. 2005, Friedrich et al. 2011).

Section 3.4.c. Conclusions

Overall, my data offer tentative support for the conclusion that cryptogams are influential in alpine biogeochemical cycling. In the most general terms, it appears that different cryptogams influence the soil matrix in different ways. Plots with the prostrate cryptogams, *L. neglecta* and *P. piliferum,* for example, were consistently associated with higher total soil N and C. The fruticose lichen mixture of *F. cucullata- C. islandica*, on the other hand appeared to hold some influence on the levels of NH_4 available. In all cases, the mechanisms behind the effects are unknown, and in the case of the prostrate cryptogams whether attached soil is considered an experimental artifact is a critical question for interpreting these results. If these results are considered legitimate, from other studies it seems likely to be a combination of indirect physical and chemical pathways. Certainly, the microclimate data we have gathered indicate that cryptogams are critical in shaping the near-surface microclimate.   Regardless, these findings suggest a variety of future studies.

First, a logical next step would be to investigate the biogeochemical relationships between individual cryptogam and vascular plant species. Both fine-scale survey work and manipulative experiments could prove fruitful. For example, a fine-scale survey of alpine soils and their spatial relationships to plants and cryptogams in several landscapes could provide some insight into whether cryptogams are consistently associated with different alpine soil properties.

Another avenue could be to try to tease apart the physical and chemical components of cryptogam influence; to that end measuring soil respiration, enzymatic activity, and microbial biomass after repeated applications of different lichen extracts or applications of lichen biomass with a physical barrier to throughput could provide some insights.

Potential restoration applications using cryptogams in terms of biogeochemical significance are intriguing as well. If one is trying to improve soil fertility in a denuded alpine or cold region area, which cryptogams offer the best prospects? The prostrate cryptogams I worked with seem to offer the most benefit in terms of total soil N and C, but is this offset by other biochemical actors I did not account for? Disentangling potential nonlinearities is critical to effective larger-scale modeling efforts. Thus I contend that the only way to truly predict the long-term trajectory of alpine ecosystems and their associated ecosystem services in a warming world is to account for these relationships, both within and across trophic levels.

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Section 3.6. Figures and Tables

Table 3.1. Inorganic N levels in soils from other cold region sites. PRS data are reported in the literature on many different time scales; I converted all values to the full time of burial. Where a range of values was reported for a particular community type, I report the minimum and maximum, as opposed to mean ± 1 SE. The use of ≈ reflects values estimated from figures and not taken directly from text.

			Values reported as min – max or mean ± 1 SE, μg N 10 cm^{-2})			
Region	Community Type	Time	NO_3	NH_4	NH_4NO_3	Author(s)
Colorado Rockies (Niwot LTER)	"Dry Meadow"	Growing season	*NA*	*NA*	≈ 10 – 39	Berdanier and Klein (2011)
	"Dry Meadow	2 Days			0.24 ± 0.03	Litaor et al. (2008)
	"Moist Meadow"	2 Days			0.26 ± 0.03	
	"Snowbed"	2 Days			0.22 ± 0.03	
Mt. St. Helens	Spirit Lake pyroclastic flow	84 days			≈ 26 – 35	Gill et al. (2006)
Northern Alaska	Moist nonacidic tundra	49 days (2 year average)			≈ 26.0	Kelley and Epstein (2009)
Northern Sweden	Tundra heath	84 days			≈ 25 ± 5	Aerts (2010)

Nunavut, Northern Canada	Wet sedge tundra	58 days	≈ 4.1 – 8.7	≈ 10.4 – 22.6		Elliott and Henry (2011)
Kluane Lake, Canada	Arctic grassland	46 days	≈ 1900 – 3000		≈ 2000 – 3000	McLaren and Turkington (2010)
NE Greenland	“Ablation plateau”	43 days	≈ 20.7 ± 5.0	≈ 4.8 ± 1.3		Schmidt et al. (2010)
	“Cassiope heath”		≈ 4.6 ± 0.7	≈ 5.1 ± 3.0		
	“Salix snowbed”		≈ 4.3 ± 0.6	≈ 4.3 ± 1.5		
Southern Norway	“Low alpine grassland”	43 days	*NA*	*NA*	≈ 0.5 – 2.5	Martinsen et al. (2012)

Figure 3.1. Sandbox experiment, Snowshoe Mountain, 2007. PRS ion exchange resin probes were placed in sand then the entire surface in each planter was covered with one of the three cryptogams of interest or left bare (control).

Figure 3.2. Kernel density plots showing the relative frequency of total N and total C (from soil cores), and NO_3 and NH_4 (from PRS ion-exchange resin probes). The y-axis is the proportion of all values. Data are from all cryptogam transplant experiment plots. The grey line in each plot represents the mean.

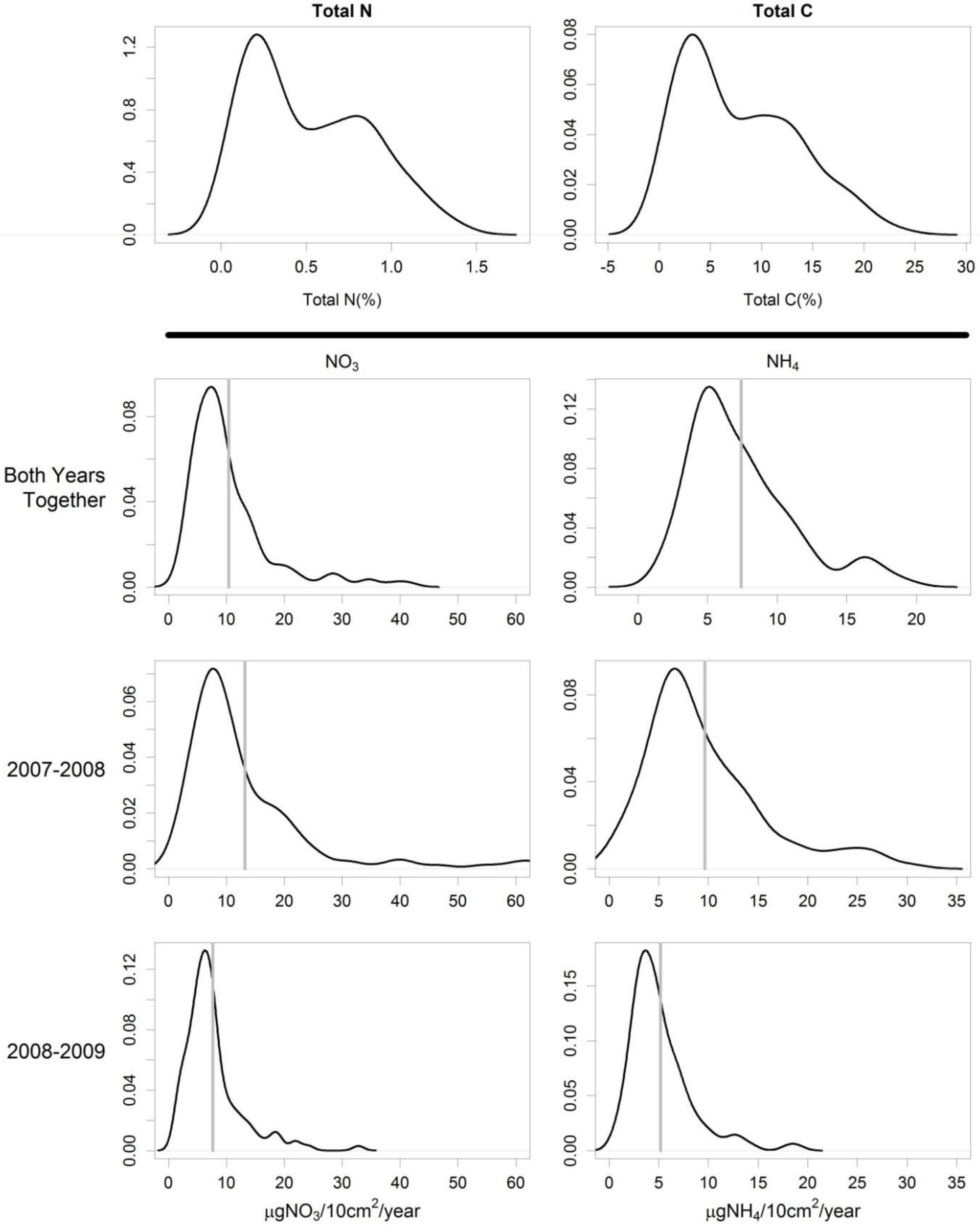


Figure 3.3. Total N, C, and C:N from soil cores in undisturbed "control" plots across communities on Snowshoe Mountain, 2009. Different letters indicate significant differences (Tukey's HSD, $p \leq 0.05$ except where indicated with *, where $0.1 \geq p \geq 0.05$). Values are displayed as mean ± 1 SE. N was between 10 and 12 for each site.

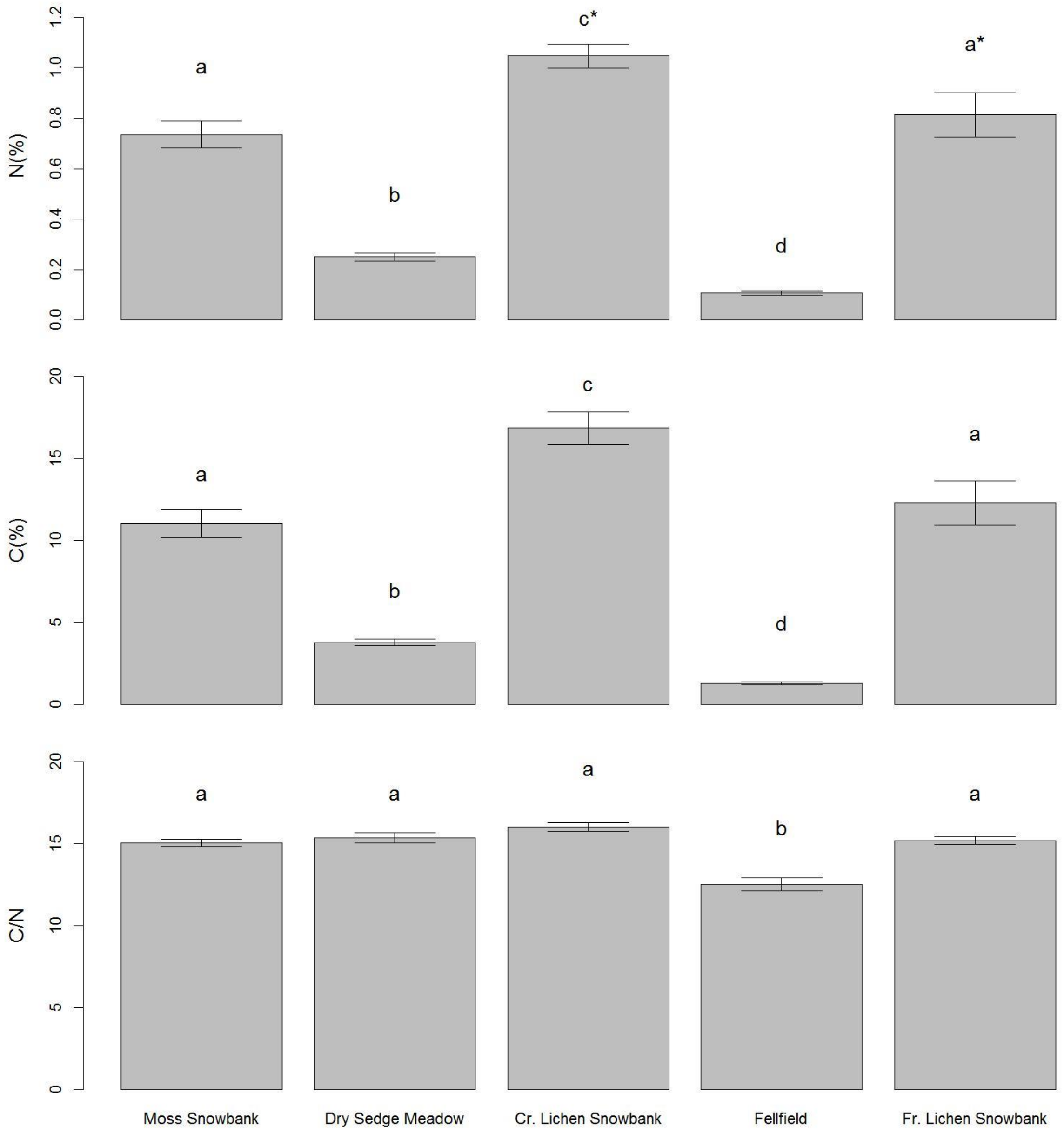


Figure 3.4. NO_3, NH_4, and ratio of NH_4 to NO_3 across communities on Snowshoe Mountain, 2007-2008 (post-treatment year one) and 2008-2009 (post-treatment year two). Data are from PRS ion-exchange resin probes in undisturbed “control” plots of the cryptogam transplant experiment. Different letters indicate significant differences (Tukey’s HSD, $p \leq 0.05$ except where indicated with *, where $0.1 \geq p \geq 0.05$). Values are displayed as mean ± 1 SE. N was 11 or 12 for each site.

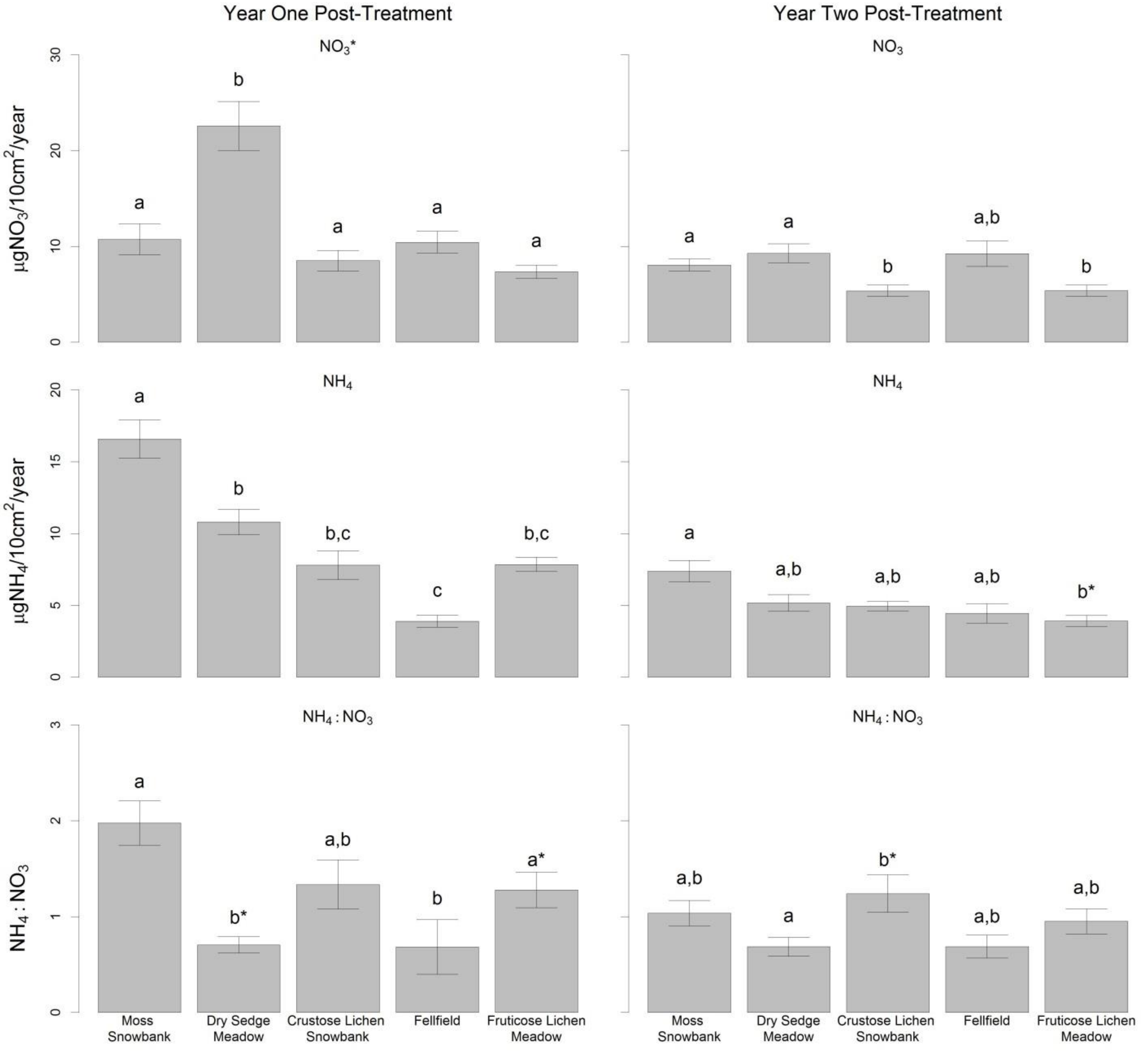


Figure 3.5. Total N, C, and C:N from soil cores taken from cryptogam transplant experiment plots (removals and additions) on Snowshoe Mountain, 2009, two years following treatment. Significant treatment effects are noted (linear mixed model, Signif. codes: * 0.1 ≥ p ≥ 0.05, **p ≤ 0.05). Values are displayed as mean ± 1 SE. N=12, except where indicated otherwise.

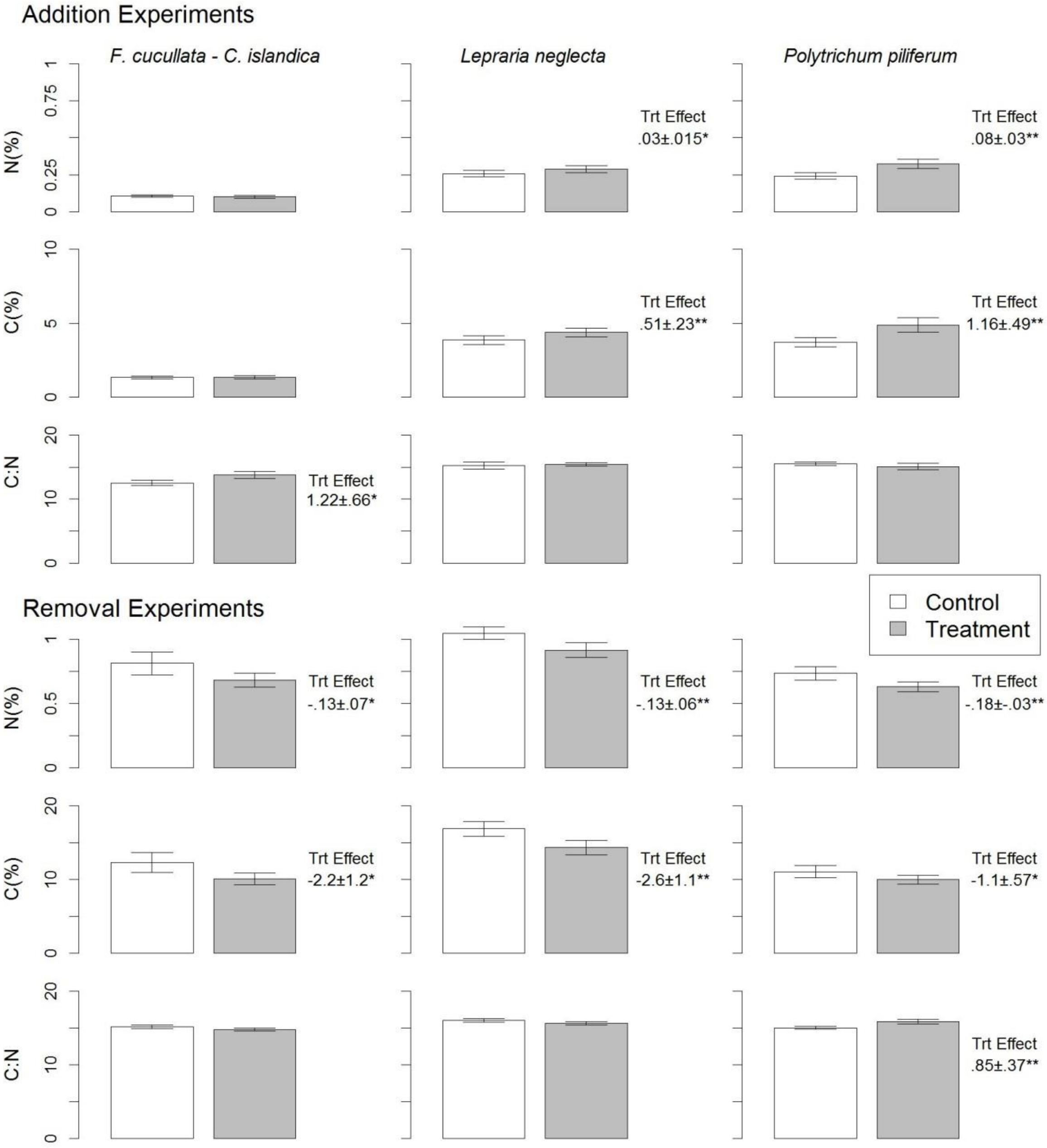


Figure 3.6. NO_3, NH_4, and ratio of NH_4 to NO_3 from PRS ion-exchange resin probes in cryptogam transplant experiment on Snowshoe Mountain, 2007-2008 and 2008-2009, one and two years following treatment. Significant treatment effects are noted (linear mixed model, Signif. codes: * $0.1 \geq p \geq 0.05$, **$p \leq 0.05$). Values are displayed as mean ± 1 SE. N=12, except where indicated otherwise. Total N, C, and C:N in planter box experimental plots on Snowshoe Mountain, 2009, two years following treatment.

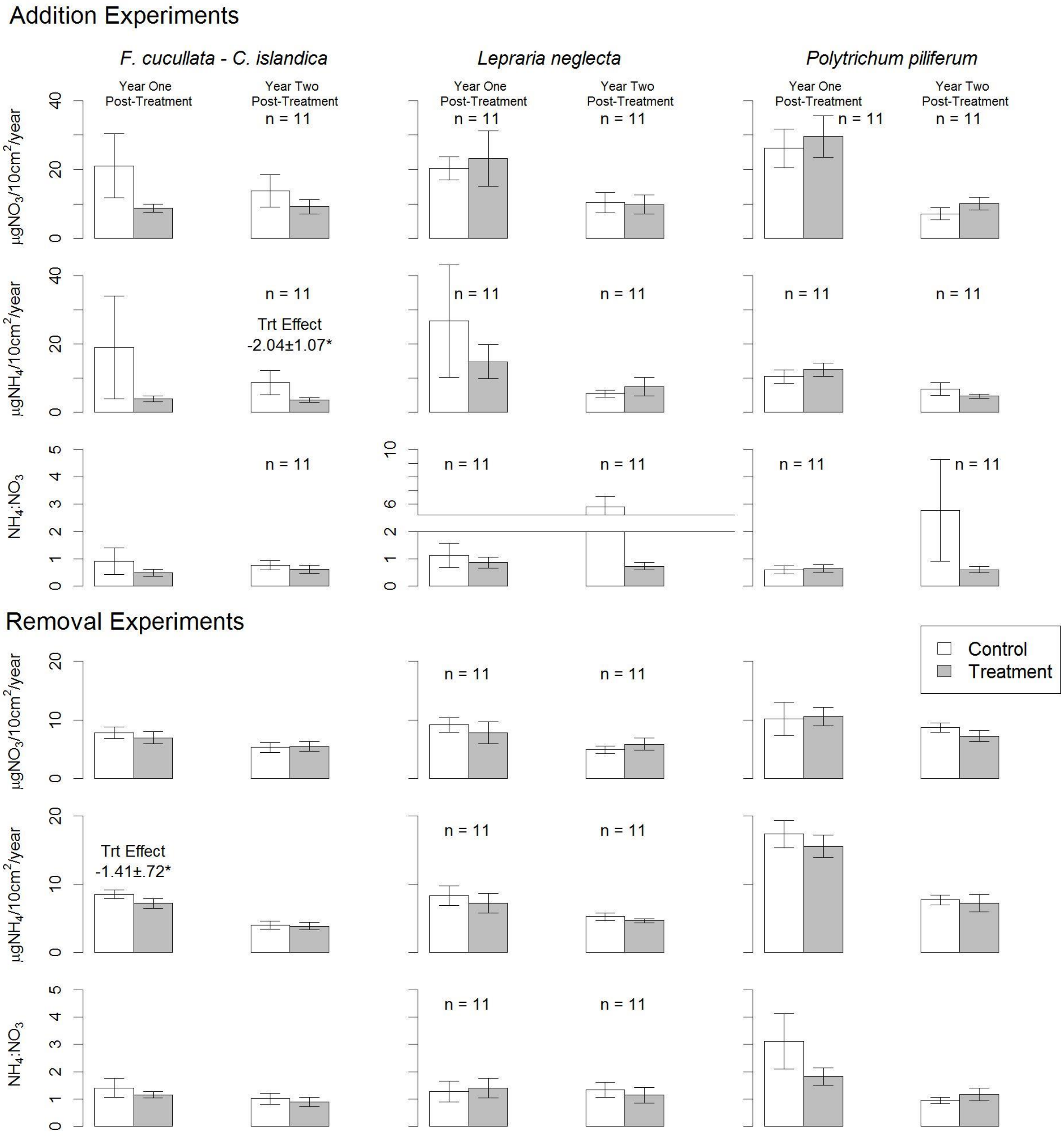


Figure 3.7. Total N and C from soil cores taken from sandboxes in 2009, two years following treatment. Different letters indicate significant differences (Tukey's HSD, $p \leq 0.05$ except where indicated with *, where $0.1 \geq p \geq 0.05$). Values are displayed as mean ± 1 SE. N =5.

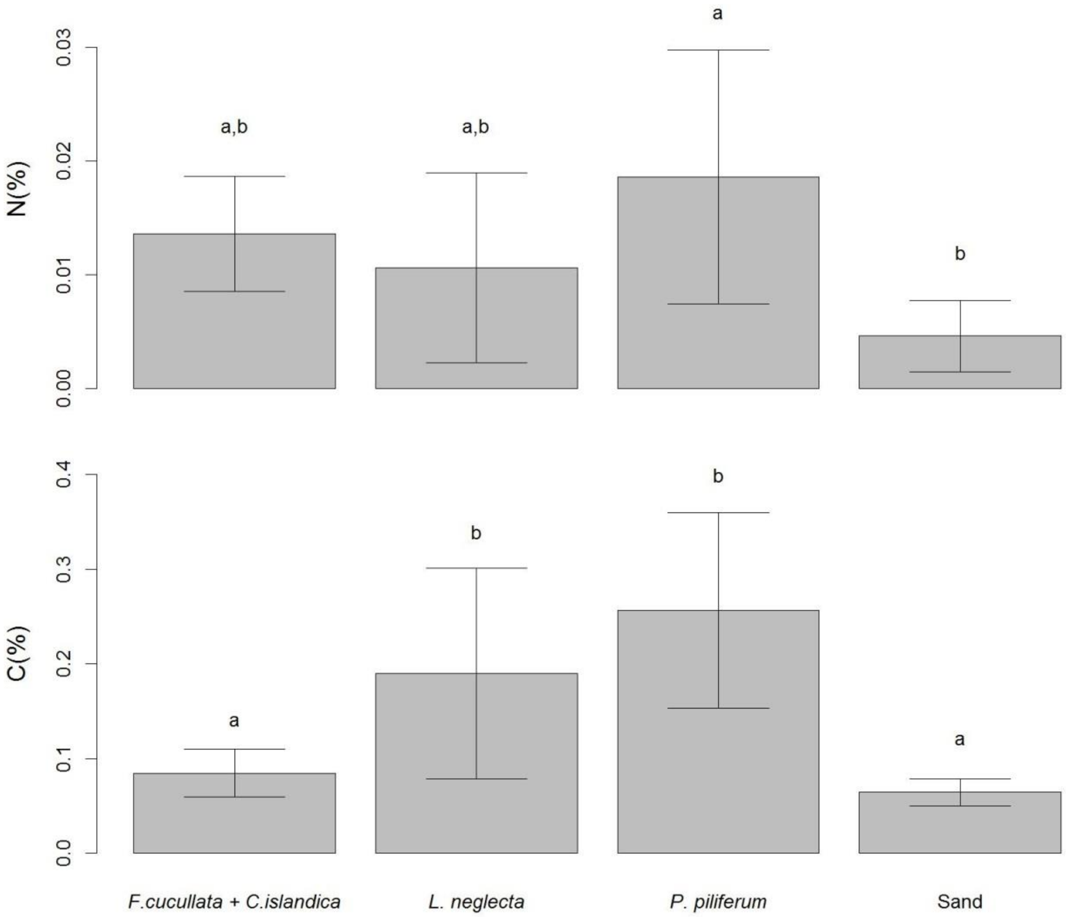
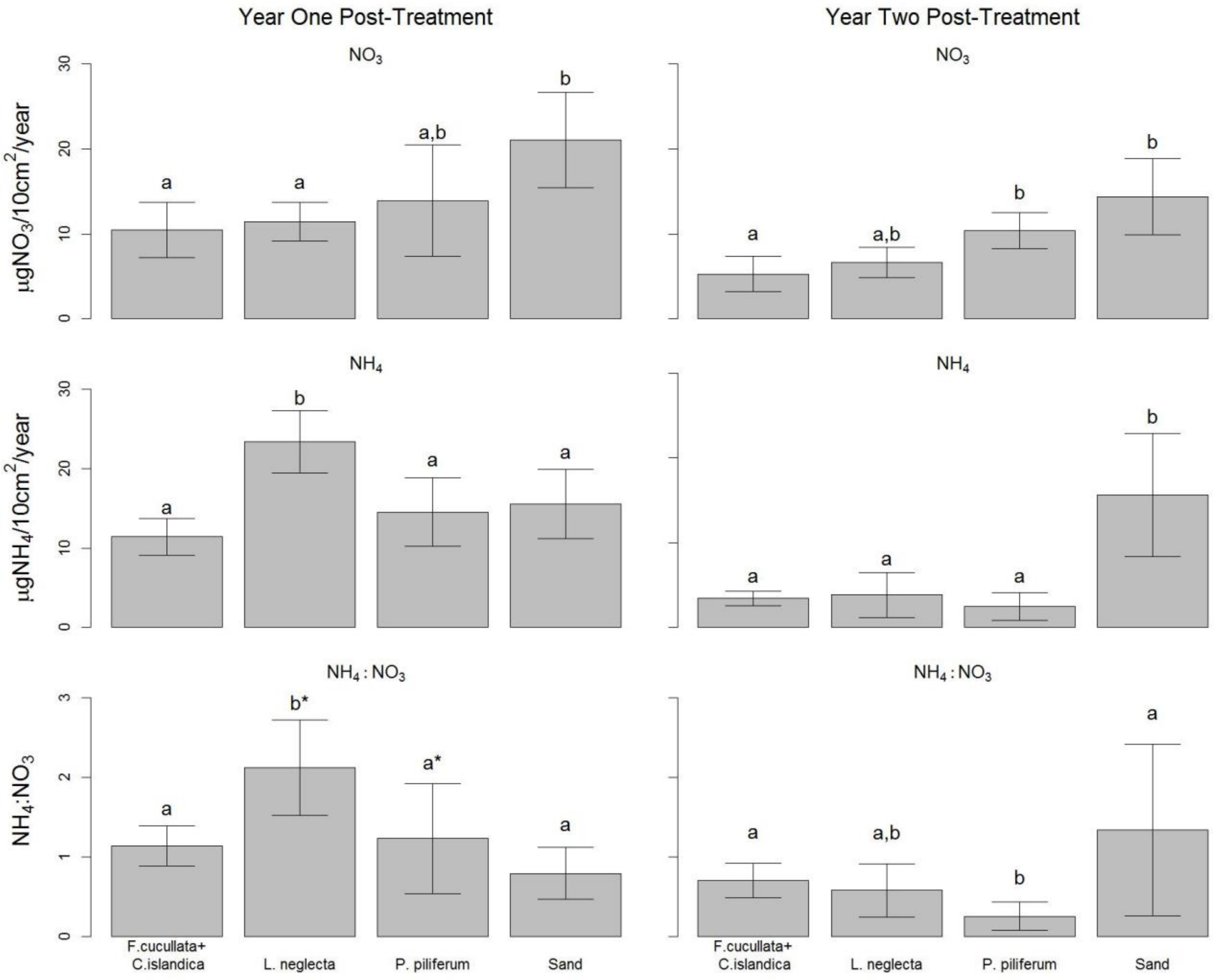


Figure 3.8. NO_3, NH_4, and NH_4:NO_3 from PRS ion-exchange resin probes in sandbox experiment, 2007-2008 and 2008-2009, one and two years following treatment. Different letters indicate significant differences (Tukey's HSD, $p \leq 0.05$ except where indicated with *, where $0.1 \geq p \geq 0.05$). Values are displayed as mean ± 1 SE. N =5.



Chapter 4: Experimental investigations into the influence of some alpine cryptogams on alpine plants in the North Cascades and Fuegian Andes

Section 4.1. Introduction

Traditional models of alpine plant distribution have had a distinct abiotic bias, focusing on plant-climate relationships. Fueling this is an extraordinary literature detailing individual and community vegetation responses to the alpine physical environment (Bliss 1971, Billings 1974, Walker et al. 1994, Körner 2003). However, a growing body of evidence linking alpine plant distributions to plant-plant interactions has highlighted the need for a more holistic assessment of species interactions in alpine ecosystems (Callaway et al. 2002, Kikvidze et al. 2005). The broad goal of my research was to expand understanding of species interactions in alpine plant communities beyond plant-plant interactions.

Alpine landscapes in the Pacific Northwest are mosaics of plants, bare ground, and a thin layer of lichens and bryophytes (Gold et al. 2001) referred to in the ecological literature as a biological soil "crust" (other common names are cryptogamic or cryptobiotic crust). Biological soil crusts are well-studied in arid and arctic ecosystems worldwide – they fix nitrogen, stabilize soils, and serve as a reservoir for soil moisture (Evans and Johansen 1999, Belnap and Lange 2001). Despite their long-recognized abundance in alpine ecosystems, their ecological functions in the alpine have not been well documented (Belnap and Lange 2001, Gold et al. 2001). In this chapter I present the results of experiments designed to determine if cryptogams influence the germination and growth of alpine plants. First I make the argument that cryptogam-containing soil crusts have unique properties that make them likely to influence alpine plant growth. In support of this, I review the literature surrounding two critical questions: (1) what factors limit alpine plant growth, and (2) how do cryptogams affect these factors in systems where they are well-studied?

Section 4.1.a. Limits on alpine plants

Section 4.1.a.1. Environmental

In the broadest terms, alpine plants outside of the tropics are limited by the sub-freezing temperatures common at high elevations for much of the year (Bliss 1971). Beyond this, regional climate, local topography, and wind interact to create extraordinary spatial heterogeneity in the timing and duration of snow cover and an unparalleled diversity of growing season lengths within a landscape (Hiemstra et al. 2002, Körner 2003). Variation across the landscape in the effective duration of winter and its snowpack correlates tightly with spatial patterns in alpine plant community composition and productivity (Billings and Bliss 1959, Douglas and Bliss 1977, Oberbauer and Billings 1981, Talbot et al. 1992). The microtopographic setting is also important for the growing season climate experienced by plants (Oberbauer and Billings 1981), and alpine landscapes are immensely variable in this respect as well. Two alpine plants growing just meters apart are often experiencing climates reminiscent of elevations hundreds of meters apart (Körner 2003). In spite of the immense heterogeneity in growing season length and microclimate in a typical alpine landscape, soil moisture, temperature, and nitrogen consistently interact to limit plant growth in most high mountain plant communities (Billings and Bliss 1959, Kuramoto and Bliss 1970, Ehleringer and Miller 1975, Bowman et al. 1993, Bowman et al. 1995, see Körner 2003 for review).

Moisture limitation in alpine plants is partially reflected in the positive relationships between soil moisture and alpine community primary productivity common in the alpine literature; across a broad geographic range moist and wet meadows have been found to be more productive than more xeric plant communities (Scott and Billings 1964, Kuramoto and Bliss 1970, Fisk et al. 1998). A similar positive correlation holds for individual plants within a single growing season (Billings and Bliss 1959). Growing season soil moisture is related to the amount of snow received, the timing and duration of snow coverage, and site physical characteristics (Bliss 1971). From a plant's perspective, much of the surface area of alpine landscapes in western North America often experiences periodic mild to severe summer drought (Ehleringer and Miller 1975). This is the common explanation for the correlations between discrete vegetation boundaries and steep moisture gradients that are typical throughout the mountainous parts of western North America (Mooney et al. 1965). These phenomena can be traced more directly to high evapotranspiration resulting from thin soils with low total organic matter and high radiation loads and associated high surface temperatures (Taylor and Seastedt 1994). The driest conditions in alpine soils are found in near surface layers, which can be particularly problematic for germinating seeds, seedlings, and/or shallow-rooted species (Chambers and Macmahon 1994, Körner 2003).

Soil temperatures present complex and even contrasting limitations to alpine plants at different stages in their life cycles. In the broadest sense, most established alpine plants are limited by prevailing low root-zone temperatures (Bliss 1956, 1966). Soil temperatures measured at 10 cm depth across alpine landscapes in Europe suggest that monthly averages rarely exceed 0° C, and often are well below freezing during the winter months (Körner 2003). On Niwot Ridge mean *summer* soil temperature at 10 cm depth was 2.6° C (http://culter.colorado.edu/exec/.extracttoolA?soiltemp.ss). Thus for much of an alpine plant's life its roots are forced to operate near the freezing point of water. This is in stark contrast to the temperature extremes found at the soil surface, where midsummer bare ground temperatures have been observed as high as 80°C, with a mean temperature at 1 cm depth of 7.3°C found on Niwot in these same years (Körner 2003). Such temperatures are potentially lethal to plant tissues, particularly an emerging seedling whose structure is confined to this near-surface environment.

Nitrogen is generally considered to partially limit total primary productivity in alpine plant communities (Bowman et al. 1993). In spite of high amounts of organic N in alpine soils, low atmospheric inputs, slow decomposition and mineralization, and acidic soils all contribute to limited inorganic N availability (Bowman et al. 1993, Körner 2003). A number of fertilization studies have recast this limitation as species and life-form specific, and Körner has argued that because community composition often changes with additions of N, current alpine plant communities cannot be considered N-limited (Theodose and Bowman 1997, Körner 2003, Suding et al. 2005). However, though I may not consider extant alpine communities to be N-limited, I can safely assert based on available evidence that some alpine plants are N-limited, and many could be expected to respond to perturbations of their N supply (Bowman and Conant 1994, Bowman et al. 1995, Soudzilovskaia and Onipchenko 2005).

Section 4.1.a.2. Biotic

While it is broadly agreed upon that moisture, temperature, and nitrogen combine to limit alpine plant growth, recent findings suggest that the critical levels of these factors may be set not only by regional climate interacting with local topography, but also by community constituents themselves. For example, cushion plants ameliorate local habitat extremes in both temperate and sub-polar climates in biologically important ways (Cavieres et al. 2007, Haussmann et al. 2009, Haussmann et al. 2010). In the temperate Chilean Andes, Cavieres et al. (2007) found that individual cushion plants lowered daily maximum soil temperatures by 10-15 °C and increased soil matric potential by 10-20 kPa, enabling improved local survivorship of conspecific and heterospecific seedlings.   In subpolar tundra, Haussman et al. (2009) observed that similarly-structured *Azorella spp.* cushions reduced frost heave in their surroundings, with benefits for seedling survivorship of associated species (Haussmann et al. 2010). Likewise, recent findings suggest alpine plant species exert considerable influence over their biogeochemical surroundings. For example, Suding et al. (2004) demonstrated that the resource utilization patterns of individual species are important in shaping the growth trajectories of neighboring plants in alpine meadows. The influence can come through preferential uptake of forms of soil N (Ashton et al. 2008), root exudates (Meier et al. 2009), and litter chemistry (Bowman et al. 2004). However, while this literature has deepened my understanding of plant community dynamics, to date the scope of these investigations have been limited to vascular plants. For reasons to be discussed, cryptogams are promising candidates to be added to the list of local biotic factors which may influence the alpine biogeochemical setting.

Section 4.1.b. Potential for the cryptogams to influence alpine plants

Taking the environmental controls on alpine plant growth into account, the crust literature offers multiple pathways through which cryptogams might influence alpine plants. In arid systems, soil crusts redistribute precipitation and are often the dominant source of inorganic nitrogen (Evans and Ehleringer 1993, Bromley et al. 1997, Bliss and Gold 1999, Prasse and Bornkamm 2000). Cryptogams of all forms wield considerable influence over near surface soil temperatures (both raising and lowering, see Chapter 4 for detailed review) in arctic, arid, and boreal systems (Kershaw 1977, Gold 1998, Gold et al. 2001, George et al. 2003, Breen and Levesque 2008). In some cases plants growing near crusts exhibit higher growth, fecundity, and leaf nutrient levels than other plants (Pendleton et al. 2003, Beyschlag et al. 2008, Langhans et al. 2009). Improved germination and establishment on crusts have also been reported in cool and hot deserts (St Clair et al. 1984, Rivera-Aguilar et al. 2005), while species-specific germination responses to crust presence were found in Florida scrubland (Hawkes 2004). In one of the few studies from a high elevation system, Soll (1994)found higher seed germination and first-year survival of *Abies lasiocarpa* seedlings on a lichen crust than in areas with established dwarf shrub, forb, or rush communities, areas that would presumably be cooler at the soil surface.

Recent findings also suggest the potential for negative cryptogam-plant interactions. For example, lichen exudates can inhibit seed germination and mycorrhizal colonization (Sedia and Ehrenfeld 2003), and for some species it appears crusts may inhibit establishment by serving as a physical barrier to root penetration or emergence (Zaady et al. 1997, Zamfir 2000). Given the physical complexity and taxonomical medley of cryptogams comprising "crusts," it is not surprising that the effects on germination and establishment have been found to vary. Thus it seems likely that cryptogams could influence the germination, establishment, and productivity of alpine plants either positively or negatively through both physical and chemical pathways.

Section 4.1.c. Research Questions

To begin to address the function of cryptogams in alpine plant communities, I posed the following two research questions: (1) Do crusts influence alpine plant growth, and (2) Do crusts influence seed germination? In an ideal natural experiment one might find that otherwise identical plants would grow or germinate differently with cryptogams as neighbors. However, in my search for a study site, I encountered no reasonable natural experiments. Certainly I have encountered conspecific plants with and without natural cryptogam cover around them, but the topographic and environmental differences between such sites appeared to be and were thus assumed to be too great to isolate cryptogams as an influence. Acknowledging this constraint, I used an experimental approach to investigating the effects of crusts on plant growth and seed germination.

Section 4.2. Methods

Section 4.2.a. Cryptogam transplant experiment

To examine the effects of cryptogams on alpine plant growth, I performed cryptogam transplant experiments at the Snowshoe Mountain and Cara de Indio field sites. The transplant experiment procedure was already described in detail in Chapter 2; here I describe briefly only the cryptogam transplants. In each community on Snowshoe Mountain (five total) and Cara de Indio (three total), I located pairs of $400cm^2$ plots having nearly identical topography, vegetation, and substrate that were within one meter of each other, and had at least three individuals or ramets of my study species (See Chapter 2, Appendix 2.2 for images of communities and study species). In four of the five communities on Snowshoe Mountain and in all four communities on Cara de Indio, I established twelve pairs of plots. Because I could not locate another naturally cryptogam-free community on Snowshoe Mountain, I established twenty-four pairs of plots in the dry sedge meadow community. On Snowshoe Mountain I established 72 total pairs, and on Cara de Indio I established 48 pairs.

Within each pair I randomly assigned one plot to retain its natural substrate (cryptogam or bare soil, depending on the natural cover at the site) and one plot to have cryptogam cover removed or added to all interplant spaces, depending on the natural cover in the community (Chapter 2, Appendices 2.1 and 2.2). The same cryptogam species was always used for addition replicates. In the dry sedge meadow community (Snowshoe Mountain), where there were twenty-four pairs, twelve pairs were used for *L. neglecta* additions and twelve for *P. piliferum* additions. After the end of the growing season in 2007 (late September), all cryptogam material was carefully removed from removal plots. For plots with *F. cucullata* and *Cetraria islandica*, this involved simply lifting loose lichen tissue out of the plots. For plots with *L. neglecta* or *P. piliferum*, the two cryptogams directly attached to soil, the cryptogam tissue was cut out of the plot using a knife and a bucket trowel. As much soil was removed from the base of the cryptogams as possible without breaking the pieces apart. In some cases this resulted in a cryptogam-soil layer 2 cm thick, but generally this layer was ≈ 1 cm thick. In all cases, this represented a removal or addition of > 60% (see Chapter 2, Appendices 2.1 and 2.2 for plot cover before treatment) of the total ground cover. Following the removals, this cryptogam tissue, along with additional tissue harvested nearby, was used to cover all bare ground in the addition plots.

Section 4.2.a.1. Measurements

Section 4.2.a.1.a. Field

I considered aboveground biomass at the whole-plot level a more robust indicator of long-term community influence than a more detailed set of measurements on a single individual plant. To non-destructively (I was limited to non-destructive techniques by my permitting agency at both sites) estimate whole-plot aboveground biomass of the focal plant species, I selected several measurements that had been standardized for use in the International Tundra Experiment (ITEX) and were specific for many of the same taxa I had on site (Arft et al. 1999, Chapin et al. 1996). Thus beginning in 2007, in each plot I measured the length and width of the longest leaf and counted the total number of green leaves for the three tallest plants for each focal species.

Next, as an initial step towards understanding the mechanisms behind any cryptogam influence on plant growth, I measured leaf temperature in a subset of my experimental plants (2008 and 2009 growing seasons only). I inserted fine wire copper-constantan (“Type T”) thermocouples into leaves in treatment and control plots in all of my experimental communities. Values were recorded on Campbell Scientific CR-21X dataloggers at hourly intervals. Only three dataloggers were available for this purpose, so I was not able to simultaneously record on all sites. Also, many thermocouples were disturbed by rodents and large precipitation events, thus the data I present are only from situations where multiple leaves were monitored per plot for at least one week.

Section 4.2.a.1.b. Image-based Data

Prior to beginning the transplant experiment, I suspected that traditional non-destructive indices of plant productivity (point cover, cover estimate, subsampling) would be too imprecise to be effective. Because this experiment was intended to last three years and changes in alpine plants are notoriously slow, any treatment effect I observed was likely to be small. Thus beginning in 2007 I captured digital RGB (red, green, blue spectra) images once annually after plants had reached their peak size (mid-late August) with the intent of using the images later in a then-unidentified image classification process. Images of each plot were captured from a height of approximately 30cm using a Canon PowerShot S3 IS 6.0 megapixel camera. A 20 x 20 cm PVC frame was placed around the plot, and the appropriate camera height and angle were determined to be the minimum height where the entire PVC frame was included in the image and appeared square. To minimize light variability all images were captured in a site within 30 minutes of each other. At all sites, images were taken during peak daylight hours during a day with consistent natural light. All images were then cropped manually using Microsoft Office

Picture Manager to include the minimum amount of frame possible while still including the entire 20 x 20cm plot, defined as the entire area inside the PVC frame.

To analyze the images for percent cover of my target species, I used eCognition Developer 8.64 and eCognition Grid 8.64 (Trimble, USA). The entirety of the work was performed in Developer; Grid simply batch processes images using the classification schemes created in Developer. The steps in the image analysis process were segmentation, classification, and post-processing.

I first used the "multiresolution segmentation" process in eCognition, which treats each individual pixel as an "object" and proceeds to merge objects with neighbor objects according to a homogeneity criterion, a user-defined combination of shape and color. This merging process is eventually limited by the user-defined scale parameter, which sets an upper bound on the size of image objects permitted. I used different homogeneity criteria and scale parameters for each site (Appendix 4.1). These were obtained via a lengthy trial-and-error process, with the primary criteria being that the edges of all foliage were accurately defined by image objects. While I still needed to manually edit and merge many objects, taking these preliminary steps reduced the amount of time needed for tracing individual leaves. Next, I used the "nearest-neighbor classification" process in eCognition, a sample-based classification algorithm which required that I select objects to serve as reference samples for the classes of interest. However, regardless of the care taken in sample and feature choice, I found it impossible to achieve a reasonable classification using the nearest-neighbor classification alone. Thus the final and most cumbersome (9 months) step in the analysis process was "post-processing," or manual cleanup. I considered post-processing complete when all of my objects classified as one of my focal plant species contained greater than 50% of the class assigned. I chose 50% because this was the only threshold I believed I could correctly determine rapidly. However, the pixel area in most objects of interest (objects with plants) was either entirely or almost entirely correctly classified.

From these classified images I simply computed the percentage of the image represented by each of my species of interest. *Carex scirpoidea* proved difficult to discern from *Carex phaocephala* in the communities where these two co-occurred with high frequency. To avoid classification errors in these communities, I grouped *Carex* sp. together and performed the analysis accordingly.

Section 4.2.a.2. Analysis

Section 4.2.a.2.a. Allometric

Before analyzing the experimental data, I tested the validity of my methods for estimating aboveground plant biomass. In 2008 I collected both field and image data for a set of ten randomly placed 20x20 cm plots in each community type at the end of the growing season. After all field data were collected, I clipped all vascular plant biomass to the ground level (belowground structures and cryptogams were left intact to ensure regrowth). In the lab these clippings were sorted by species and tissue type (stem, leaf, live, dead), oven-dried at 70°C until mass had stabilized (about 72hours in most cases), and weighed.

From my field measurements I computed mean length and width of longest leaf of each focal species at the plot level for each year. From my images I calculated percent cover for the species of interest. I then applied linear regression models to test whether these measures provided reasonable estimates of aboveground vascular plant biomass (Appendix 4.2). Because the field measurements correlated poorly to biomass at the plot level (note the low R^2 values for field-based measurements in Appendix 4.2—mean R^2 was 0.28), I did not consider these data further in my analyses. My image-based cover values, on the other hand, were well-correlated with biomass at the plot level (Appendix 4.2) in most cases (mean R^2 was 0.77). My analyses of the transplant experiments thus rely exclusively on the image data.

Section 4.2.a.2.b. Transplant Data

Several factors influenced my choice of statistical models for the image data. First, I needed a model to include random effects-- although I paired my plots according to topographic and cover similarity, the actual values of slope, aspect, and vegetative cover in each plot were not specifically chosen. Rather, the pairs themselves were trivial and drawn randomly from a theoretical population of pairs. Second, because treatments were applied after first year measurements were taken, I had a time-varying factor. Finally, repeated measures were made on the same plots for three consecutive years (two for the plots on Navarino island). These considerations led me to choose the linear mixed effects model (lmer procedure in lme4 package, R version 2.15.0). Repeated attempts to fit a model using data from all three years of the form

Y_{ijk} = intercept + overall mean + treatment(i) + pair(j) + year(k) + error

resulted in too many parameters to estimate given the sample size ("an overfitted model"). Therefore, I decided to use a simpler mixed model using just two years' of data per model of the form

Y_{ij} = intercept + Year1Cover + treatment(i) + treatment*Year1Cover + pair(j) + error

where Y_j represents growth at either year two or three. Two unanticipated benefits arose as a result of using this particular model. First, I was able use year one growth (pre-treatment) as a predictor of the following years' growth instead of the overall mean, which is ecologically sensible. Second, by moving to this particular model form I was able to fit a treatment interaction term, thus enabling a non-homogeneous estimate of treatment effect, conditioned on initial percent cover.

Section 4.2.a.2.c. Leaf Temperature Data

I calculated the mean hourly temperature for all of the cryptogam by plant combinations with at least two replicates and seven days of undisturbed data. I present these data in graphical format only. I deemed statistical analyses unnecessary, as these data were intended only for commentary on possible patterns in growth data, and there was often a lack of replication.

Section 4.2.b. Seed Germination Experiment

To address the effects of crusts on seed germination I performed two experimental germination trials, one in the field and one in the lab. Because the field trial resulted in zero germinates for two consecutive years, here I describe only the laboratory germination trial (see Appendix 4.3 for details of field germination trial). In 2009, I collected seeds from seven plant species and live biomass from seven cryptogam species (Table 4.1) on Snowshoe Mountain. In the lab I sowed 30 seeds of each plant species on each of nine substrate types (eight cryptogam surface types and bare soil) in a standard potting soil mixture in 5cm peat pots (“Jiffy Pots”, Figure 4.1). Because *Cetraria islandica* and *F. cucullata* occur most often in the field together (Chapter 2, Appendices 2.1 and 2.2, see description of the fruticose lichen meadow), I used an equal mixture of the two as one of the cryptogam cover types. Seeds were sown directly onto the surface of *P. piliferum* and *L. neglecta* because these effectively are the soil surface. There were ten replicates per plant x cryptogam treatment. Trays were placed in two growth chambers (Conviron, Pembina, ND) located in the laboratory on the University of Washington-Bothell campus.

Because most alpine seeds germinate during or immediately after spring snowmelt, I exposed the seeds to a synthetic snowmelt event in the growth chambers by covering the germination trays evenly with approximately 20 centimeters of freshly collected, compacted snow. Next, I programmed the growth chambers to follow a diurnal temperature pattern similar to that found in early to mid-summer at my field site (Table 4.2), although maximum light levels in the growth chambers were about 30% less than I observed in the field. Similar greenhouse studies using excised cryptogams and soil have been published from other systems (Zaady et al. 1997, Zamfir 2000, Serpe et al. 2006).

Section 4.2.b.1. Analysis

The germination data were Poisson-distributed (due to an abundance of zeros) with unequal variances. Thus all of my statistical tests used a generalized linear model procedure (glm with poisson family and log link function, R v 2.15.0), which is robust to violations of the normality and homogeneity of variance assumptions of a two-way ANOVA.

Seed characteristics were similar within the Carices and Asters I worked with. Achenes from the three Carices all possessed extremely hard, tight epidermal layers, presumably due to the presence of silicone bodies characteristic of many *Carex* species (Gordon and Norton 1990). In contrast, all of the Asters had thin, flexible epidermal layers over their fruits. Because of these similarities within the families in their seeds, I first analyzed the germination data grouped according to family. Likewise, because of the similarities I observed in the microclimate influence of fruticose (large) cryptogams (see Chapter 3), I also consider the germination data with surfaces grouped by physical structure, which I refer to henceforth as “surface form.” Next I compared germination rates of the different plant growth forms on each individual surface type. Finally, I compared the germination rates of all different plant species across all surfaces. In all cases, additional pairwise comparisons within plant species were made using Tukey’s HSD procedure for Type I error control.

Section 4.3. Results

Section 4.3.a. Cover

Section 4.3.a.1. General Patterns

At both study sites, the year-to-year patterns for both additions and removals in the control and treated plots tended to parallel each other. Therefore, subsequent patterns for each site are discussed separately. On Snowshoe Mountain, percent cover tended to decline over the three years I collected data for most species in most of the communities in which I worked (Figure 4.2), with much of the decline occurring between the second and third study years. Across communities, cover tended to decrease; the range of cover losses was between approximately 0.2% and 2.7% cover with a mean of 1.2%; in relative terms this represents an average loss of about one third of initial cover of my target species from 2007 to 2009. The only exceptions were *Antennaria lanata* in the crustose lichen snowbank community and *Carex scirpoidea* in the dry sedge meadow community, which tended to increase in cover between the first and second study years, but ultimately seemed to decline as well by the third year. On Cara de Indio, in the only species whose cover was estimated, *Festuca contracta*, cover tended to decline between year one and two (year one mean ≈1.7%, year two mean ≈1.2%, a loss of about one third of initial cover). The variables used to estimate *S. humifusus* biomass (stem length, canopy diameter) were unsuited for year-to-year comparisons of this variety as they tend to go up consistently through time.

Section 4.3.a.2. Transplants

The cryptogam transplants demonstrated negative effects on cover of the focal species in six of the ten study communities in at least one of the post-treatment years (Figure 4.2). On Snowshoe Mountain, *Erigeron aureus* responded negatively to both removals and additions of the moss *P. piliferum*. Between 2007 and 2009 *E. aureus* percent cover declined 40% more in removals than controls; between 2007 and 2008 *E. aureus* declined 60% more in additions than in controls. *Carex nardina* and *Antennaria lanata* both responded negatively to removals of *Lepraria neglecta*, as did *E. aureus* in response to *L. neglecta* additions. Between 2007 and 2008, *Carex nardina* lost one third of its initial cover in *L. neglecta* removals, whereas cover remained nearly constant in controls. Likewise, whereas *A. lanata* cover increased in both *L. neglecta* removals and controls between 2007 and 2008, cover increased 40% less than in the control plots. *E. aureus* cover declined over twice as fast from 2007 to 2009 when *L. neglecta* was added that when the bare ground was undisturbed. Over the duration of the entire study (2007-2009) *Carex scirpoidea* cover declined approximately 17% more when *Flavocetraria cucullata* and *Cetraria islandica* were removed than when they were left intact. Finally, on Navarino Island, plots where *Usnea trachycarpa* had been removed lost three times more of their *Festuca contracta* percent cover after one year than plots where it was left intact (treatments lost 51% of their initial cover, whereas controls lost 16%). In the remaining four communities, I found no statistically meaningful response to the cryptogam transplants during the two years following treatment in either focal species (Figure 4.2).

In most cases where I found a statistically significant treatment effect, the magnitude of the estimated effect changed depending on the initial coverage of the focal species (i.e . the Year1Cover*Treatment term in the model significantly improved model fit, Figure 4.3). In all but one of these cases, the estimated interaction term was negative— the model predicted a higher loss of percent cover in treatment plots with higher initial percent cover. This can be seen clearly in Figure 4.3, as the slope of the relationship between Year 2 or 3 and Year 1 cover tended to be flatter for treatments than controls. For example, in the moss addition plots, *Erigeron aureus* cover was predicted to decline an additional 0.32% for each extra percent of initial *E. aureus* cover. The one exception was *Carex nardina's* response to removal of *L. neglecta*. In this case, in the first post-treatment year the estimated treatment effect decreased over the range of values observed, although not in a statistically meaningful manner. In the second post-treatment year the treatment effect was also predicted to be more negative in low cover (below 1.7%) situations, but actually increase to positive above this threshold. This was the only statistically significant Year1Cover*Treatment interaction term that was positive.

Section 4.3.b. Leaf Temperature

Of the nine unique cryptogam*vascular plant combinations with sufficient data, in three cases leaf temperatures tended to be different between plants surrounded by cryptogams versus bare soil. In all three cases the largest differences tended to appear during peak daylight hours and disappear between dusk and dawn. In the dry sedge meadow, *Erigeron aureus* leaves tended to be about 3°C warmer at midday in the presence of *Lepraria neglecta* than when surrounded by only bare soil (Figure 4.4, Table 4.3). On the other hand, at the fellfield site, *Festuca brachyphylla* leaves tended to be about 2°C cooler at midday in the presence of the *Flavocetraria cucullata – Cetraria islandica* mix (Figure 4.5, Table 4.3), and in the fruticose lichen meadow, *Carex scirpoidea* leaves tended to be about 3°C cooler at midday in the presence of the *F. cucullata – Cetraria islandica* mix (Figure 4.6, Table 4.3).

Section 4.3.c. Germination

Section 4.3.c.1. General Patterns

Examining all plant species together, bare soil tended to be the poorest germination substrate, though it was statistically inseparable from three of the eight cryptogam substrates (*Cladina mitis, Clodonia pyxidata,*and *F. cucullata,* Figure 4.7A). *Polytrichum piliferum* was the best germination substrate overall, though it was statistically inseparable from the mixture of *F. cucullata* and *Cetraria islandica* or *Cetraria islandica* alone.

Although both plant family and surface form and their interaction term were significant at the $p<0.05$ level in both models they were used in (Figures 4.7B and 4.7C), neither plant family nor surface form were consistently associated with any particularly strong patterns (only one significant pairwise comparison was illustrated in Figures 4.7B and 4.7C). When grouped together, neither the Carices nor Asters differed in their ability to germinate across the different surface forms (Figure 4.7C). Likewise, the two plant families did not differ from each other in their ability to germinate on each surface form (bare soil, crustose, fruticose), though the Carices tended to germinate slightly better across all (Figure 4.7C). Finally, the Carices and Asters did differ somewhat more in their germination patterns when the surfaces were not grouped together as surface forms. This derived almost entirely from exceptionally low germination of the Carices with *Stereocaulon paschale* (Figure 4.7B).

Section 4.3.c.2. Species-Level Patterns

Germination was much more variable at the species level than at the plant family or surface form level (Figure 4.8). For example, *Carex phaocephala* displayed the highest ($\bar{x}$ =73 %) and most variable germination of all plant species tested, with its poorest germination (≈57%) on bare soil and highest (≈97%) on *P. piliferum*, while the two other Carices tested, *Carex scirpoidea* and *Carex nardina*, displayed the lowest ($\bar{x}$ =3 % and $\bar{x}$ =8 %, respectively) and least variable (ranges: 0-3% and 0-13%, respectively) germination of all species tested. For these last two Carices, no differences were found in their ability to germinate across the difference substrates.

The Asters were somewhat more consistent in their germination rates overall (Figure 4.8); the highest germination rate was 28% (*S. multiradiata*) and the lowest 19% (*A. lanata)*. The range of values found across the different surfaces was also similar for all of the Asters tested; germination ranged between 12 and 33% germination for *S. multiradiata*, between 10 and 23% for *A. lanata*, and between 13 and 42% for *E. aureus*. In the Asters, differences were found for both *E. aureus* and *S. multiradiata* in their ability to germinate across the different surfaces. In particular, both showed low germination under *S. paschale* statistically identical to that found on bare soil. *A. lanata*, on the other hand, showed little variation across surface types but tended to have higher germination under *S. paschale* than on bare soil.

Section 4.4. Discussion

Section 4.4.a. Plant Growth – Broad Trends

The decreases in cover of most of my study species could be interpreted a number of different ways. High interannual variability in aboveground biomass has been found in other alpine studies (Walker et al. 1994, Fisk et al. 1998). Because I focused on only two species per site I do not know if the decreases in percent cover of my focal species represent a broader drawdown in total aboveground community biomass. Considering that the focal species were chosen for their prominence and consistency in cover, this is certainly a possibility. If so, interannual variability in aboveground alpine plant community biomass has generally been linked to interannual climate variability (Walker et al. 1994). A brief comparison of air temperature and precipitation on Snowshoe Mountain (I did not have climate data for both years for Navarino) among the years of my study finds modest evidence to support interannual climate variation as the source of the change in cover; some aspects of the 2006 (the year prior to my study) and 2007 climate indicate they may have been particularly good years for growth (Figure 4.9). For 2006, considerably higher precipitation was observed than in the subsequent three years. The year prior to the study is relevant because environmental effects on alpine vegetation are notoriously lagged due to bud preformation and reliance on carbon stores (Aydelotte and Diggle 1997). Next, snowmelt in 2007 was unusually early, and July 2007 was the warmest month of any during the study. This time coincides with emergence and leaf elongation for most of my species at these sites (Jespersen, personal observation).

An equally, if not more plausible explanation for the broad decreases in focal species cover comes from looking at longer-term climate trends. Compared to the prior three decades, the years of my study tended to be warmer (≈2º C warmer, although closer to 5º warmer in July) with lower overall precipitation and an earlier snowmelt (Figure 4.9). In this context the decreases in focal species percent cover I observed could be interpreted as part of a broader climate-induced shift towards different species assemblages. Shifts in community composition have been observed at many tundra sites globally (Elmendorf et al. 2012b), and experimental results have linked these shifts to warming and changes in snowmelt timing seen in the latter part of the 20th century (Galen and Stanton 1995, Sandvik et al. 2004, Schob et al. 2009, Wipf et al. 2009, Carbognani et al. 2012, Elmendorf et al. 2012a). Finally, it is important to acknowledge that without any measures of belowground productivity it is impossible to put the decreases in aboveground cover into the proper ecological context; however, white it is theoretically possible that they could represent allocation shifts or overall productivity changes, several authors have found limited plasticity in alpine plants (Bechtold et al. 2002, Jonsdottir et al. 2005, Myerburg et al. 2011).

Section 4.4.b. Plant Growth – Transplant Experiments

To some degree, the experimental results confirmed my expectation that adding or removing cryptogam cover would impact plant growth. In most of the plant communities where I worked, for at least one of the focal species the relationship between pre- and post-treatment cover in plots where the cryptogam cover had been manipulated was statistically different from plots where the natural cover was left intact. Surprisingly, though, all of the statistically significant treatment "effects" were negative – in no case did adding or removing cryptogams lead to improved growth in either of the years following treatment (Figure 4.2). Unfortunately, this raises the possibility of an experimental relict, that some aspect of the cryptogam transplants in general was more influential than the particular form of the transplant in affecting plant growth. Two possible interpretations of this puzzling finding stand out, the first being that the disturbance associated with the transplants simply had negative effects on plants. This hypothesis gains traction in light of the majority of statistically significant effects being found at cryptogam removal sites, as the physical disturbance to the rhizosphere and plant tissues was certainly more profound in removal plots than addition plots. If this was the case, it would be interesting to follow-up over several more years to see if the treatment effects all remain negative, or if different signals could be obtained from the transplant plots. The second possibility is that the effects were not disturbance-related, but rather legitimate negative treatment effects. Below I will highlight some of the more promising cases.

Perhaps the most intriguing findings involve the fruticose cryptogams, as the disturbance to the rhizosphere and surrounding plant tissues during transplant was minimal. Removing *U. trachycharpa* involved simply clipping a single branch of lichen thallus tissue above the substrate attachment point whereas for the mixture of *F. cucullata—Cetraria islandica*, removal involved lifting the loose, unattached 'leaves' of the Cetrarioid lichens by hand and clipping sparse moss fronds. On Snowshoe Mountain, *Carex scirpoidea* cover declined more in plots where the mixture of *F. cucullata* and *Cetraria islandica* had been removed, and on Cara de Indio, *Festuca contracta* declined more after *Usnea trachycarpa* had been removed (Figure 4.2). In both cases, the growth reduction occurred in tandem with sharp increases in the amplitude (approximately 5°C) of the diurnal temperature swings at 1cm depth (See Chapter 2 for details). To put this into context, the differences in diurnal soil temperature swings between treatments and controls were similar to the wider swings in soil surface temperature inside of warming chambers on Niwot Ridge (Walker et al. 1999); these chambers have been linked to profound changes in species composition, community productivity, and nitrogen cycling in tundra communities worldwide (Walker et al. 2006, Borner et al. 2008). Another possible explanation involves freeze-thaw cycles and soil denitrification (Deluca et al. 1992). While I do not know whether freeze-thaw events were more frequent in treatment plots, I did monitor other covariates of denitrification on Snowshoe Mountain (*F. cucullata - Cetraria islandica* removals). There the more rapid reduction in *Carex scirpoidea* cover in removal plots also corresponded to more rapid drying of near surface soils (Chapter 2, Figure 2.9), lower total soil N and C (Chapter 3, Figure 4.5), and lower soil NH_4 levels (Chapter 3, Figure 3.6). These observations are consistent with an increase in denitrification and a decrease in mineralization (Fisk and Schmidt 1996, Fisk et al. 1998, Makarov et al. 2003, Miller and Bowman 2003, Zhang et al. 2012). Also, diurnal leaf temperature swings were considerably wider in *Carex scirpoidea* leaves from removal plots. Although I did not measure leaf temperatures on Cara de Indio, on Snowshoe Mountain I did add the *Flavocetraria cucullata-Cetraria islandica* mix to fellfield habitat with *Festuca brachyphylla*, a congener of *F. contracta* with nearly identical physiognomy and growth habits. In this setting fruticose lichens helped modulate leaf temperatures, reducing daily midday maxima by about 3°C (Chapter 2, Figure 2.6A and 2.6B). While I do not know the shape of the relationships between leaf temperature and other physiological parameters for any species I worked with, data from other studies indicate a shift of this margnitude might be sufficient to influence net photosynthetic activity (Körner 1982), mesophyll resistance (Lloyd and Woolhouse 1979), and freezing resistance (Sierra-Almeida and Cavieres 2010). Thus I have a variety of evidence suggesting the naturally-occurring mixture of *Flavocetraria cucullata* and *Cetraria islandica*, and perhaps *U. trachycarpa* as well, maintains growing season soil moisture, prevents losses of N and C, and regulates leaf temperatures, ultimately improving *Carex scirpoidea* growth.

Next, several of the cases of significant treatment effects involved *E. aureus.* Perhaps the most credible of these was the negative response of *E. aureus cover* to additions of *L. neglecta.* These reductions in cover occurred in tandem with some strong patterns in the other covariates measured in these plots— both leaf temperatures in *E. aureus* and near-surface soil temperatures were considerably warmer at midday when *Lepraria neglecta* was present compared to the bare soil control plots in the dry sedge meadow (Chapter 2, Figure 2.6A). Consistent with these microclimate trends, there appeared to be a slight tendency towards lower NH_4 in these plots with *L. neglecta* as well (Chapter 3, Figure 3.6). For reasons already discussed, these shifts in the near surface microenvironment could well explain these cover reductions.

My most dubious finding was that *E. aureus* responded negatively to both the addition and removal of the moss *Polytrichum piliferum*. In light of the similar response to additions and removals I consider these results to be disturbance-driven. However, there are still some interesting points that can be gleaned from some of the covariates I measured. Despite the considerable heating of *P. piliferum* under full sun (Chapter 2, Figure 2.7A) it did not appear to influence leaf temperatures in either *Carex scirpoidea* or *E. aureus*. *P. piliferum* was associated with higher N and C levels (Chapter 3, Figure 3.5), but no effects were observed with regard to inorganic N levels. At the removal site, *P. piliferum* was associated with cooler soil temperatures (Chapter 2, Figure 2.6B) and higher soil moisture (Chapter 2, Figure 2.9), in spite of its impressive foliar surface temperatures (Chapter 2, Figure 2.7B). If I were observing the *P. piliferum* removals in isolation, these findings could be invoked to explain the growth reduction in removal plots, but I am uncomfortable doing so given the circumstances.

Given that nearly half of the statistically significant treatment effects involved *E. aureus*, it is worthwhile to consider why this particular species may have been uniquely sensitive to the surface disturbances I engineered. To the best of my knowledge, no published studies document the responsiveness of this species to either climate or disturbance-related habitat change. Evidence regarding the sensitivity of other alpine *Erigerons* is mixed. De Valpine and Hart (2001) reported negative responses to experimental warming in *Erigeron speciocus*, and Inouye (2008) has reported significant frost damage to buds in *E. speciocus* related to early snowmelt. On the other hand, in the Finnish alpine, one alpine *Erigeron* was shown to be less responsive to grazing than its community associates (Eskelinen 2008), and Utelli (1995) reported considerable phenotypic plasticity in another alpine *Erigeron.* Ultimately, I believe a combination of factors led to the sensitivity of *E. aureus* to my treatments. First, leaf temperature data suggest that *E. aureus's* physiological status was tightly linked to its surface surroundings, perhaps more so than some of my other plants. For example, leaf temperatures in *E. aureus* tended to be more responsive than in *Carex scirpoidea* to *L. neglecta* additions (Figure 4.4), and these same *E. aureus* plants declined in cover relative to control plots (Figure 4.2), whereas *Carex scirpoidea* cover was unresponsive. Given the low stature (and hence, proximity to the soil surface) and relatively large leaf areas in *E. aureus*, it is not surprising that these leaves might be more subject to changes to the soil surface. Second, of the plants I examined *E. aureus* was the only one lacking rhizomatous growth, suggesting a higher degree of physiological isolation for *E. aureus* individuals. Taken together, this evidence suggests that *E. aureus* individuals may be more prone to be exposed to the effects of shallow disturbances in their immediate surroundings.

Next, *Carex nardina* and *Antennaria lanata* responded negatively to the removal of *Lepraria neglecta*. Because *L. neglecta* is essentially part of the soil matrix, disturbance to the rhizosphere was relatively high in these plots, thus I am choosing to interpret these results cautiously. Additionally, there are few related findings which add to the case for legitimacy. Total N and C both declined in the near surface soils of removal plots (Chapter 3, Figure 3.5), but beyond that soil temperatures were unaffected by *L. neglecta* removals (Chapter 2, Figure 2.6B), soil moisture actually appeared to decline faster following precipitation events in plots with intact *L. neglecta* (Chapter 2, Figure 2.9), and no reliable leaf temperature data was obtained.

Finally, the significance of many of the interaction terms could be interpreted to mean that the magnitude of the effects were density-dependent. In most cases this would result in more negative treatment effects predicted for higher initial densities. To put it another way, the higher the initial density the more of an absolute reduction in cover one would expect for treatments relative to controls (Figure 4.3). However, I believe it critical that these “interaction” terms be interpreted in a more ecologically relevant manner. That is, I believe it is more appropriate to view the “treatment effects” as acting on proportions. Under this interpretation, both treatments and controls either add or lose a fixed proportion of the previous year’s cover; the difference between the treatment and control proportions, essentially the difference in slope for the lines in Figure 4.3, is then the treatment 'effect.' For example, if the "absolute" treatment effect predicts a loss of 0.2% cover given a starting cover of 1% but a loss of 1% cover for a starting cover of 5%, I consider these ecologically similar—they both represent a loss of 20% of initial cover, a similar loss in a species' ability to compete for and utilize available resources.

Section 4.4.c. Germination

Because of the high number of species of plants and cryptogams I worked with in the germination trial, these particular results are challenging to distill. Nonetheless, several findings stand out. First, for most of the alpine plants I worked with *Polytrichum piliferum* is an exceptionally good germination substrate. Bryophytes in general have been reported to have both positive and negative effects on germination and emergence (Bell and Bliss 1980, reviewed in During and Vantooren 1990, Equihua and Usher 1993, Zamfir 2000, Morgan 2006, Serpe et al. 2006), with current opinion moving towards a nuanced, life stage- and species-specific model of influence (Godinez-Alvarez et al. 2012). *P. piliferum* in particular has been reported to have positive effects on germination (Delach and Kimmerer 2002), while Sedia and Ehrenfeld (2003) reported net neutral effects for seeds treated with extracts from the closely related *Polytrichum juniperum*. Positive effects on germination such as those I observed have been attributed elsewhere to improved moisture conditions (Sohlberg and Bliss 1987), while negative effects have been most commonly attributed to lack of available moisture (Serpe et al. 2006), light (Equihua and Usher 1993), or allelopathy (Steijlen et al. 1995, Michel et al. 2011). In my opinion, the positive effects I observed are driven by higher temperatures found on *P. piliferum* (See Chapter 3 for details), but these effects are absolutely dependent on consistent, plentiful moisture. Without consistent moisture, the heating of *P. piliferum* can become rapidly hostile; for example, despite improved germination, Delach and Kimmerer (2002) saw no enhancement of seedling survival on *P. piliferum* mats. In nature, the moist conditions necessary to realize the benefits of *P. piliferum* cover are likely to be restricted to the period during and immediately following snowmelt, making it necessary to test my findings under field conditions before extrapolating further. Nonetheless, given the other positive assocations between *P. piliferum* and soil moisture, N and C, and soil temperature amelioration, there is sufficient reason to suspect this moss could be a valuable component of alpine restoration efforts when used appropriately (with sufficient moisture).

My next major finding was that for many of the plant species tested, bare soil is a relatively poor germination substrate ($\overline{x}$ = 23% overall, the next poorest was *C. mitis*, $\overline{x}$ = 27% overall). Whether this was due to the use of standard potting soil, as opposed to a field soil, is unknown, but potting soil has been used in published arctic/alpine germination studies elsewhere (Müller et al. 2011). Bare soil has previously been found wanting as a germination substrate (Marchand and Roach 1980). However, Zamfir (2000) found higher germination on bare native soil than with bryophytes or lichens, suggesting the possible importance of soil type and cryptogam species used. I believe this finding is likely related to moisture available to the seed. Given the physical structure inherent in a cryptogam surface versus a bare soil surface and the capillary water rise associated with mosses, it seems likely that seeds have a higher probability of contact with multiple moist surfaces on, for example, a moss surface versus a bare soil surface. Such multiple contacts would facilitate the transfer of moisture to the seed coat and enhance germination. In this light, partial to full burial of the seeds would probably have improved germination on this particular substrate, but this would have made the direct comparison with various cryptogam surfaces more complicated.

An interesting finding was that for two of the three composites (*Erigeron aureus* and *Solidago multiradiata*), *Stereocaulon paschale* is an unusually difficult germination substrate. How and why this occurs is unknown, though I believe this may be an example of secondary metabolites influencing germination. No previous studies address the impacts of *S. paschale* on germination, but three facts support this line of reasoning. First, other *Stereocaulon* species are known to exude a wide variety of biologically active secondary metabolites (Perezurria et al. 1989, Hickey et al. 1990, Huneck 1999, Morita et al. 2009, Boustie et al. 2011), including atranorin and orcinol derivatives, which have known phytotoxic qualities (Rojas et al. 2000, Marante et al. 2003). Second, the particularly thin and permeable seed coats of *E. aureus* and *S. multiradiata* make their seeds ideal candidates to be influenced by secondary chemicals. Finally, in the case of *S. multiradiata,* the fact that this decline was not echoed under *Cetraria islandica* (a cryptogam of similar physical structure) would indicate the mechanism is not purely physical, and that perhaps *Cetraria islandica* and *S. paschale* represent opposite ends of an unidentified chemical spectrum of influence.

Finally, in *Festuca brachyphylla* a noticeable increase in germination occurred under the mixture of *Flavocetraria cucullata* and *Cetraria islandica,* making this the best surface for *Festuca brachyphylla* germination. In *S. multiradiata, E. aureus,* and *Carex phaocephala* a similar slight uptick occurred under *Cetraria islandica* alone. I do not know what might make the cetrarioid lichens I worked with somewhat more attractive to germinate under for these particular species. On a purely physical basis, the cetrarioid lichens comprise a thick boundary layer which is very effective at insulating the soil surface (see Chapter 3 for details), but this should not differentiate it in any way from *Cladina mitis* or *Cladonia* pyxidata. The cetrarioid lichens are also known to often exude bioactive secondary metabolites (Boustie et al. 2011), but particularly usnic acid, which has well-documented antifungal properties (Cardarelli et al. 1997, Halama and Van Haluwin 2004), but also the capacity to stimulate cell growth (Cardarelli et al. 1997). Further, the seeds of both *F. brachyphylla* and *S. multiradiata* have a particularly thin seed coat (personal observation), which would make them particularly susceptible to fungal pathogens or chemical stimuli. While I cannot demonstrate conclusively that chemical influence occurred in my germination experiments, the evidence outlined here is sufficient to warrant further investigation along these lines.

Section 4.4.d. Conclusion

Here I attempted to address the very basic question of whether cryptogams affect the lives of the higher plants with which they cohabitate above treeline. I did this through manipulative experiments involving the soil-plant-cryptogam matrix, using both the seed and adult phases of the plant life cycle. Although I anticipated some difficulties working in this environment, several factors had an enormous influence on my study. First, change in alpine systems is very slow, in part because the climate is harsh, and in part because there is only a small portion of the year during which most of the biological activity can happen. Second, the weather during my study years (2006—2009) appears to have been drier and warmer with consistently earlier snowmelt than the previous few decades. Thus, the treatments and subsequent data are set against a backdrop of potentially stronger environmental and ecosystem change. Third, there is no history of experimental alpine work at this site and little in this region. In particular, without the detailed natural history knowledge that comes from a long, consistent history of working at a site, it is really difficult to contextualize my findings appropriately.

With these reservations in mind, I tentatively find that cryptogams do indeed influence their higher plant neighbors. The particular cryptogam a seed lands on appears to influence its germination rate, and which cryptogam is preferred differs for different plants. Further, with adult plants my most reliable results suggest that large-bodied, fruticose cryptogams play some role in maintaining growth, particularly in grass-like species. My preliminary results suggest this influence may arise through a combination of insulating the near surface soil layers and leaves from temperature extremes common at higher altitudes in the short Pacific Northwest summer. While my results are far from conclusive, for alpine scientists and land managers involved with restoration and conservation of subalpine and alpine lands they provide a theoretical and experimental baseline from which to proceed. For example, if one were charged with restoring a degraded alpine habitat, cryptogams might enhance or diminish the success of transplants or alter soil chemistry in beneficial or harmful ways. Likewise, if one were attempting to predict the abundance of particular alpine plants over the coming century, if these plants commonly share space with cryptogams it may be worthwhile to investigate the nature of their relationship and their physiological tolerances in order to anticipate possible nonlinearities in the community response to climate change.

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Section 4.6. Figures and Tables

Table 4.1. Plants and cryptogams used in the indoor germination trial.

Plant species (Family)	Cryptogam cover types
Solidago multiradiatw (Asteraceae)	*Stereocaulon paschale*
Erigeron aureus (Asteraceae)	*Lepraria neglecta*
Antennaria lanata (Asteraceae)	*Solorina crocea*
Carex scirpoidea (Cyperaceae)	*Flavocetraria cucullata*
Carex phaocephala (Cyperaceae)	*Cetraria islandica*
Carex nardina (Cyperaceae)	*Cladina mitis*
Festuca brachyphylla (Poaceae)	*Cladonia pyxidata*
	Polytrichum piliferum (moss)
	Cetraria islandica + *Flavocetraria cucullata*

Table 4.2. Growth chamber settings for germination experiment.

Time period	Air Temp (°C)	Halide Lights (out of 3)	Sodium vapor lights (out of 3)	Approximate Photosynthetic Photon Flux Density PPFD at Soil Level (µmol $m^{-2}s^{-1}$)
20:00 - 6:00	12	0	0	0
6:00 - 8:00	15	1	1	100
8:00 - 11:00	20	1	1	100
11:00 - 13:00	25	2	2	580
13:00 - 16:00	30	3	3	810
16:00 - 18:00	25	2	2	580
18:00 - 19:00	20	1	1	100
19:00 - 20:00	15	1	1	100

Table 4.3. Summary of leaf temperature relationships between cryptogam and bare soil plots across all communities with sufficient data. *No statistical models were used with these data. A “strong” tendency is considered on where the standard error bars do not overlap during some portion of the day.

Community	Cryptogam(s)	Vascular Plant	Leaf temperature Cryptogam relative to Bare	Strong Tendency*
Dry Sedge Meadow	*Polytrichum piliferum*	*Carex scirpoidea*	>	No
		Erigeron aureus	≈	No
	Lepraria neglecta	*Carex scirpoidea*	<	No
		Erigeron aureus	<	Yes
Fellfield	*Flavocetraria cucullata – Cetraria islandica*	*Festuca brachyphylla*	<	Yes
Fruticose lichen meadow	*Flavocetraria cucullata – Cetraria islandica*	*Carex scirpoidea*	<	Yes
		Solidago multiradiata	<	No

Figure 4.1. Seed germination experiment. Top: the eight different cryptogam surfaces displayed. These larger trays were used in looking at soil temperature under different surfaces. Bottom: a student counts seedlings in germination trays arrayed in the growth chamber.

Figure 4.2. Percent cover of focal species in experimental plots across all measurement years. For, *S. humifusus*, stem length and canopy diameter were used in place of percent cover and y-axes are labeled as such. Values are reported as mean ± 1SE. Where sample size does not equal 12 (i.e. data were lost), the sample size is noted. “I” indicates significant (at least $P \leq 0.1$ level) interaction term *as well as* significant mean treatment effect. Significance relates only to treatment versus controls, not differences among years, which were not tested. “I-O” indicates only interaction term significance. No letters indicated no interaction term significance (See Discussion for details. Significance codes: *** $P \leq 0.01$, ** $P \leq 0.05$, *$P \leq 0.1$

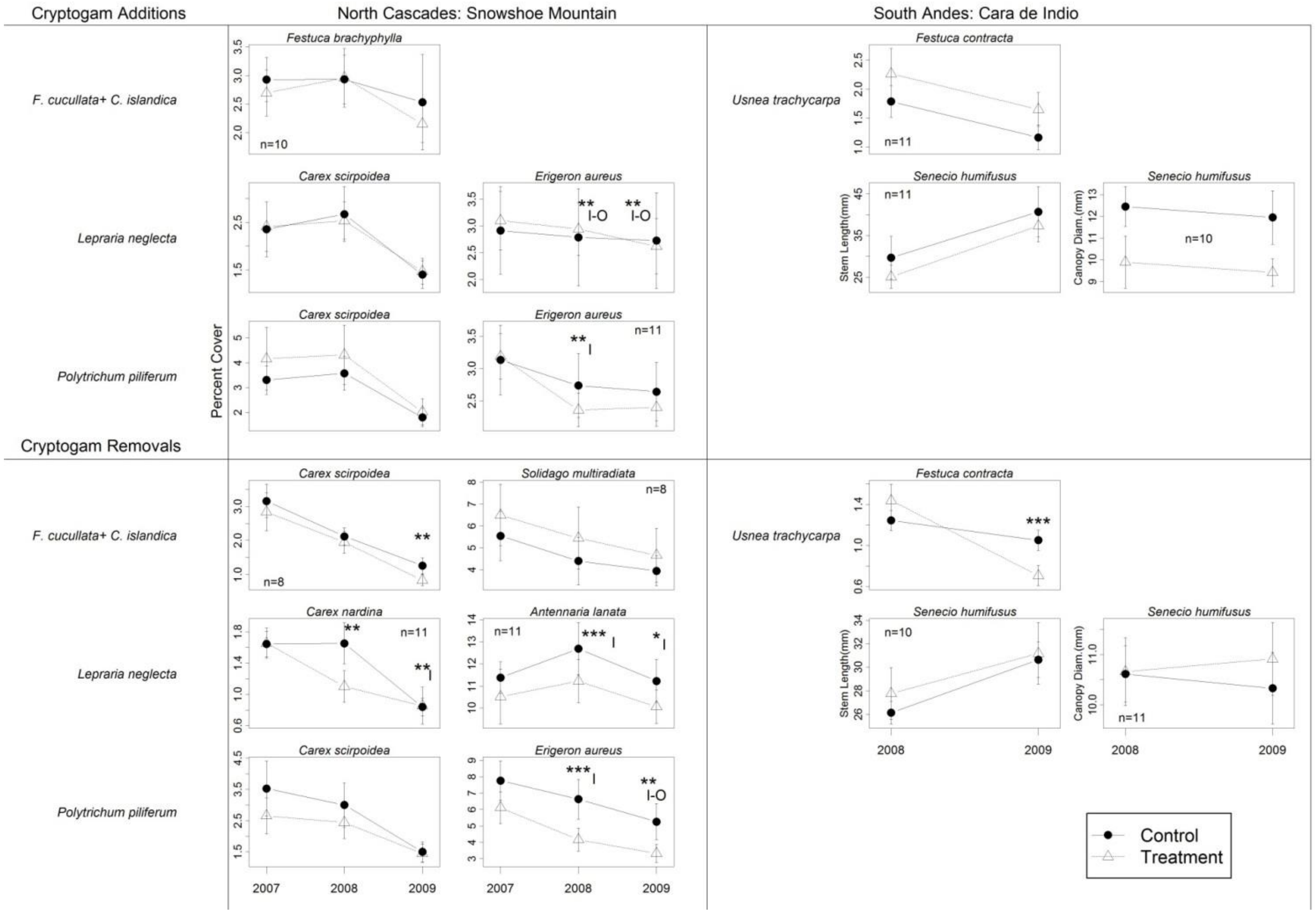


Figure 4.3. Post- versus pre-treatment percent cover in experimental plots for experiments with significant treatment effects. Significant model coefficients are listed in the lower right corner of each plot. α_{Trt} = Treatment coefficient; $\alpha_{Year1Int}$= Interaction coefficient. The basic treatment coefficient can be interpreted as an expected difference in the relationship between pre- and post-treatment cover for treatments versus controls. A significant interaction coefficient can be interpreted to mean that the predicted difference between these two regression lines (treatment and control) differs depending on the pre-treatment cover. Significance codes: *** $P \leq 0.01$, ** $P \leq 0.05$, *$P \leq 0.1$.

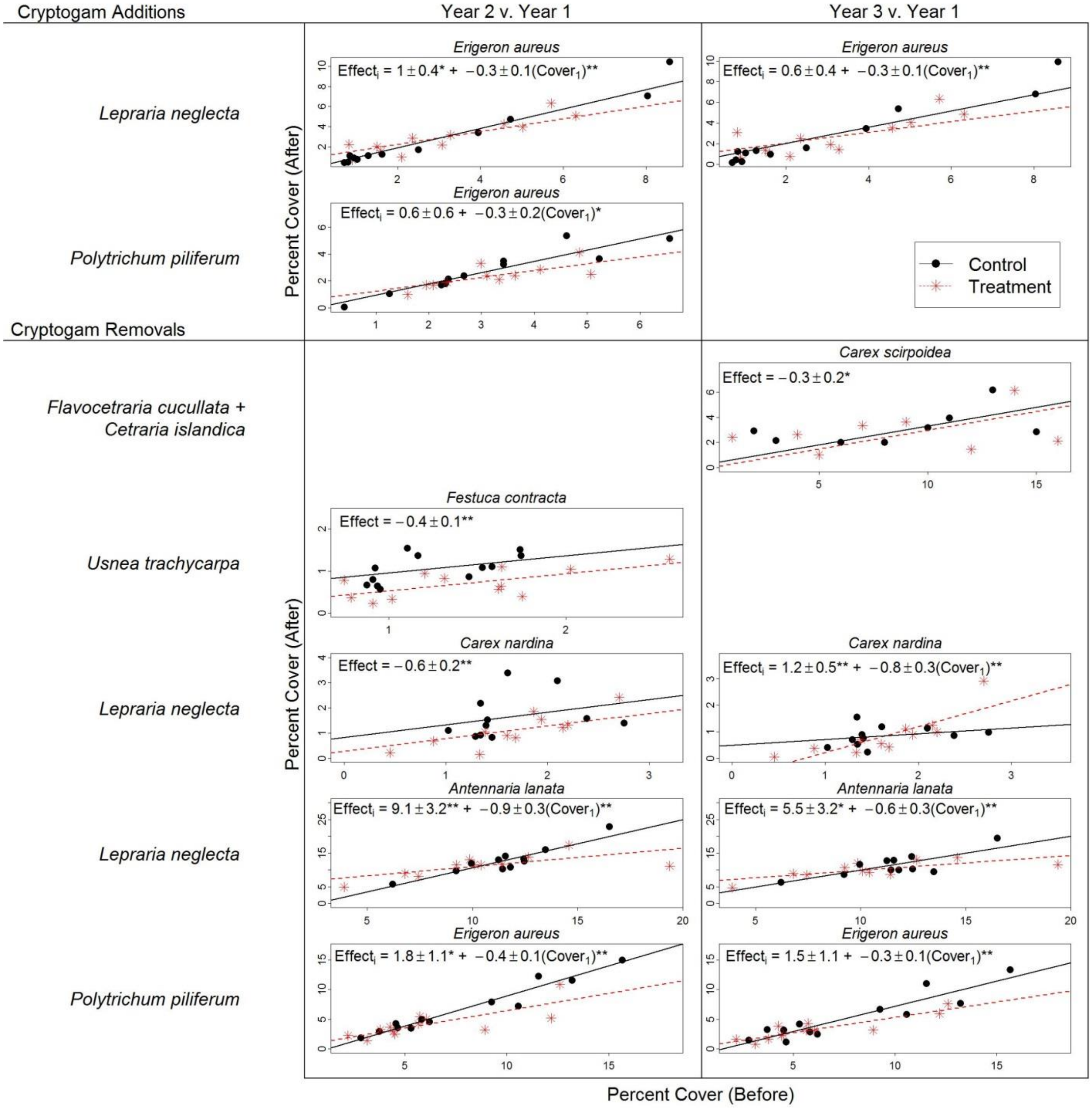


Figure 4.4. Mean hourly leaf temperatures for two plant species surrounded by two cryptogam types in the dry sedge meadow, August 16 — October 3, 2008. Values reported as mean ± 1 SE.

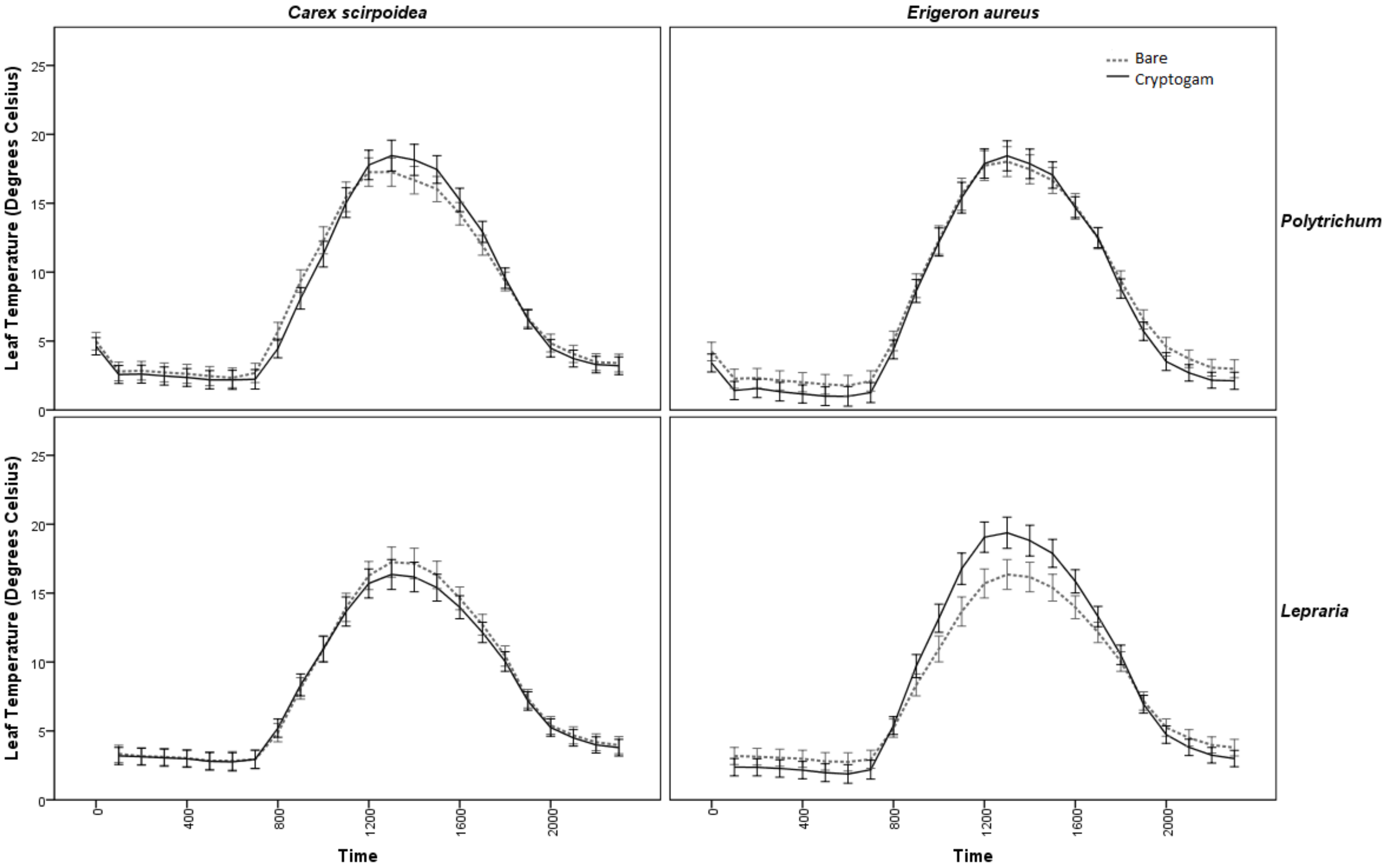
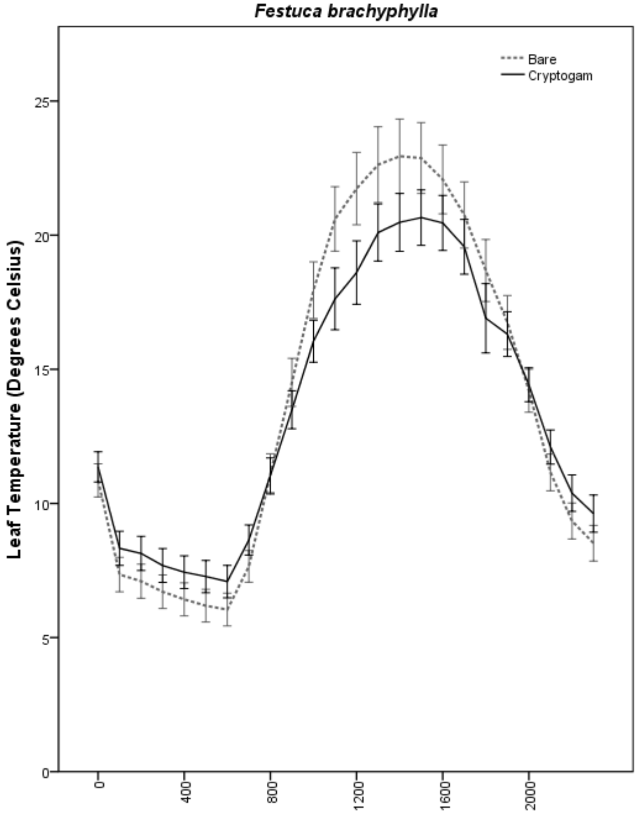


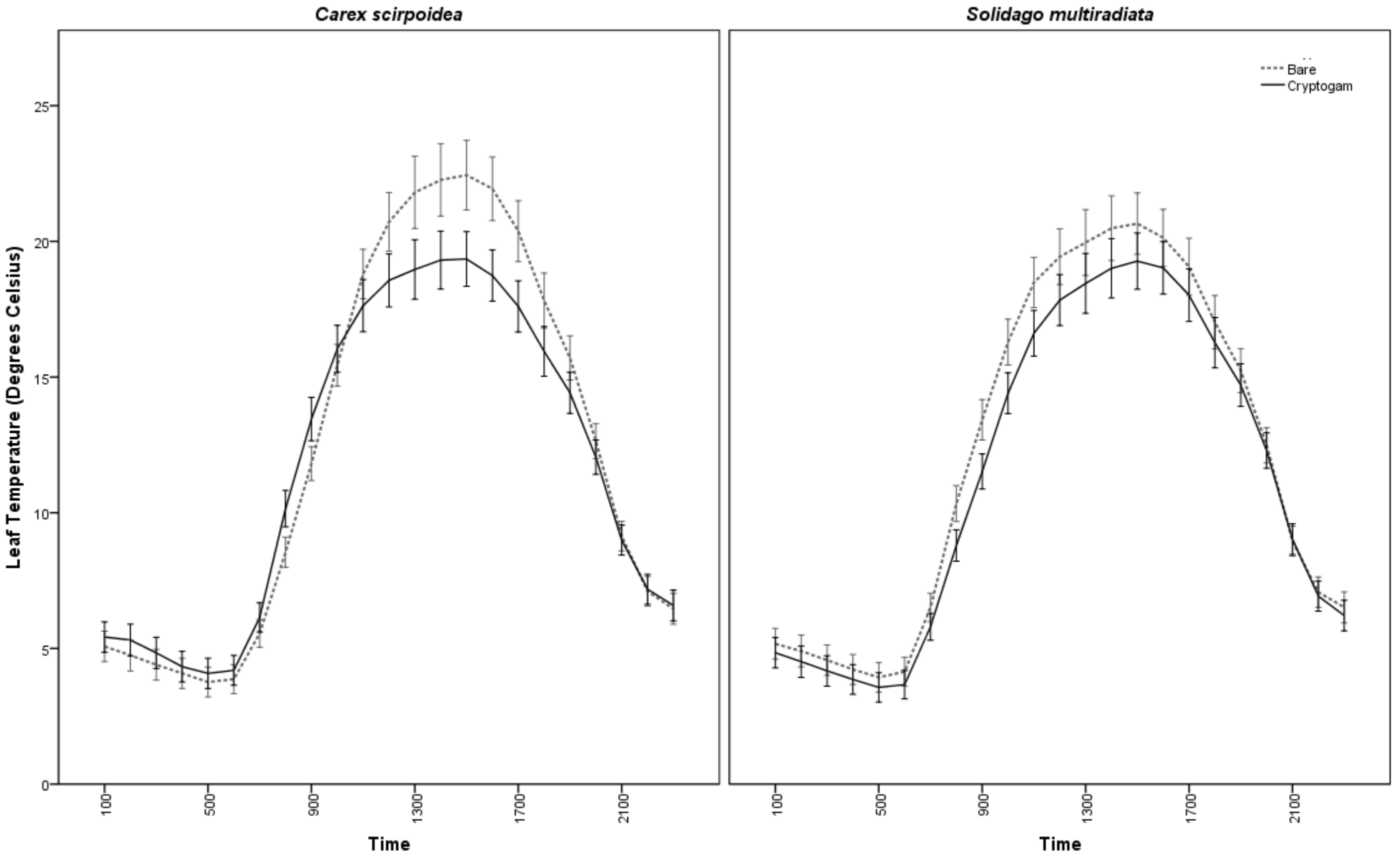
Figure 4.5. Mean hourly leaf temperatures for one plant at the Fellfield site, July 8 – August 15, 2009. Values reported as mean ± 1 SE.



Flavocetraria cucullata –

Cetraria islandica

Figure 4.6. Mean hourly leaf temperatures for one plant at the Fruticose Lichen Meadow site, June 28 — August 15, 2009. Values reported as mean ± 1 SE.



Flavocetraria cucullata – Cetraria islandica

Figure 4.7. Seed germination data when with plants or crusts grouped according to structure or taxonomy. A. All plant species together across all different surfaces. B. Carices and Asters grouped together across all different surfaces. C. Data grouped according to Carices or Asters across different surface forms. Values are mean germinates ± 1SE (maximum possible was 30). Asterisk on left of plot indicate which model parameters provided an improved model fit, as compared to a null model. Significance codes: *** $P \leq 0.01$, ** $P \leq 0.05$, *$P \leq 0.1$. Groups sharing a letter within a plot are statistically inseparable (at a minimum $P \leq 0.1$ level). Asterisk next to letter indicates $0.05 \leq P \leq 0.1$ between the groups sharing the asterisk. No asterisk next to letter indicates $P < 0.05$.

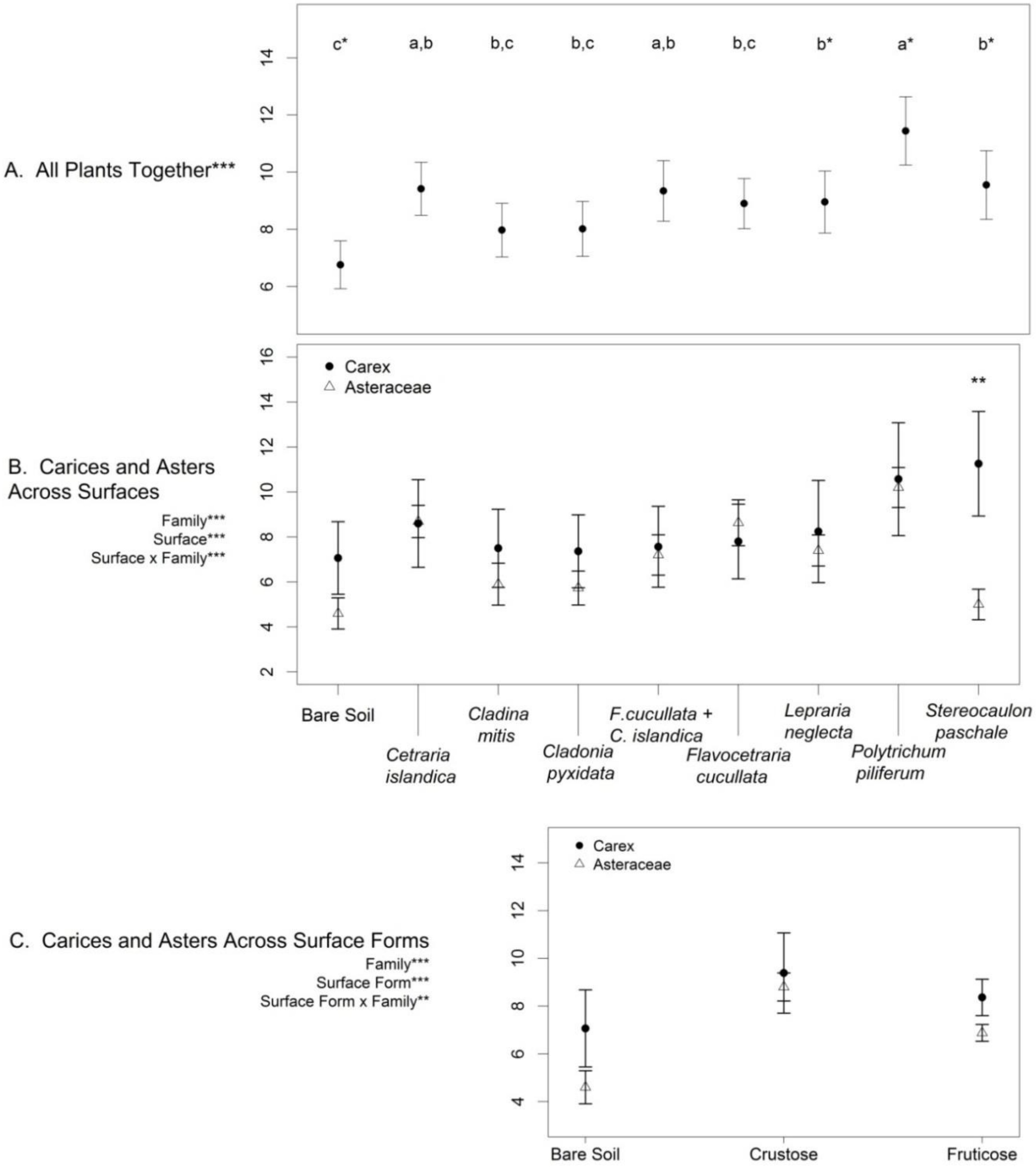


Figure 4.8. Seed germination data for each species tested across all different surfaces. Values are mean germinates ± 1SE (maximum possible was 30). Asterisk (*) on left of plot indicate whether surface type on the whole was a significant model parameter. Significance codes: *** $P \leq 0.01$, ** $P \leq 0.05$, *$P \leq 0.1$. Groups sharing a letter within a plot are statistically inseparable (at a minimum $P \leq 0.1$ level). Asterisk indicates $0.05 \leq P \leq 0.1$ between the groups sharing the asterisk. No asterisk next to letter indicates $P < 0.05$.

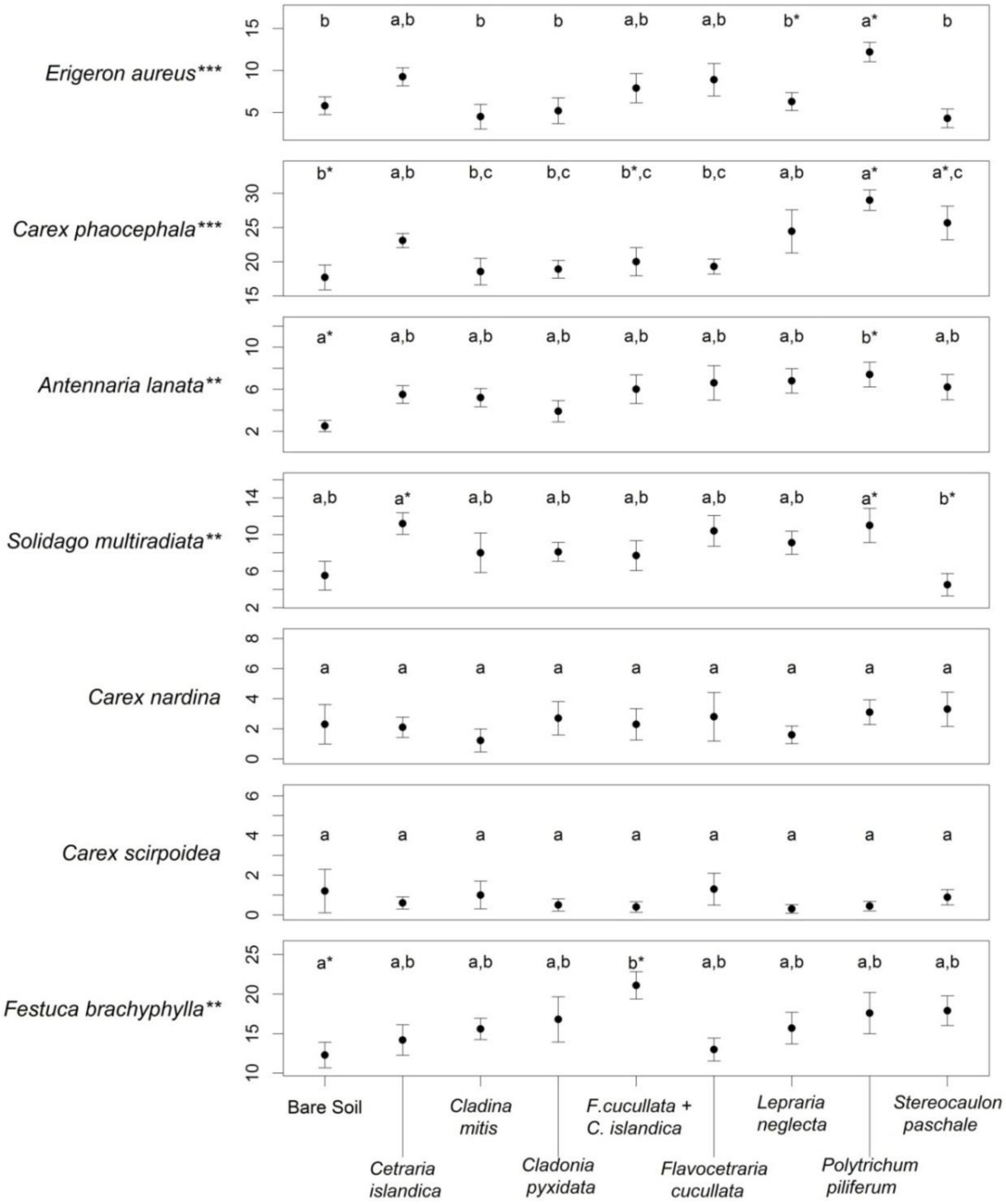
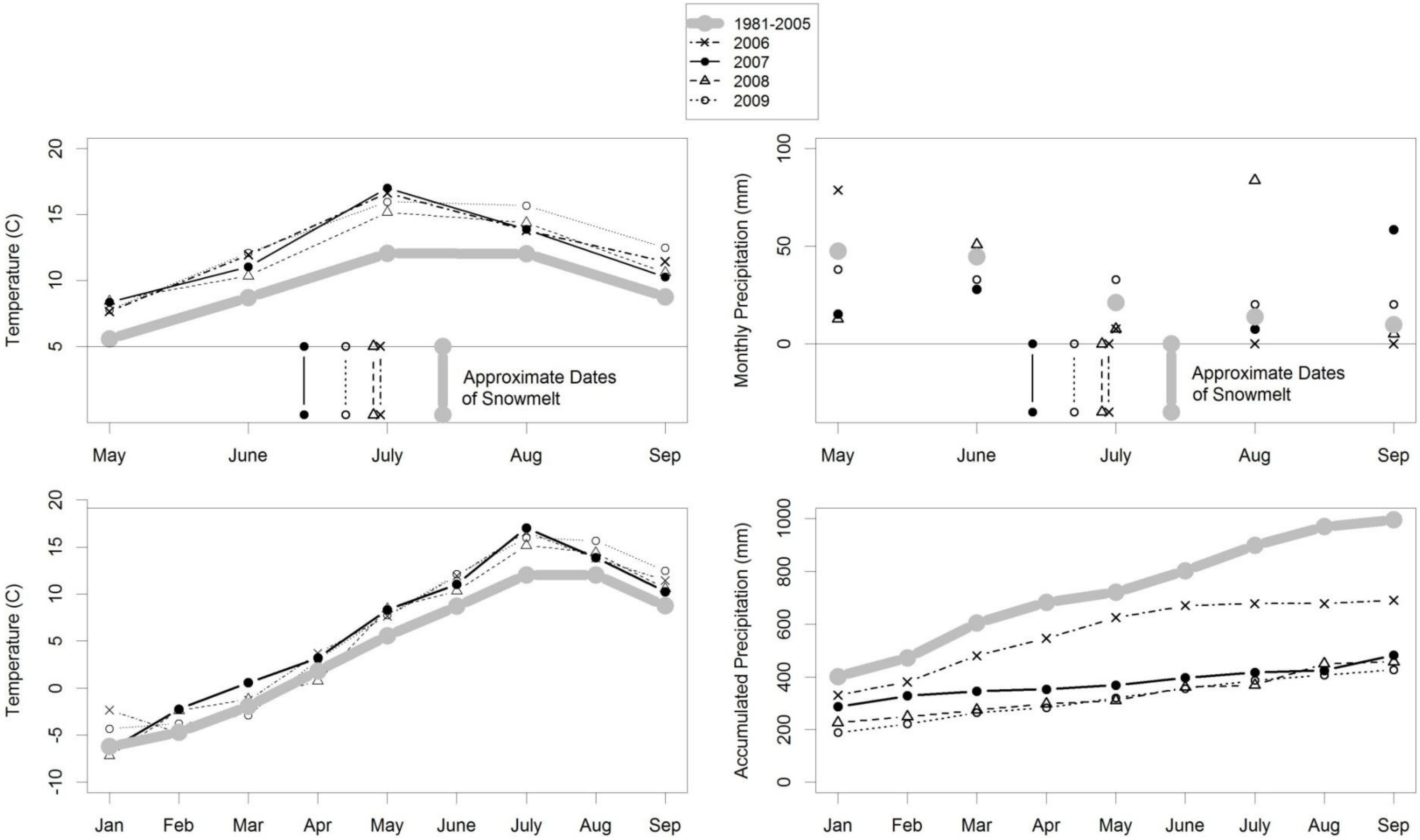


Figure 4.9. Air temperature and precipitation data from Salmon Meadows (Snotel site 728, 48° 39‘ 119° 50’W, elevation 1359m). Data in the top row include only May – September for more resolution in comparing the years of the experiment, whereas the bottom row contains January – September for better historical context.

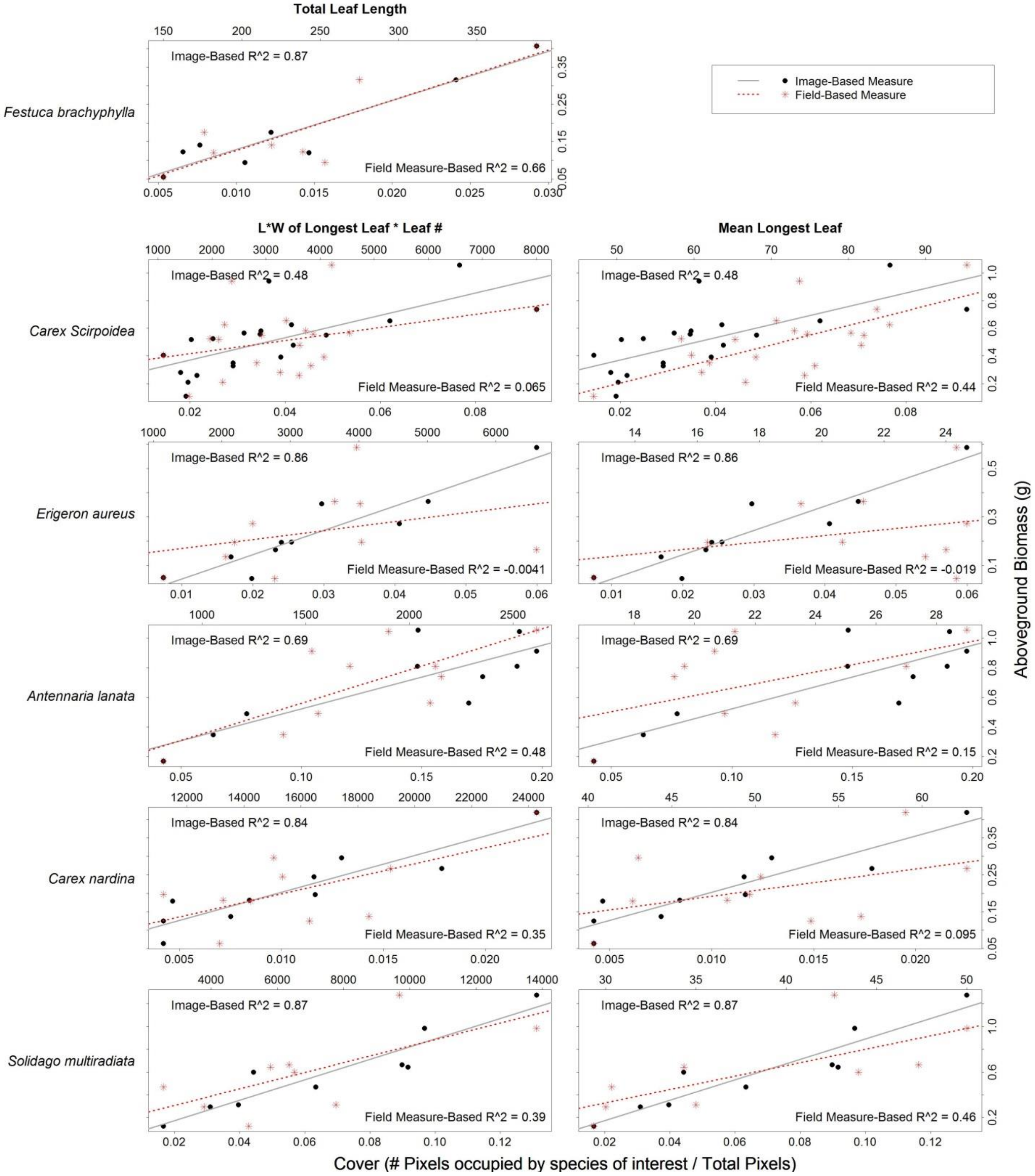


Section 4.7. Appendices

Appendix 4.1. Parameter settings used in the nearest-neighbor image classification procedure.

			Segmentation Parameters				Classification
Site	Community	Plant Species Classified	Weights	Scale	Shape	Compactness	# Classes
Navarino	All	*F. contracta*	2,2,1	25	0.2	0.2	11
Snowshoe	Moss Snowbed	*Carex spp. , E. aureus*	2,2,1	20	0.2	0.2	9
	Dry Sedge Meadow	*Carex spp. , E. aureus*	2,2,1	20	0.2	0.2	9
	Crustose Lichen Snowbank	*C. nardina., A. lanata*	2,2,1	20	0.5	0.1	13
	Fruticose Lichen Meadow	*Carex spp., S. multiradiata*	2,2,1	40	0.2	0.2	13
	Fellfield	*F. brachyphylla*	2,2,1	30	0.1	0.5	8

Appendix 4.2. Linear regressions of allometric data, comparing traditional field measurements to image analysis. On the y –axis is aboveground live biomass (oven-dried), and the bottom x-axis is image-based cover. The secondary (top) x-axis are the units for the field measure.



Appendix 4.3. Field seed germination experiment

From 2007-2009, I performed a seed germination experiment on Snowshoe Mountain. Although no seedlings were observed, here I detail the methods used. In 2007 and 2008, I collected seeds from seven plant species on Snowshoe Mountain (beginning in September). Seeds were prepared and counted in the lab. For the carex species this involved brushing the spikes against a soil sieve (≈3mm mesh) to remove the perigynia from the spike. Most of the perigynia were separated from the achene in this fashion, however those remaining were removed by simply rubbing between two palms, leaving only the achene. Composite seeds were removed from the flower head by brushing the flowers against a soil sieve and collecting the fallen seeds. For all species, filled seeds were combined and homogenized by species.

In the field we used the surfaces of the "sandboxes" detailed in Chapter 3 for our germination substrates. Briefly, these were thirty PVC rings (25 cm diameter X 8.5 cm tall) arrayed randomly in a relatively flat barren area on the Snowshoe Mountain ridgeline (approximately 20 m^2). Each ring had porous landscape fabric fastened across the bottom. Each sandbox was filled to 6 cm depth with pure sand (≈ 3 liters) and randomly assigned one of the following four surface treatments (Figure 1) to each: P. piliferum, F. cucullata - C. islandica, L. neglecta, or control (bare sand). For the cryptogam treatments, the entire sand surface of the sandbox was covered with the cryptogam assigned.

Using a cardboard frame, each sandbox was divided into eight equally-sized wedges. Thirty filled seeds of each species were sown into one randomly assigned wedge per sandbox. In 2007 seeds were not sown until mid-October, by which time snow had already begun to accumulate on-site. About five centimeters of snow was scraped from the tops of the sandboxes, and seeds were sown into a thin (≈1cm thick) layer of snow and covered with some fresh snow to prevent seed loss in the wind. In 2008 seeds were sown directly onto the surface of the sandbox, either cryptogam or bare sand.

In both 2008 and 2009, no seedlings were visible in any of the sandboxes, nor were any seeds visible (although this was not inspected particularly closely). Unfortunately, without knowledge of the seed fates, I have no evidence to support a hypothesis to explain why no seeds germinated and survived to seedling stage in the sandboxes. Either the or seeds did not germinate, or seeds were removed from the sandboxes. I believe these are equally likely to have occurred. Poor germination on any of these surfaces could have been due to poor soil moisture. This particular area holds very little snow in winter, being flat, at the crest of the ridge, and nearly devoid of vegetation—the combination of these characteristics and extremely porous substrate (sand) would not have promoted moisture retention. As to seed loss, seeds on bare soil and *L. neglecta* (the surface of which appears “smooth” relative to even bare soil) may have simply blown away during the winter. However, this offers little explanation for the lack of seedlings in the the *F. cucullata—C. islandica* or *P. piliferum* sandboxes. It seems unlikely seeds would have blown away out of either of these surface types given their relative roughness.