PIKES PEAK FRECKLES: SPATIAL PATTERN FORMATION OF ALPINE TUNDRA ON PIKES PEAK, COLORADO

A THESIS

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Abstract:

Spatially-organized patches primarily composed of Alpine avens (*Geum rossii*) on Pikes Peak, CO give the tundra of the 14,000ft mountain a freckled appearance. The mechanisms causing formation and maintenance of these patches were examined using parameters such as vegetation height, species abundance, micro-topography, C:N ratios of soils and plants, and soil moisture. This study focused on eight patches by evaluating the above parameters along eight, horizontal 15-18 m transects that ran through the centers of the patches. Shockingly, vegetation height was two times greater within the patch compared to open tundra. This suggests nutrient accumulation within the patch parameters. In this thesis we analyze abiotic, top-down and bottom-up processes, to evaluate these patches. We conclude that this ecosystem is a bi-stable dynamical structure (Lotka-Volterra). In addition, scale-dependent feedback mechanisms (short-distance facilitation and long-distance inhibition) may be a primary contributor to patch formation and maintenance.

Key words: Alpine avens (Geum rossii), scale dependent feedback, bi-stable equilibria, Pikes Peak, CO, alpine tundra

Introduction:

The importance of endogenously-generated spatial pattern formation in ecology has become increasingly explored in the past few years (Rietkerk and Koppel, 2007). Up until this point, most of the theory in ecology has been a-spatial. By analyzing ecosystems within a spatially focused mindset, we have been able to discover new and fascinating ecological findings that often reverse the conclusions drawn from a-spatial investigations (Begon *et al.,* 1996). In the remotely sensed images of alpine tundra of

Pikes Peak, CO patches of darker vegetation suggest spatial self-organization. These patches dot the alpine tundra giving Pikes Peak a freckled appearance. By investigating the tundra patches within a spatial framework we have been able to hypothesize possible mechanisms contributing to patch formation and maintenance. These include bi-stable dynamical structure as explained through Lotka-Volterra competition dynamics and scale dependent feedback mechanisms.

Evidence of patches on Pikes Peak can be traced back to 1938 via aerial photographs of the alpine tundra. When geo-referenced, these photographs show that the tundra patches have become slightly more numerous but overall have stayed in the same size and location for ~75 years (preliminary personal observation). Given the long lifespan of tundra plants, this patterning is likely to be the result of centuries of slow-moving, spatial self-organization. These patches are primarily composed of Alpine avens (*Geum rossii*) and seem to be localized in moist alpine meadows. The presences of Alpine avens in moist alpine meadows has been studied thoroughly at the Niwot Ridge Long Term Ecological Research Station in Boulder, CO (Komárková and Webber, 1978), however studies investigating the self-organization of this species and the processes that create and sustain its organization have not previously been conducted. Therefore, the focus of my thesis was to explore the possible mechanisms via abiotic variables such as micro-topography, vegetation height, species abundance, soil moisture, and soil and plant C:N ratios. Using these variables, I provide hypotheses for patch formation and maintenance under the framework of bi-stable equilibria and scale-dependent feedback.

Spatial self-organization is the process in which large-scale patterns are generated from disordered initial conditions through local interactions (Rietkerk and Koppel, 2007).

One possible mechanism to describe the formation and maintenance of the regular pattern formation on Pikes Peak is scale-dependent feedback. Scale-dependent feedback relies on two mechanisms that operate at different spatial scales: short-distance facilitation and long-distance inhibition. When these feedbacks affect an ecosystem simultaneously, they have the capacity to create regular patterns in ecosystems (Rietkerk and Koppel, 2007). Short-distance facilitation occurs when an organism creates beneficial conditions for establishment, growth, or reproduction of its own species by increasing resources, decreasing environmental stress, or eliminating competitors. These positive local interactions create groups, or patches, that further modify the environment for their benefit. For example, in arid ecosystems patches of higher vegetation density facilitates water infiltration into the soil, therefore increasing their resources and limiting drought stress within the patch (Rietkerk and Koppel, 2007).

Long-distance inhibitions can occur as a result of short-distance facilitation. For example, isolated patches of trees in savanna grassland have positive effects because their closeness results in nutrient accumulation within the patch (short-distance facilitation). However, the nutrient accumulation within the patch is a result of nutrient transfer from the surrounding grassland into the patch (Rietkerk and Koppel, 2007). This creates a nutrient deficit outside the patch, therefore inhibiting growth of conspecifics in the grassland. This depression of nutrient availability outside of the patch is an example of long-distance inhibition. By living together, the trees decrease nutrient stress (short-distance facilitation), but are simultaneously limited from expanding their patch because of nutrient deficit in the grassland (long-distance inhibition). These patches are spaced far enough away that the long-distance inhibition from one patch no longer affects the

nutrients in the soil. In this way, regular pattern formation via scale-dependent feedback can emerge from simultaneous short-range facilitation via modification of the organisms' environment and long-range competition for resources (Rietkerk and Koppel, 2007).

Long-distance inhibition determines the regularity of the pattern by restraining the patches from expanding outwards. This affect decreases with increasing distance from the patch. Therefore, new patches are more likely to form at longer distances from existing patches. The distance of inhibition-effect therefor determines the spatial distance and regularity of the pattern.

Short-distance positive feedback is known to be responsible for the sharpness of the patterns (Rietkerk and Koppel, 2007). Because the Alpine avens patches encountered on Pikes Peak have sharply defined parameters and a regular lattice-like orientation, it is likely that both short-distance positive feedback and long-distance negative feedback mechanisms play a large role in the development and maintenance of the regular pattern formation exhibited here. In fact, Bertness and Callaway hypothesize that facilitation may be a more important structuring force than competition in environments where levels of physical stress is high such as the alpine tundra (1994).

In order to understand the mechanisms that are potentially responsible for short-distance facilitation and long-distance inhibition, we need to understand the factors that control the tundra ecosystem. Physical factors, such as wind, snow cover, length of the growing season, and temperature, help to shape a tundra community in tandem with biological factors such as bottom-up plant-resource interactions and top-down grazing by alpine animals. Soil moisture, in combination with timing of snowmelt, greatly influences the species composition and nutrient availability in tundra ecosystems (Fisk *et al.*, 1998).

With high soil moisture, nutrient availability is high and these together promote the formation of a moist tundra meadow (Komárková and Webber, 1978; May, 1976). The Alpine avens patches examined in this thesis were located in the moist meadows ecosystem.

Early snowmelt in the moist meadow extends the length of the growing season, which ranges from 100-150 days compared to tundra with heavy snow cover which can have 50 day growing seasons (Komárková and Webber, 1978; Bowman and Seastedt, 2001). Nutrient uptake, shoot growth, and flowering may commence under snow before melt in many of the plants found at our field site such as Alpine avens, *Bistorta bistotoides*, and Marsh Marigold (*Caltha leptosepala*) because their leaf primordia and flower buds are preformed during prior growing seasons (Bowman and Seastedt, 2001).

Temperatures in moist meadows were typically temperate. In the winter, snow cover provides the tundra with insulation, keeping the snow bed community relatively warm at -1°C compared to the open-air temperature of -15°C or below. In moist meadows, temperatures are typically intermediate during both the winter and early summer. Below ground temperatures are a few degrees warmer than the air temperature during the winter and few degrees cooler in the summer (May and Webber, 1982). The moderate temperature allows for plants like Alpine avens to flourish as it consistently flowers only after the soil temperature at 3cm deep exceeds 10ºC, regardless of aboveground temperatures (Holway and Ward, 1965).

These abiotic factors also have a large impact on the species composition. Interactions between the topography and snow cover contributes to microclimates and the distribution of vegetation (Bowman and Seastedt, 2001). Moist meadows are known to be

primarily composed of fobs, such as Alpine avens. Because of the abiotic factors listed above, moist meadows tend to be particularly productive tundra ecosystems (Billings and Bliss, 1959; Stanton *et al.,* 1994).

In addition to abiotic conditions, biological interactions also strongly influence the alpine tundra community. Bottom-up resource-plant interactions control a large part of the alpine tundra. Plants manipulate soil nutrient cycling in order to maintain a low nutrient supply, which limits competitive exclusion (Tilman, 1988). Specifically, Alpine avens has been known to manipulate the N mineralization rate in alpine tundra ecosystems. Because Alpine avens is N insensitive (Bowman and Seastedt, 2011) and manipulates the soil nutrients in this manner, this could contribute to the dynamics controlling the patch formation and maintenance.

Top-down processes also contribute to the tundra community via direct feeding by alpine animals, such as birds, pika, marmots, insects, and gophers. Alpine avens has been known to compromise 60-77% of the North American Pika (*Ochotona princeps*) (Bowman and Seastedt, 2001) and 7% of the elk diet (*Cersus elaphus*) (Baker and Hobbs, 1982). There was a strong presence of the Northern Pocket Gopher (*Thomomys talpoides*) at our field site. While the diet of the gopher is not fully understood (Bowman and Seastedt, 2001), the prevalence of these animals in and around the patches (Hebert, 2014) makes us believe that gopher induced top-down processes may be contributing to the patch effect exhibited on Pikes Peak.

We focus on determining how these parameters are driving – or are a result of – short-distance facilitation and long-distance inhibition. Given the appropriate spatial scale, these factors can form these self-organized spatial patterns on Pikes Peak. Abiotic,

top-down and bottom-up processes can be capable of this scale-depend feedback. In this paper we aim to carefully describe differences in the physical, chemical, and vegetation parameters within the patches and in the open tundra in order to evaluate whether these parameters contribute to the patch formation and maintenance. In particular, we hypothesize that the patches in the open tundra form a bi-stable dynamical structure. We further hypothesize that this structure is driven by facilitation among the patch community and by competition for nutrient and resources such as light and nitrogen (N). Finally, we hypothesize that long-distance inhibition via herbivory on patch species by the Northern Pocket Gopher creates the regularity of the spatial distribution of the patches.

Methods:

Site Description:

The site for this experiment is located on the western-facing side of Pikes Peak in Pikes Peak National Forest, Colorado Springs, CO. The coordinates for the site are 38° 51'02.19" N 105° 05' 26.07" W. The elevation of the field site is 3,796 m.

The site was a moist tundra meadow (Komárková and Webber, 1978) on a shallow sloping, western-facing hillside which bordered a small unnamed, spring-fed creek. Approximately 25 patches dominated by Alpine avens spotted the hillside. For our experiment eight of these patches were examined within a smaller research plot identified by the polygon in Diagram 1 of approximately 14,000 m^2.

Transect Assembly:

First, each patch was measured in diameter. We then tripled the diameter to get distance of the transect. Seven of eight patches were approximately five meters in diameter, therefore all except one patch (Transect 7) was 15 meters in length. Transect 7 was 18 meters in length for the diameter of the patch was six meters. The transect was then laid perpendicular to the slope through the center of the patch with 5 m in the open tundra, 5 m within the mat, and 5 m again the open tundra (Diagram 2).

Micro-topography Field and Lab Methods:

Next we collected data on micro-topography at every 10 cm along each transect. We assembled and leveled an optical level base station (Bosch GOL Professional, 26 D) downhill from the center of the patch. Using a leveled meter stick, we used the optical level to read the height on the meter stick as we moved along the transect.

The data collected from the field yielded a picture that was "upside-down" and sloped because we measured the distance downwards from an imaginary horizontal plane. To flip them "right-side-up," each data point was subtracted from the elevation of the imaginary horizontal plane above the lowest point of each transect.

In the field we worked hard to make each transect as horizontal as possible by placing it perpendicularly to the slope of the hill, however some transects still had a slight slope to the left or right when graphed. To correct for such sloping in the data, a linear line was fit to each transect. We then used this equation to create a series of points that represent this line. We called this "Line of Best Fit data" and it was calculated by multiplying the slope of the linear line times the distance along the transect and added to the y-intercept. Essentially, this data is just the line of best fit in data points. Then we calculated the difference between the line of best fit data and the collected micro-topography and called it the "residual." We multiplied the residual by the cosign of the arctangent of the slope to rotate the data horizontally. Then we subtracted the horizontal height at zero meters from the heights along the transect. This was our final rotated data.

Vegetation Height and Species Abundance Field and Lab Methods:

All species within a two-centimeter radius neighborhood were identified and measured for vegetation height at every 10 cm along each transect. The vegetation height for any particular specimen was defined as the distance from the base of the stem to the tip of the highest leaves (n=150 per transect). If no species was found inside the 2 cm neighborhood, the area was classified as "bare ground" or "disturbed-bare ground." A disturbed-bare ground classification indicated that gopher activity had recently buried the tundra vegetation under a gopher mound, or earth pushed by gophers from its tunnels to

the surface. Bare ground either indicated that this neighborhood was within the parameters of an older disturbed-bare ground site or that this neighborhood was a small patch of vegetation-free ground.

The data was then used to develop the species abundance both in and outside of the mat. Species abundance can be interpreted as the frequency that one would encounter the species in that environment. More specifically, in my data the percent abundance refers to the proportion of the two-centimeter neighborhoods that contain the given species.

Soil Collection Field Methods:

At every meter along each transect, ~20 grams of soil was collected for soil moisture and soil C:N analyses. First, aboveground organic matter was removed. Then using a standard soil core, the soil was removed and placed into small plastic bags. The bags were kept cool inside a portable cooler with multiple icepacks until the soil could be frozen and stored.

Soil Moisture Lab Methods:

To analyze soil moisture, the soil collected earlier was thawed and sieved through a 3 mm sieve. The weight of the soil was recorded before and after drying for at least 24 hours in a drying oven at ~60°C.

Soil C:N Lab Methods:

The soil dried for soil moisture analysis was then repurposed for soil C:N analysis. The dried soil was ground to a fine powder using a mortar and pestle before being processed for percent carbon and nitrogen by high temperature combustion, the resulting gases of which were eluted on a gas chromatography column, detected by

thermal conductivity, and integrated to yield carbon and nitrogen content. The analyses were performed on a Thermo Quest CE Instruments NC2100 Soil.

Plant C:N Lab Methods:

Random individuals of Alpine avens were collected from in and out of the patch parameters. They were then brought to the lab where they were rinsed to remove excess dirt and dried for at least 36 hours at ~60°C. The above-ground and below-ground vegetation were separated and labeled. The root was then prepared for C:N analysis: First, the root's outer epidermis was delicately shaved off to remove any remaining non-plant material. Then we removed the top 10 mm of root. The next 10 mm of root was then cut off and ground to a fine powder using a mortar and pestle and was used for plant C:N analysis.

This ground plant material was then processed for percent carbon and nitrogen by high temperature combustion, the resulting gases of which were eluted on a gas chromatography column, detected by thermal conductivity, and integrated to yield carbon and nitrogen content. The analyses were performed on a Thermo Quest CE Instruments NC2100 Soil.

Results:

Vegetation Height:

Perhaps the most obvious visual difference of these tundra patches is the change in vegetation height. This difference allowed the observer to identify a visible line (down to centimeters) between patch area and open-tundra. Vegetation height for all species was recorded every 10 cm along the transect within a two centimeter radius. On average, the vegetation height inside of the patch was almost two times larger. Average patch height was 8.21 cm and average open-tundra height was 4.24 cm (Figure 1) ($t = -15.78$; $df = 556.499$; $p < 0.0005$). Figure 1a -1h illustrate cross-sectional views of vegetation height along each transect. Areas with 0 cm of vegetation height were areas with no vegetation. The vegetation height along each transect comes to a peak close to the start and end lines representing the patch parameters. This demonstrates nicely how the patch parameters can easily be defined by vegetation height.

Species Abundance and Diversity:

Relative abundance was used to describe the species composition of the mats. Relative abundance in this study can be interpreted as how frequent one would encounter that species in or outside of the patch and are therefore described using percentages. All species were identified within a two-centimeter radius at every ten centimeters along each transect. This yielded a large sample of 1,237 data points for all eight transects. We encountered 24 species (Table 1) on Pikes Peak, 18 of which were commonly found along the transects. These 18 species are listed on Tables 2a and 2b in order of most abundance in and out of the patch.

By examining relative abundance we were able to identify where it would be most likely to encounter a species: in or outside of the patch. Tables 2a and 2b list the relative abundances inside and outside of the mat.

Alpine avens was the most abundant inside of the patch at 66.17%. A common alpine forb, *Bistorta bistortoides,* was the second most abundant at 26.87% and Grass Type 1 was third most abundant at 11.19% (Table 2b). The top three most abundant species in the open tundra were Grass Type 1 at 35.53%, Alpine avens at 25.24% and *Phacelia sericea* at 17.70% (Table 2a). Alpine avens, although dominant inside the patch was still present in the open tundra but played a subdominant role in terms of species composition. Similarly, Grass Type 1 was dominant in open tundra but was present as a subdominant species in the patch. Additionally, the most abundant species n open tundra was only encountered in 35% of the neighborhoods while Alpine avens was encountered in 66% of the neighborhoods. This indicates that the diversity of the open tundra is greater than that of the patch.

After running multiple t-tests on these data, we were able to deduce where a species preferred to live: inside the patch or outside in the open tundra (Table 3). We corrected this t-test using Bonferoni correction for multiple comparisons. We labeled species that showed a strong correlation (significant t-test after Bonferoni correction) towards living inside of the patch as "patch-dominant species;" those species that showed strong correlation (significant t-test after Bonferoni correction) towards living outside the patch in the open tundra were labeled as "open-tundra-dominant species." Species labeled "impartial species" were those found to have no significant difference in their abundance between the patches and the open tundra. The species that were to have significant

differences using a t-test but insignificant differences after a Bonferoni correction, were labeled "almost patch-dominant species" or "almost open-tundra-dominant species" depending on if they were more abundant in the tundra or in the patches. Therefore, we have established a gradient of where the species encountered on this experiment can be most likely found.

To further examine the diversity of the two ecosystems, we created rank-abundance curves (Figure R-A). Patch communities had high initial slopes, steep initial slopes and steeply sloping midsections. Open tundra communities had low initial slopes, shallow-sloping initial slopes, and long, shallow-sloping midsections.

Micro-topography:

In general, micro-topography showed that each patch rests on top of a small hill. Figures 3A-3H, give cross-sectional views of the micro-topography along each transect. The start and end of the patch parameters are marked. Micro-topography did not abruptly change at the patch parameters but instead gradually increased to a peak in the middle of the patch and then declined on the other side, creating a small hill. The size of these small hills varied from five to 20 centimeters in height over 15 meters. Transects 1-3 rose to a peak height of approximately 20-25 cm while transects 2, 5, 6, 7, and 8 only had peak heights of ~5cm (Figures 3A-3H).

While these changes are quite small, especially over 15m of distance, the difference between micro-topography inside and outside of the patch was statistically significant ($t = 14.256$; $df = 693.156$; $p < 0.0005$). On average micro-topography (cm) inside the patch was 8.05 cm and the micro-topography outside of the patch was found to

be 2.91 cm. (Figure 3). Therefore, the micro-topography inside the patch was found to be ~2.75 times that found outside the patch.

Soil Moisture:

Soil moisture was measured at every meter along each transect. Soil inside of the mat was found to be on average 0.0375 ml/g soil drier than soil outside the mat when using a paired t-test for all 8 transects (t = -4.160; df = 7; p = 0.004) (Figure 4). However, when a standard t-test evaluated the soil moisture for each transect individually, soil moisture in the mat was found to be significantly drier in only 2 of 8 transects. There was no significant difference in soil moisture between in and outside of the mat in the remaining six transects. Of these six transects, three showed that the mean moisture content was drier inside the mat; two transects had mean moisture content exactly the same inside and outside of the mat; only one transect had mean moisture content greater within the mat than outside of the mat. Overall, the soil appeared to be slightly drier within the mat but this result was quite variable.

Soil and Plant Carbon-to-Nitrogen Ratios:

Soil samples taken at every meter along each transect were used to collect data on the carbon-to-nitrogen (C:N) ratios. C:N ratios were found to be higher in soils outside of the mat compared to soils within (t=-3.040; df = 4; p =0.038) (Figure 5). The mean soil C:N ratio for soils within the mat was 13.3040 while C:N ratios outside the mat averaged at 13.8760. Although this difference is small the difference in data is still consistent enough to make the data significantly different inside and outside of the mat.

Plant C:N ratios were quite high for tundra vegetation averaging at 45.64 in the mat and 46.56 outside of the mat (Figure 6). Unlike soil C:N ratios, there was no

significant difference between plant C:N ratios in and outside of the mat (t = -0.159; df = 2; p = 0.888).

Bare Ground and Disturbed Bare Ground:

There was no significant difference in the abundance of neighborhoods classified as bare ground in and out of the patch (t = -0.502; df = 1236; p = 0.616) (Figure 7). Inside the patch, bare ground neighborhoods were encountered 21% of the time and encountered outside of the patch 22% of the time. Similarly, there was no significant difference in the abundance of neighborhoods in and outside of the patch classified as disturbed bare ground (t = -0.588; df = 1236; p = 0.556) (Figure 8). Disturbed bare ground was found 18% of the time inside of the patch and 19% of the time outside of the patch.

Discussion:

The major question of this paper was, "which processes and mechanisms contribute to the formation and maintenance of the avens patches?" Patchiness is typically associated with a system structure that contains multiple equilibria, and therefore in this discussion we will first address whether our system can be thought of as a bi-stable dynamical structure. We will accomplish this by first comparing species abundance and individual height within the patch in in the open tundra. Second by addressing abiotic variables associated with the patchiness. The theory of spatial self-organization also postulates that patterns form by a combination of short-distance facilitation and long-distance inhibition. We will proceed to examine our data to see if we can see signatures of these mechanisms in them.

The patches were primarily composed of Alpine avens while Grass Type 1 dominated the open tundra. The density of Alpine avens in the patch (~66% abundance) was about ~2.6 times greater than Alpine avens living in the surrounding tundra (~25% abundance). Grasses dominated the open tundra (~36% abundance) but were subdominant in the patch (11% abundance). The height and therefore the biomass of patch vegetation were significantly greater in the patch compared to the outside tundra. Vegetation in the patch was two times the height of vegetation in open tundra. This change in vegetation height could easily create a four-fold increase in biomass, although we did not measure this parameter directly. In addition the height and thus biomass of the Grass Type 1 was taller in the outside tundra compared to grass of the same species found inside the patch.

Therefore individuals of each of the two key species were doing better (had greater height and biomass), in the environment where they were most abundant. This relationship between individual performance and population size is congruent with the bi-stable outcome of Lotka-Volterra competition dynamics --- also know as the saddle point. In the classical Lotka-Volterra competition theory, competition between two species can lead to two alternative stable states described by carrying capacities of the two species. The system also includes an unstable equilibrium (the saddle point, Diagram 3),which lies on a threshold line called the separatrix. The separatrix separates the basins of attraction to the two alternate stable equilibria. In our case the two alternative stable states are patches of Alpine avens and open tundra. In the competition context the bi-stable system develops when the strength of the between species competition is greater than the strength of the inter-species competition (Begon *et al.,* 1996). In other words individuals of each species are more harmful to individuals of the other species than to their own kind. Congruent with the theory, Alpine avens growing within the patch is significantly taller and has greater biomass than Alpine avens growing in the open tundra and grass growing in the open tundra is taller than grass growing in the Alpine avens patch. This indicates that within species interactions are less harmful than between species interactions.

Even though the overall simplified dynamics of the system are congruent with the theory, there are two significant differences. First in our system each equilibrium is represented by a whole community type rather than by a monoculture of a single species as dictated by the theory. Second, positive interactions my also play a role in our system, which we will discuss later in the paper.

The Lotka-Volterra competition theory is a phenomenological theory built on the impact of each species onto the carrying capacity of its competitor. In real systems it is important to identify the mechanisms of such effects. Here we explore interactions via depletion of light and via manipulation of soil resources (N).

Open tundra species, such as grasses, sedges, lichens and cushion plants were less abundant and shorter in the patches compared to their height outside of the patches. Importantly, the open tundra species were also shorter than the patch species (e.g. Alpine avens, *Bistorta bistortoides*) growing within the patch. Because the vegetation is lush and very tall in the patch there does not appear to be much light available at the soil surface (personal observation). Therefore, open tundra species, which are shorter than patch species, may be out-competed for light. Comparatively there is a large amount of light that penetrates to soil surface while in open tundra and therefore light competition may not play a decisive role in the open tundra.

On the other hand, competition for nutrients may play an important role in the open tundra. This is consistent with the findings that competition for soil nutrients is very important in moist meadows (Bertness and Callaway, 1994). From the mechanistic perspective, one way to maintain the bi-stability of the system is by structuring the competition dynamics: the Alpine avens patches may be structured by competition for light and the open tundra by competition for soil resources.

What allows the switch from competition for soil resources to light? Light competition is possible only when plants are tall and large enough to block the light that reaches the sub-canopy and ground. The key therefore is to identify factors that sustain higher vegetation biomass and height. To sustain the higher vegetation biomass within

the parameters of the patch, there must be a greater nutrient pool within the patch. This suggests nutrient accumulation. The soil C:N ratios[1] revealed that soil in the patch was slightly more fertile than soil in the surrounding tundra. At first glance, one would think that perhaps this weak but significant difference could be contributing to the drastic change in vegetation height. However the accumulation of resources may not be within the soil pools but rather within the living biomass.

To look at possible nutrient accumulation within the living biomass of plants, we examined the C:N ratio of rhizomes of Alpine avens. However we found no significant difference between individuals growing inside and outside of the patch. This was surprising because the Alpine avens appeared to be greener and lusher inside of the patch, suggesting Alpine avens living inside the patch should have lower C:N ratios. However, perhaps plant C:N ratios for Alpine avens is not a plastic trait and therefore cannot manipulate its C:N ratio, or has reflected the C:N of the rhizome rather than the leaves. The patch may be much greener than the surrounding tundra because of the high-density of dark green Alpine avens (~66% abundant in patch) compared to the relatively low density of Alpine avens (~25%) in the lighter-colored open-tundra. However, the non-variant C:N ratio of Alpine avens inside and outside of the patch does not indicate that the patch is not accumulating nutrients within the plants. To address the accumulation of nutrients we must take into consideration the increased biomass of vegetation within the patch. The plant C:N ratio together with the biomass can be used to estimate the total plant-N pool. Because the patch has approximately four times the biomass but the same

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[1] Soil C:N ratios may be used as a proxy for the fertility of the soil. A low soil C:N ratio means that there is relatively little C to one N molecule; therefore, low C:N ratios describe more fertile soils. Conversely, high soil C:N ratios contain more carbon and are less fertile soils.

C:N ratio as outside of the patch, the total pool of N in the patch is four times greater than that outside of the patch. This increased pool of N within plants is an example of the nutrient accumulation of the patch.

The analysis of community structure using the rank-abundance curves is also congruent with the change in competition dynamics: as expected the light-limited patches have a simple and less diverse community (Figure R-A). Rank-abundance curves can be characterized by (1) the height of the y-intercept, the abundance of the most abundant species, (2) the initial slope, the fall of abundance from the first most abundant to the second and third most abundant species, and (3) the slope and length of the "mid section", the number of sub-dominant species and how their abundances decrease with rank. Simple communities, such as the boreal forests, tend to have high y-intercepts, steep initial slopes and short-steeply sloping mid sections. In other words, the most abundant species is very abundant, the second most abundant species is much less abundant than the first one, and there are few sub-dominant species. In contrast, more diverse communities, like the tropical rainforests, are characterized by low y-intercepts, shallow-sloping initial slopes and long, shallow-sloping mid sections. In these communities, the most abundant species is not highly abundant and not very different in abundance compared to the second and third most abundant species. Additionally, there are many subdominant species, which are relatively abundant. The rank abundance curves for the patch shows traits of a simple community, with high y-intercepts, steep initial slopes and short, steeply sloping midsections. In contrast, the open tundra shows a more complex and diverse community; open tundra rank abundance curves have low y-intercepts, shallow-sloping initial slopes and long, shallow-sloping midsections.

This change from more diverse to a more simple community is consistent with a switch from nutrient-limited competition to light-limited competition. By fertilizing or accumulating nutrients within a community, the competition for nutrients is decreased, and therefore plants compete only for light. This has the potential to drastically alter species composition and decrease diversity, as a decrease in limiting resources has been known to decrease species diversity within a community (Tilman, 1982; Interlandi and Kilham, 2001). In a study that exposed experimental grassland to continuous fertilizer from 1856 to 1949, diversity of the patch drastically decreased because community structure from competition for multiple soil nutrients to only competition for light (Tokeshi, 1993). Similarly, in our study, the diversity of plants in the open tundra was greater than that of the patch. Because the diversity is greater outside the patch, there must be fewer limiting resources within the patch (i.e. the patch is accumulating nutrients). The dynamics within the patch are likely to be driven by single resource interactions; this resource is likely to be N, as N has been found to be one of the most strongly limiting elements in tundra ecosystems (Shaver *et al.*, 1986). Alternatively, the Alpine avens are likely to be shading out tundra in the sub-canopy and soil surface.

So-far it appears that the patch is able the accumulate nutrients within the living biomass of Alpine avens, which leads to decreasing light availability in the sub canopy and soil surface creating competition for light. The areas that are able to accumulate nutrients become one stable equilibrium (the patch comprised of the Alpine avens and associated species) where as the areas that do not accumulate nutrients stay at the other equilibrium (open tundra) within the bi-stable system. Several observations of the soil nutrient dynamics complicate this simple picture.

The nutrient/resource accumulation theory would imply that soil moisture would be higher within the patch. However, soil in the patch was found to be drier than soil in the surrounding open tundra. Three things could explain this difference: First, because of the greater biomass in the patch, there may be more evapotranspiration, increasing the outward flow of water within the patch parameters and causing the decrease in soil moisture. The flow of water into the soil may be equal in and out of patch parameters, but the flow out of the patch via evapotranspiration may be greater than that of the surrounding tundra. Second, each patch rests on the crest of a small hill, revealed by the micro-topography through the patch. The hill may be shunting water away from the patch and into the open tundra. This effect is likely to be very small due to the tiny change in elevation of 5-25cm over 15m. Lastly, the soil under the patch could have better drainage. Lauren Hebert's study revealed that soil under the patch was primarily composed of gravel instead of the bedrock, which was found under the surrounding open tundra (Hebert, 2014). This may be a result of gopher burrowing and may decrease the soil moisture at the surface because of increased drainage in gravel versus Pikes Peak granite. This information muddles the simple picture established by the bi-stable equilibria theory. In this case, the open-tundra equilibrium is accumulating nutrients/resources in the form of soil water, which contradicts our original bi-stable equilibria theory.

Additionally, Alpine avens has been known to decrease the N mineralization rate by 10 fold compared to N mineralization rates of the open tundra (Steltzer and Bowman, 1998). Alpine avens leaf litter contains high quantities of phenolic compounds, which stimulate bacterial growth, immobilizing available soil N into the bodies of bacteria.

Because of the high density of Alpine avens in the patch, the supply of available N for tundra plants growing inside the patch parameters should be drastically decreased. However, the soil C:N ratios showed a slightly more fertile environment inside the patch parameters. This is because even though the N is unavailable for plant use the total N pool is increased because of the stimulation of bacterial growth. Additionally, the patch can accumulate N from atmospheric deposition and lateral soil transport because bacteria would be likely to immobilize N entering the patch. Nitrogen accumulation therefore is congruent with and confounds our bi-stable equilibria theory; on one hand, because N is immobilized in bodies of bacteria N is accumulating in the patch, however, on the other this N is unavailable to the vegetation and therefore it is hard to see how it could accumulate inside the living biomass of the plants in the patch.

It is likely that Alpine avens is able to thrive in the N-limited environment it creates because it is N insensitive (Steltzer and Bowman, 1998), which means it is able to grow and thrive on relatively low N concentrations of the available N pool in soil water. It is likely that Alpine avens is a superb N cycler, retaining the N within its body for long periods of time and allowing for its N insensitivity. Between its N insensitivity and its manipulation of N mineralization rates, Alpine avens has a competitive strategy to keep the N for itself. First, it decreases the available N in the soil by suppressing N mineralization and therefore increases N competition. Because the grasses found in the open tundra are N sensitive (Bowman and Seastedt, 2001) their growth is limited by the lack of available N in the patch. Second, it retains the N it has within its body for long periods of time. Then, once the Alpine avens are taller than the surrounding tundra the competition switches from nutrient-limited to light-limited. Plants inside the mat are now

competing for light due to the shading induced by the greater vegetation height of the patch. Therefore, Alpine avens are better competitors for both N and light resources. In addition, in order to start a mat, there must be a certain density of Alpine avens necessary to decrease the N availability in the soil enough to limit the growth of open tundra species and grow big enough to induce light competition. This critical density of Alpine avens corresponds to the threshold of the bi-stable Lotka-Volterra system.

Alpine avens' strategy is analogous to that of Engelmann spruce in the montane forests of Colorado. Engelmann spruce acidifies the soil, which affects the surrounding vegetation by indirectly changing nutrient availability in the soil (Krause, 1989). Simultaneously, spruce trees cycle N in their bodies by retaining N within non-senescing needles (CITE). In addition, because the Spruce decreases the N availability, it limits the growth of the surrounding vegetation, therefore preventing other plants from growing so tall as to become competitors for light. This has been known to lead to changes in species composition and abundance (Hallbäcken and Zhang, 1998) in stands of spruce.

Overall, Alpine avens seems to be facilitating its growth within in the patches in two ways: First, by living next to each other, the Alpine avens accumulate nutrients in their living biomass and become more competitive by decreasing the available N in the soil. Thus, few open-tundra species can survive in low N environments and are outcompeted within the patch parameters. Additionally, because of the enhanced height of the patch vegetation, the Alpine avens shades shorter open-tundra species. In this way, the patch switches from a nutrient-limited ecosystem to a light-limited ecosystem decreasing the diversity of the patch compared to the open tundra.

However, this poses some tension in our theory. What are the positive feedbacks that are facilitating the growth of the patch? Weak interspecific competition cannot be enough to facilitate patch formation and maintenance because if true, Alpine avens living with conspecifics in the open tundra would also be twice as tall. Patch retention of N might suggest facilitation, however, such retention should facilitate the growth of grasses and other open tundra species. Unless Alpine avens has a better way of accessing the N pool in the bacteria than grasses, perhaps through fungal associations, N retention in the patch cannot explain the full story behind patch formation.

How are Alpine avens within the patch preferentially helping conspecifics in a way that doesn't help (or perhaps hurts) growth of open tundra species like grasses? In truth, we don't yet know. The doubling in vegetation height clearly indicates some facilitation but the mechanisms contributing are still unknown. Nutrient accumulation could be either the cause or consequence of short-distance facilitation. In fact, in high stress ecosystems such as the high-alpine tundra, facilitation has been found to increase growth in alpine tundra more than competition for resources (Callaway *et al.*, 2002). The first step in determining whether facilitation plays an important role in structuring the patches would be to conduct a neighbor removal experiment in which all of the neighbors around a target individual would be removed in both open tundra and patch ecosystems. These would be compared to target individuals whose neighbors are left intact. If facilitation occurs, the Alpine avens inside of the patch whose neighbors were removed would be smaller because they lack the facilitation of their neighbors. Alpine avens outside of the patch whose neighbors were removed would be bigger because of decreased competition.

So far we have explored our system as a bi-stable dynamical structure and found significant but in-complete support for this view. The bi-stable Lotka-Volterra system does not explicitly take space into consideration. Therefore, in the following paragraphs we will focus on the spatial structure of this bi-stable system. Please recall from the introduction that spatial patterns form from a combination of short-distance facilitation and long-distance inhibition. Then how does our discussion so far fit into this framework? When the two equilibria are established, which processes snowball and force the community to go into one of these two categories? Can local interactions be enough?

We suggest that if the mat is started, the mat then feeds itself by short-distance local interactions. The verbal theory of Rietkerk and Koppel (2007) stipulates short-distance facilitation contributes to pattern formation, but is not necessary. On the contrary, mathematical theory makes it clear that positive feedbacks are necessary, and can come from variety of sources including facilitation and restructuring of competitive interactions (Edelstein-Keshet, 1988). Our discussion of whether the Alpine avens-tundra system falls into a bi-stable category focused on restructuring competition and potential facilitation, both of which could support the required positive feedback. The theory (both verbal and mathematical) specifies that the positive feedback has to operate on very small spatial scales. Well accepted theory of plant-plant interactions (both negative and positive) posits that these happen in neighborhoods where the canopies or roots are intermingled, thus the plant-plant interactions we discussed fall likely into "short-distance" effects. Theoretically these positive feedbacks should lead to unrestricted growth of the patches in which they operate. To stop this patch from expanding without limit, there must be some long-distance inhibition process to stop it. Next we examine the

processes that may be contributing to the long-distance inhibition with support from physical parameters examined in our experiment.

To control the expansion of the mat induced by short-distance facilitation, there must be a long-distance inhibition effect. One possible agent of long-distance inhibition is the herbivory associated with Northern Pocket Gophers. In a study conducted by Lauren Hebert on the same field site, gopher activity was localized in the patch but also "spilled" out of the patch around the edges within approximately 5 m of the patch (Hebert, 2014). In my thesis, we used the presence of bare ground and disturbed bare ground to indicate older and more recent gopher activity, respectively. We expected to find higher gopher activity within the mat, however it seems that gopher activity was equal in and within 5m around the mat. This is congruent with Herbert's findings. We believe that the gophers feed on patch species therefore inhibit the growth and expansion of the patch. This top-down predatory action restrains the expansion of the patch but does not completely eliminate the patch because the patch's facilitation effect is still greater than the inhibition effect.

Because the gopher activity decreases with distance from the patch, the strength of the long-distance inhibition also decreases. This should create regularity in the pattern, as new mats can form only in areas that are beyond the belt of the long-distance inhibition caused by the gophers. However, we could expect the pattern to be more regular if gophers weren't territorial (Bowman and Seastedt, 2001). Because some territories are larger, some smaller, the pattern is slightly less regular than a lattice formation (Hebert, 2014).

Gophers have been known to increase nutrient availability in tundra, particularly N (Liator *et al.,* 1996). If gopher activity is equal within 5 m of the patch parameters, and N mineralization is still stunted in the patch, the immediate outside of the patch would be a lush place for N sensitive plants to live. This may contribute to the sharpness of the patch parameters.

In summary, it is highly likely that the combined effect of short-distance facilitation via nutrient accumulation and long-distance inhibition via gopher predation on patch species contributes to the regular spatial formation of alpine tundra on Pikes Peak. However, many questions about the regular pattern formation still exist. How far does the long-distance inhibition extend away from the patch? How are patches organized given the territorial nature of gophers? And, most importantly, what are the specific short-distance facilitation mechanisms within the patch? This study has been observational; more studies to experimentally detect the influences of gophers, competition, and facilitation on the formation and maintenance of these patches need to be conducted.

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Appendix:

In this study, N mineralization lab and field methods were conducted. However, the results unable to be processed in time for the due date of this thesis paper. The following were the field and lab methods.

N Mineralization Field Methods:

For four of the eight transects, initial soil samples were collected from the field at every meter along each transect, kept cool, and frozen in the lab for later N mineralization analysis. Additional soil was sieved in the field to remove large rocks and organic debris and then placed in plastic bags to be buried *in situ*. These bags were picked up after at least 28 days *in situ* and frozen for later nitrogen mineralization analysis.

N Mineralization Lab Methods:

To analyze N mineralization, both initial and final soil samples were tested for ammonium, nitrite, and nitrate by using the following KCl extraction methods: First, ~5 grams of the soil sample was added to a small plastic cup with a screw-tight lid. Using a 50 ml graduated cylinder, 50 ml of 0.01M KCl solution was added to each sample cup. Then the cups were capped and shaken for two hours on a shaker table and stored in a refrigerator for at least 24 hours to settle.

After the soil-KCl solution had settled, the solution was filtered. First, the soil-KCl solution was passed through Whatman Qualitative 110 mm filters and collected into glass scint vials. Then the liquid was filtered again through a small 0.2 micrometer ion chromatograph acrodisc 13 Pall syringe filter into Thermo Scientific 5 ml Polyvials. The

solution was then analyzed for ammonium, nitrite, and nitrate in a Dionex Ion

Chromatograph System 5000. This system simultaneously detects anions and cations

through parallel duel column ion chromatography.
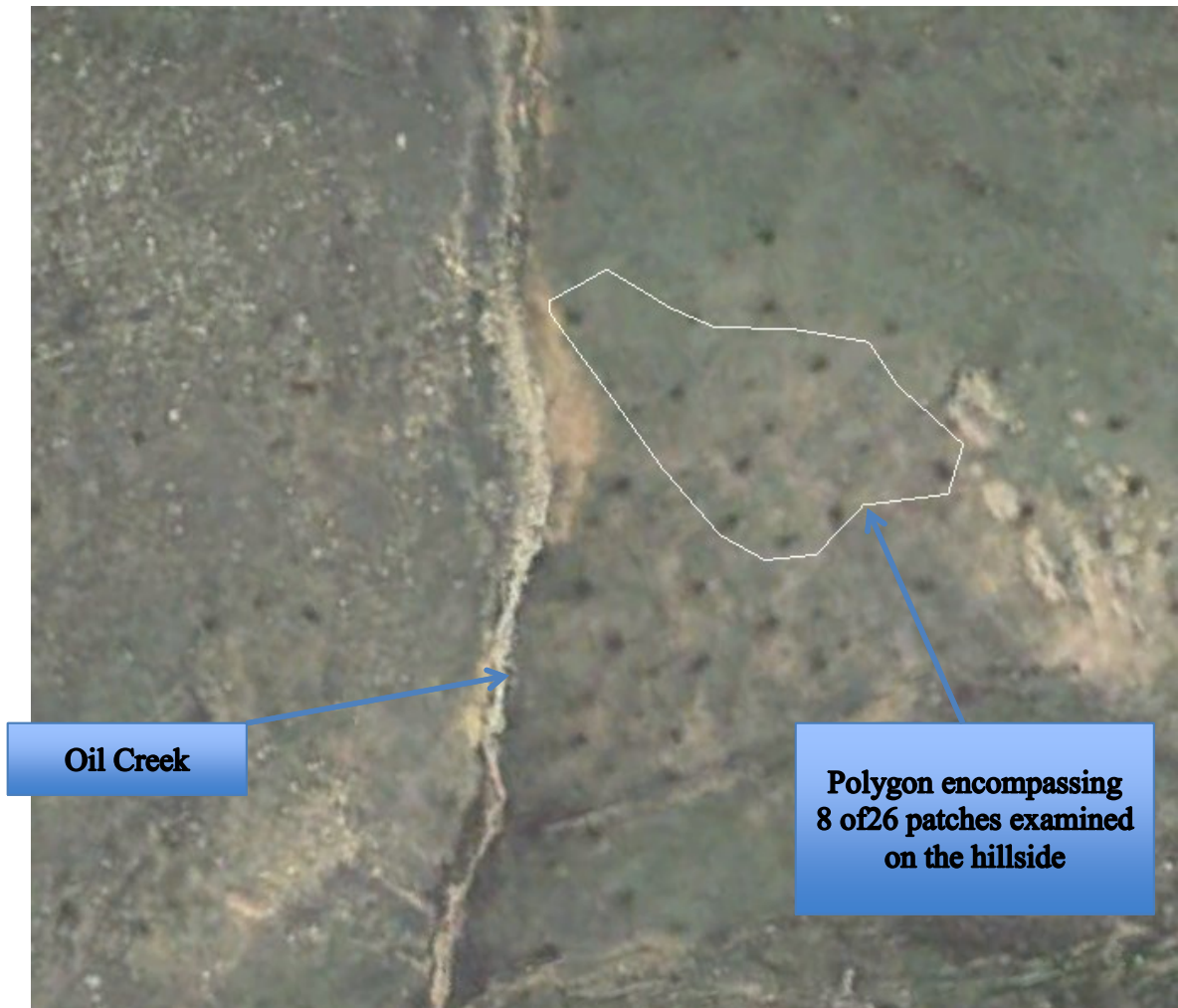
Diagram 1: Google Earth image of the field site directly east from the summit on Pikes Peak. Field site was situated on a western facing hill with approximately 26 patches. Eight of these patches were examined and are outlined in the polygon.
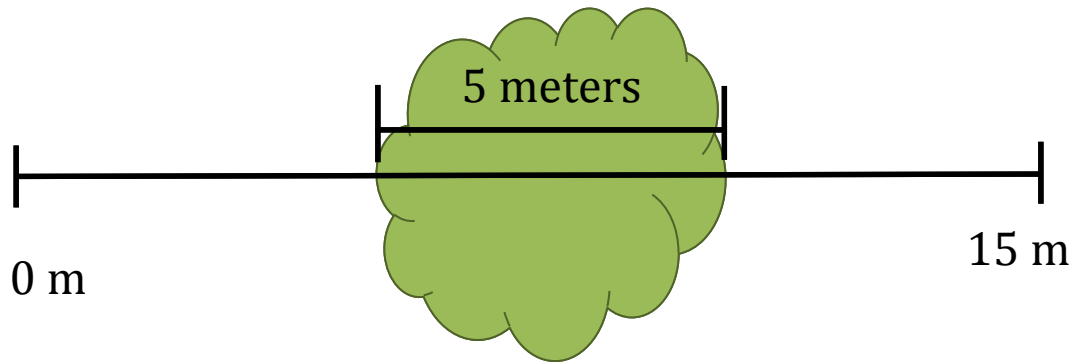
Diagram 2: Diagram of a 15m transect through a 5m patch. The transect crossed the 5m diameter of the patch and stretched into the open tundra for 5m on each side.
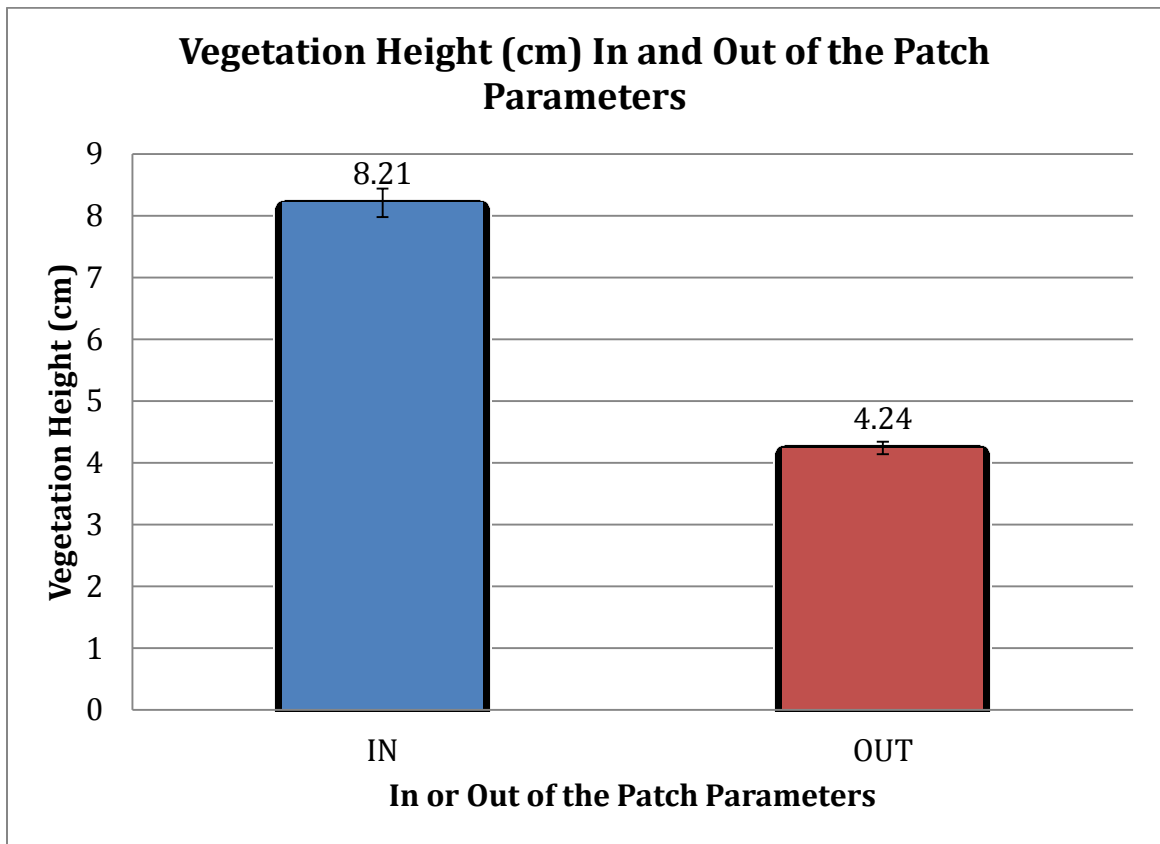
Figure 1: Vegetation Height In and Out of the Patch Parameters. Vegetation height was found to be almost two times greater inside the patch than outside.
(t = -15.78; df = 556.499; p < 0.0005).
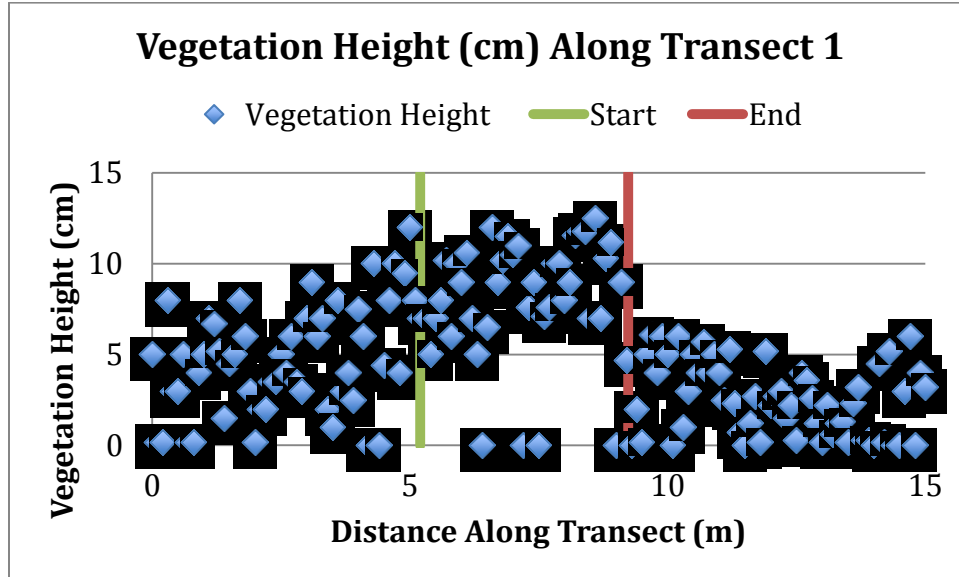
Figure 1a: Cross-sectional View of Vegetation Height (cm) along Transect 1. Green and red lines mark the start and end of the patch, respectively.
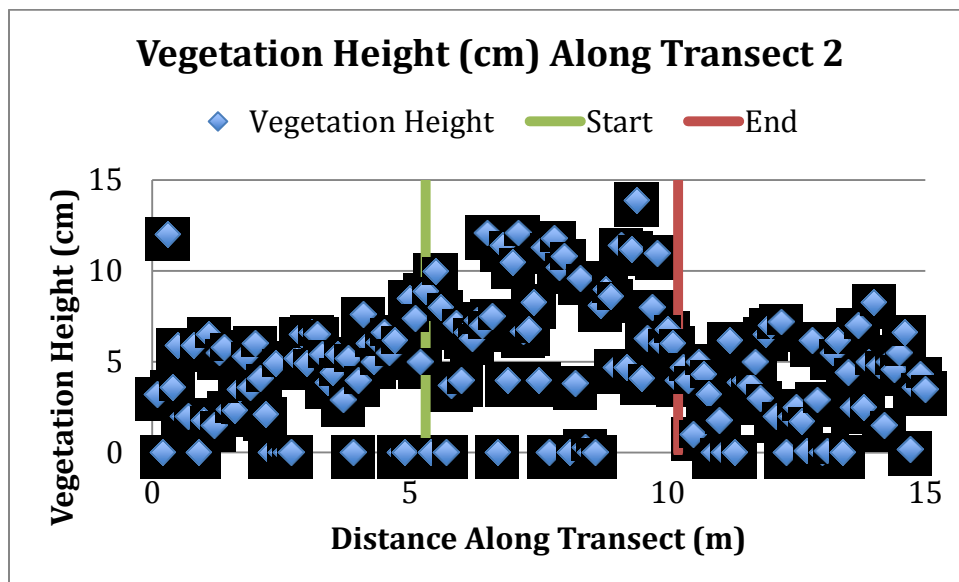
Figure 1b: Cross-sectional View of Vegetation Height (cm) along Transect 2. Green and red lines mark the start and end of the patch, respectively.
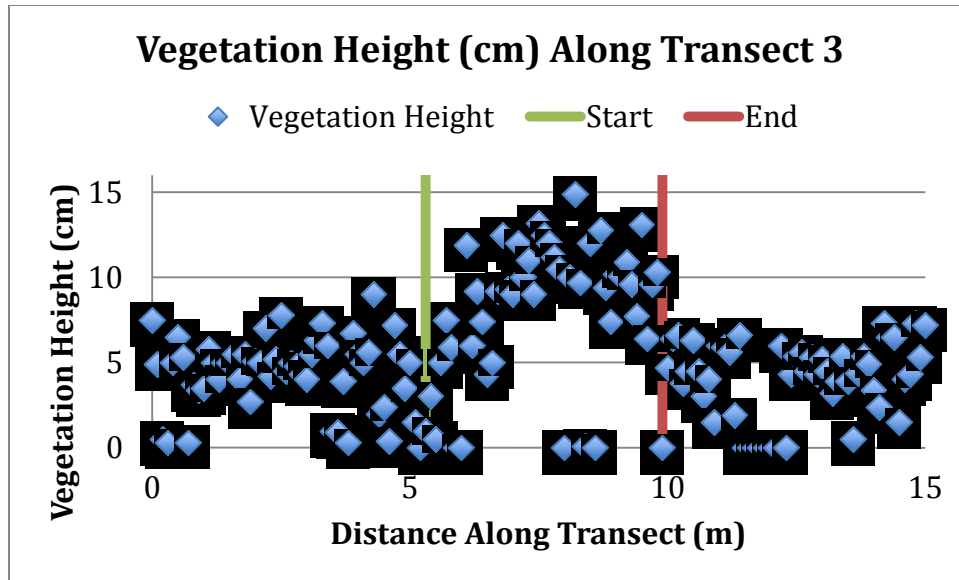
Figure 1c: Cross-sectional View of Vegetation Height (cm) along Transect 3. Green and red lines mark the start and end of the patch, respectively.
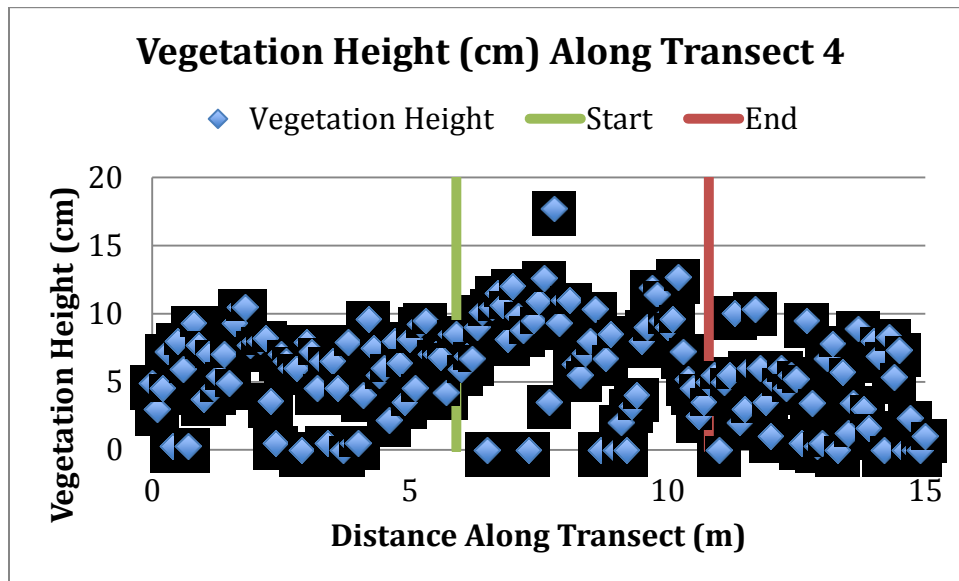
Figure 1d: Cross-sectional View of Vegetation Height (cm) along Transect 4. Green and red lines mark the start and end of the patch, respectively.
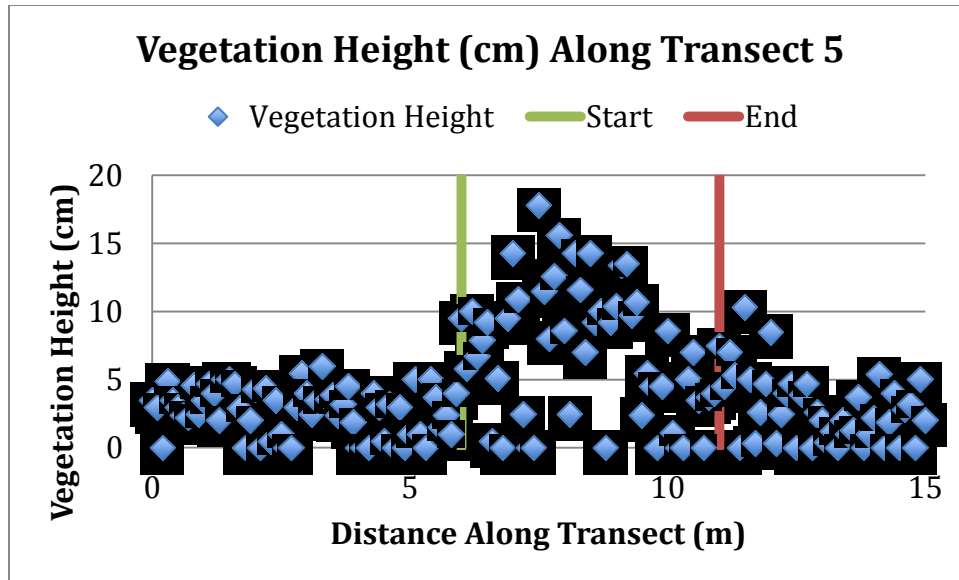
Figure 1e: Cross-sectional View of Vegetation Height (cm) along Transect 5. Green and red lines mark the start and end of the patch, respectively.
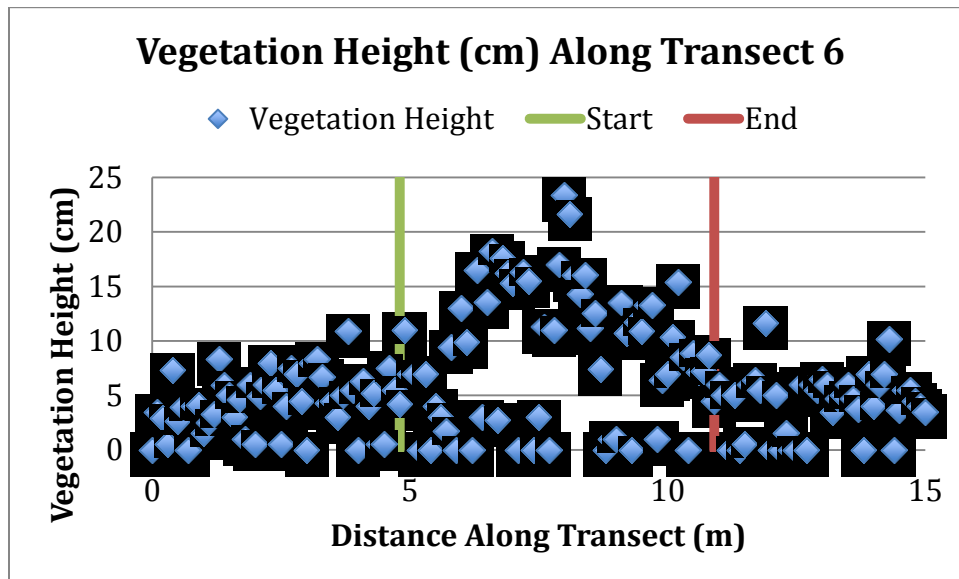
Figure 1f: Cross-sectional View of Vegetation Height (cm) along Transect 6. Green and red lines mark the start and end of the patch, respectively.
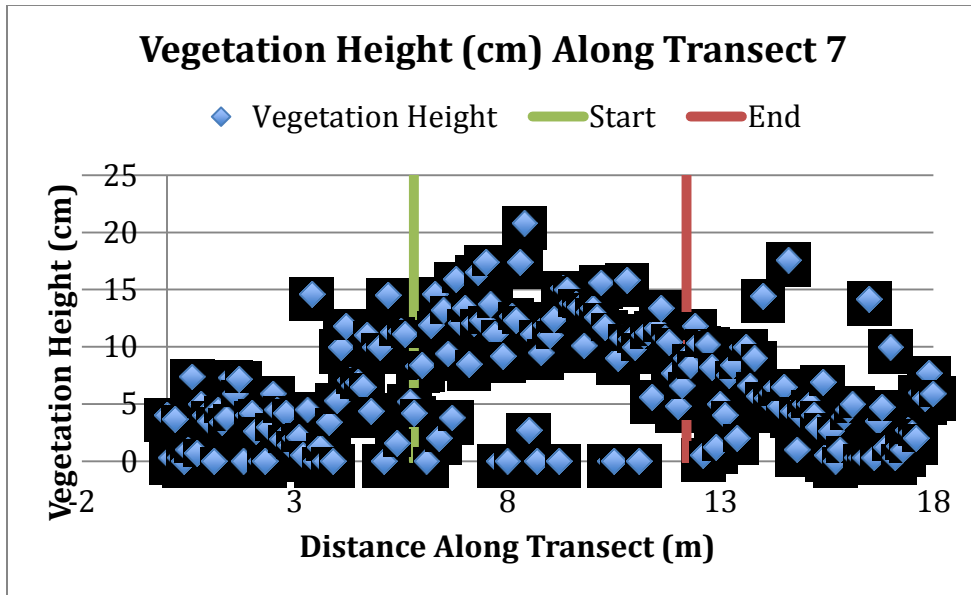
Figure 1g: Cross-sectional View of Vegetation Height (cm) along Transect 7. Green and red lines mark the start and end of the patch, respectively.
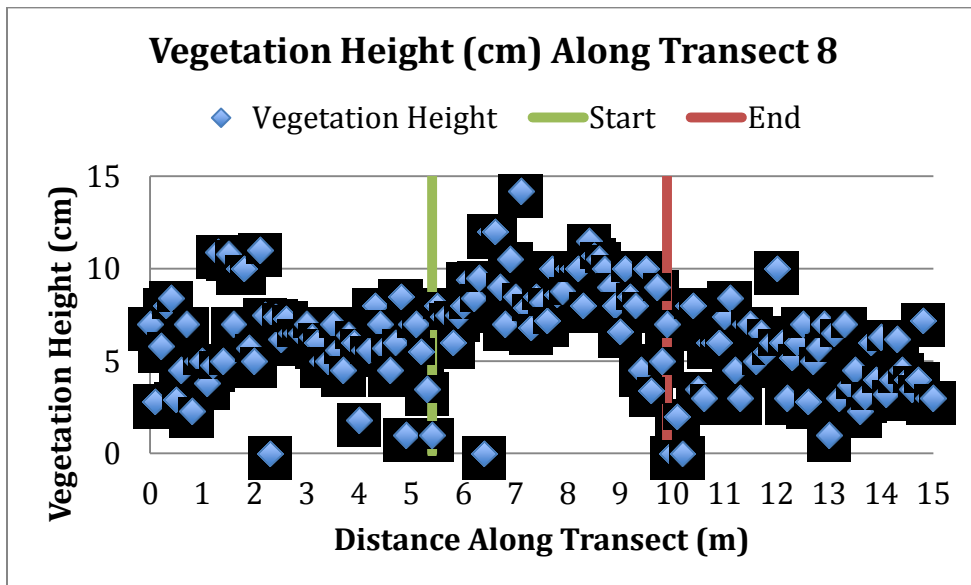
Figure 1h: Cross-sectional View of Vegetation Height (cm) along Transect 8. Green and red lines mark the start and end of the patch, respectively.

Table 1: List of all species encountered on Pikes Peak, CO during our study	
Common Name or Nick Name	**Scientific Name**
Alpine Avens	*Acomastylis rossii turbinate*
Silky Phacelia	*Phacelia sericea*
Western Paintbrush	*Castilleja occidentalis*
Bistort	*Bistorta bistortoides*
Grass 1	
Grass 2	
Alpine Lily or Alplily	*Lloydia serotina*
Lichens	
Alpine Sandwort	*Lidia obtusiloba*
Moss Campion	*Silene acaulis subacaulescens*
Alpine Parsley	*Oreoxis alpina*
Arctic Gentian	*Gentianodes algida*
Marsh Marigold	*Caltha leptosepala*
Mountain Candytuft	*Noccaea montana*
Alpine Rockjasmine	*Androsace chamaejasma carinata*
alpine clover	*Trifolium dasyphyllum*
Parry Lousewort	*Pedicularis parryi*
Alpine Forget-me-not	*Eritrichum aretioides*
Dwarf Clover	*Trifolium nanum*
Kings Crown	*Rhodiola integrifolia*
Rose Crown	*Clementsia rhodantha*
Fairy Primrose	*Primula angustifolia*
Alpine Sunflower	*Hymenoxys (Rydbergia) grandiflora*
Sky Pilot Plant	*Polemonium viscosum*

Table 2a: Abundance in the Open Tundra		Table 2b: Abundance in the Patch	
Species	Abundance OUT	Species	Abundance IN
Grass Type 1	35.53%	Alpine Avens	66.17%
Alpine avens	25.24%	*Bistorta bistortoides*	26.87%
Phacelia sericea	17.70%	Grass Type 1	11.19%
Lichens	17.22%	*Phacelia sericea*	9.70%
Grass Type 2	15.19%	Western Paintbrush	7.21%
Bistorta bistortoides	13.28%	Mountain Candytuft	7.21%
Alpine Sandwort	12.44%	Grass Type 2	4.98%
Moss Campion	7.78%	Marsh Marigold	2.49%
Alpine Parsley	5.26%	Lichens	2.24%
Arctic Gentian	4.19%	Alpine Sandwort	1.99%
Western Paintbrush	3.47%	Moss Campion	1.00%
Alpine Clover	1.79%	Alp lily	0.75%
Sweet Flower Rock Jasmine	1.56%	Alpine Parsley	0.75%
Mountain Candytuft	0.48%	Sweet Flower Rock Jasmine	0.50%
Marsh Marigold	0.36%	Arctic Gentian	0.25%
Parry Lousewort	0.12%	Parry Lousewort	0.25%
Alp lily	0.00%	Alpine Clover	0.00%

Tables RA1 an RA2: Abundance in the open tundra (RA2) and in the patch (RA1). The same species are listed, but they are rearranged in order of most to least abundant for each ecosystem.

Table 3: Species Composition of Patches and Open-Tundra

Patch-Loving Species	Almost-Patch-Loving Species	Impartial Species	Almost-Open Tundra-Loving Species	Open-Tundra-Loving Species	
Alpine Avens *Guem rossii*	Marsh Marigold Caltha leptosepala	Alpine Lily *Lloydia serotina*	Sweet Flower Rock Jasmine *Androsace chamaejasme*	Fuzzy *Phacelia sericea*	Alpine Sandwort *Lidia obtusiloba*
Broad Leaf *Bistorta bistortoides*	Western Paintbrush *Castilleja occidentalis*	Parry Lousewort *Pedicularis parryi*		Grass 1	Moss Campion *Silene acaulis subacaulescens*
Mountain Candytuft *Noccaea montana*				Grass 2	Alpine Parsley *Oreoxis alpina*
				Lichens	Arctic Gentian *Gentianodes algida*
					Alpine Clover *Trifolium dasyphyllum*

Table SC: Species Composition of Patches and Open-Tundra.
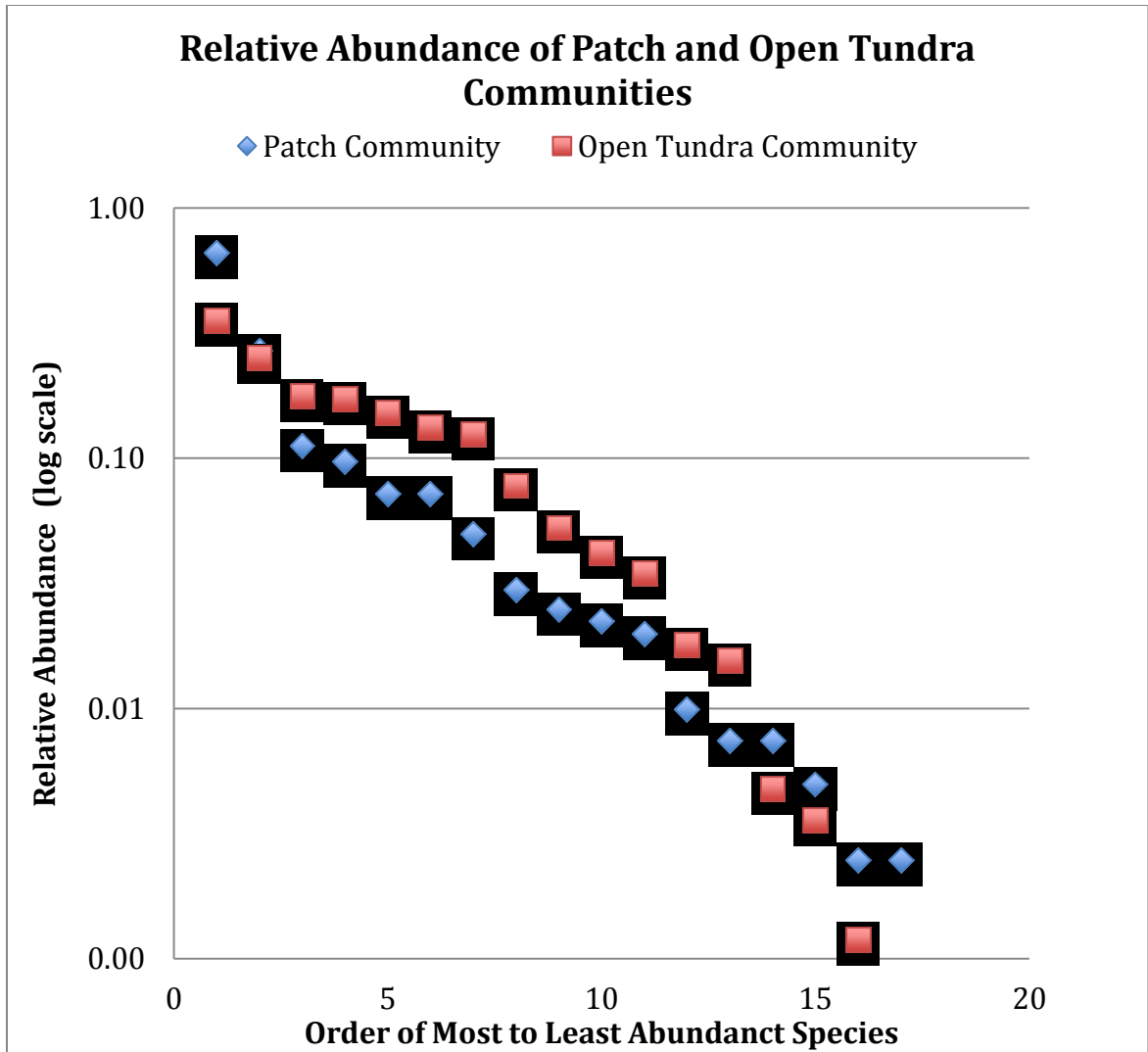
Figure 2: Relative Abundance of Patch and Open Tundra Communities.
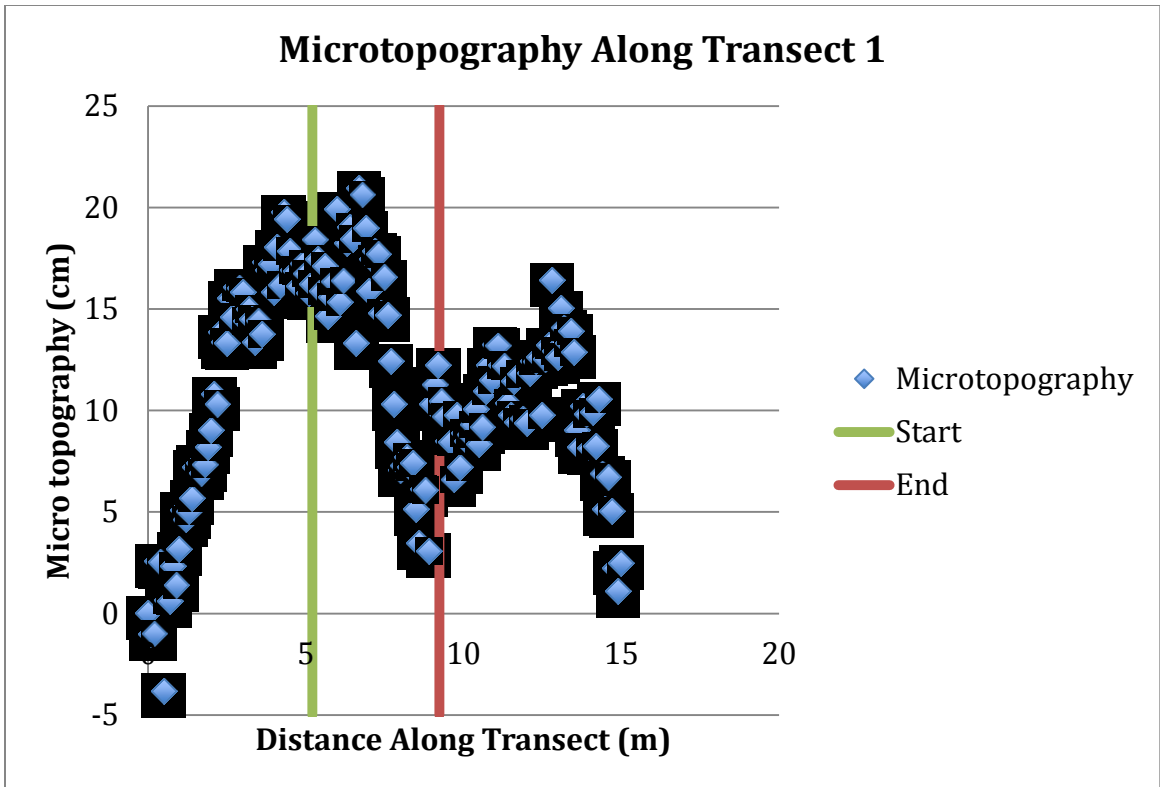
Figure 3a: Micro-topography Along Transect 1.
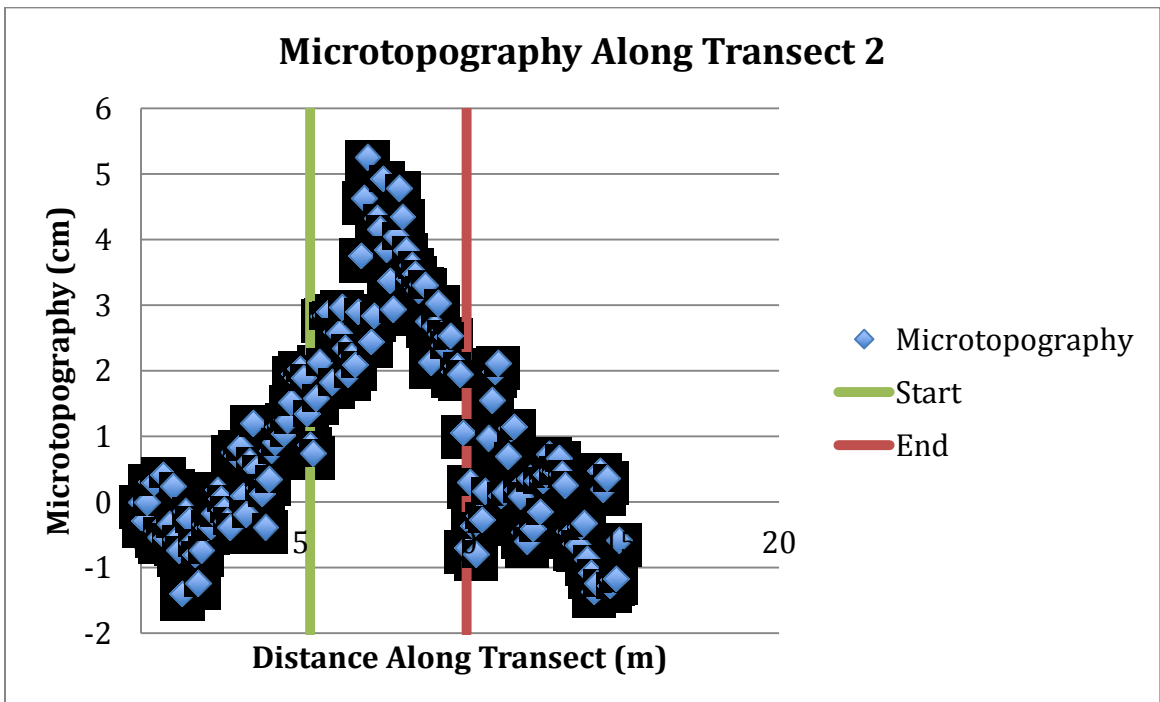
Figure 3b: Micro-topography Along Transect 2.
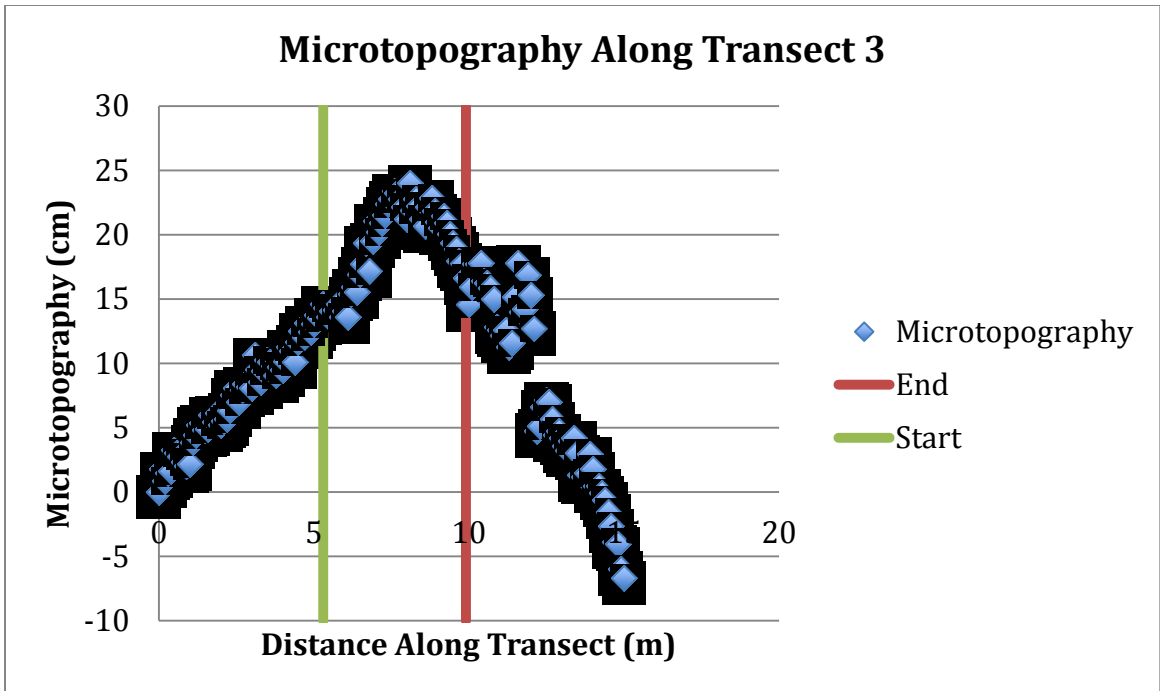
Figure 3c: Micro-topography Along Transect 3.
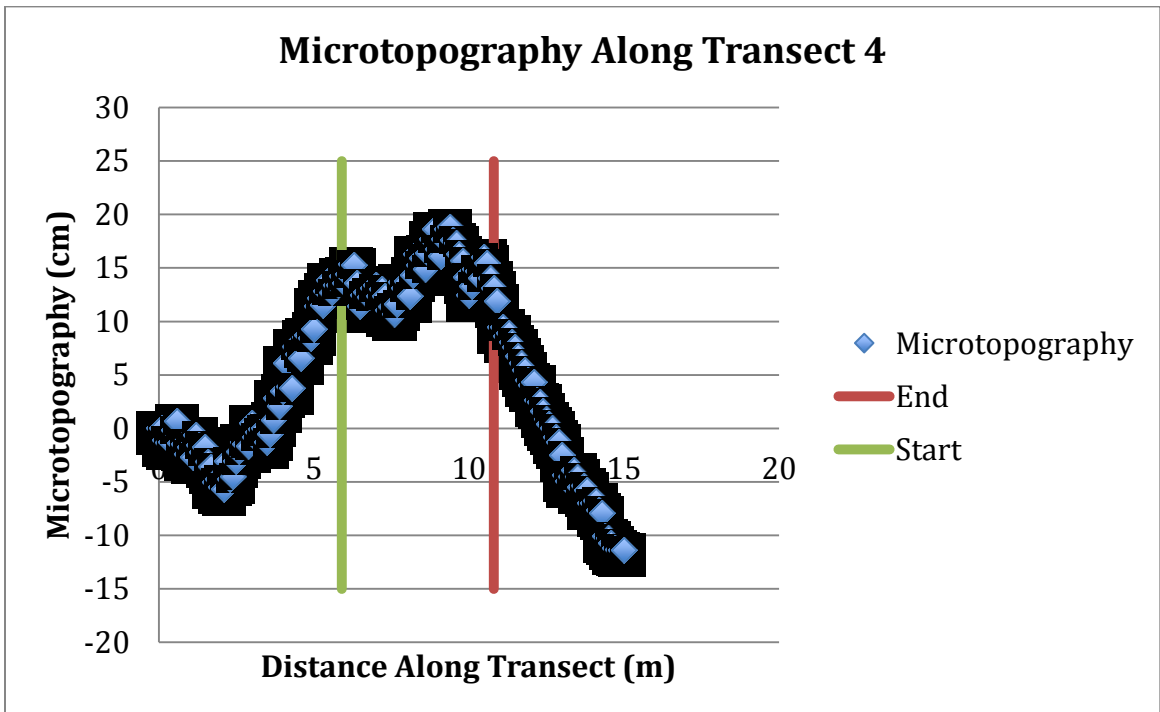
Figure 3d: Micro-topography Along Transect 4.
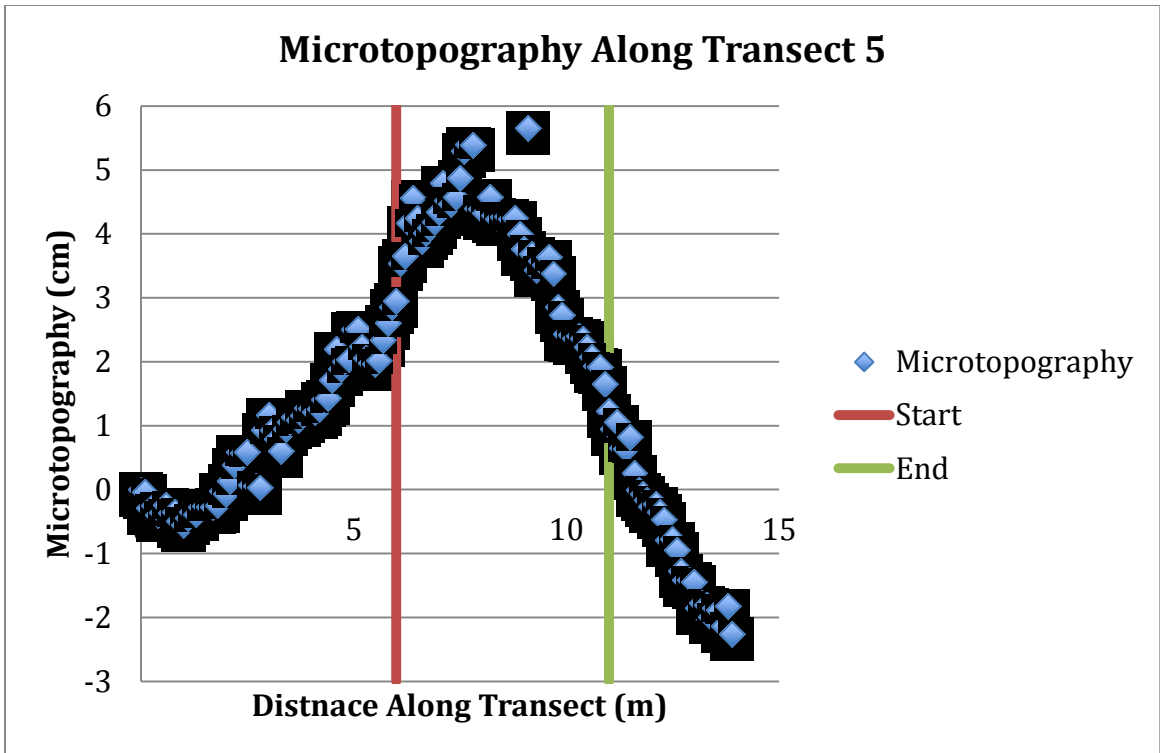
Figure 3e: Micro-topography Along Transect 5.
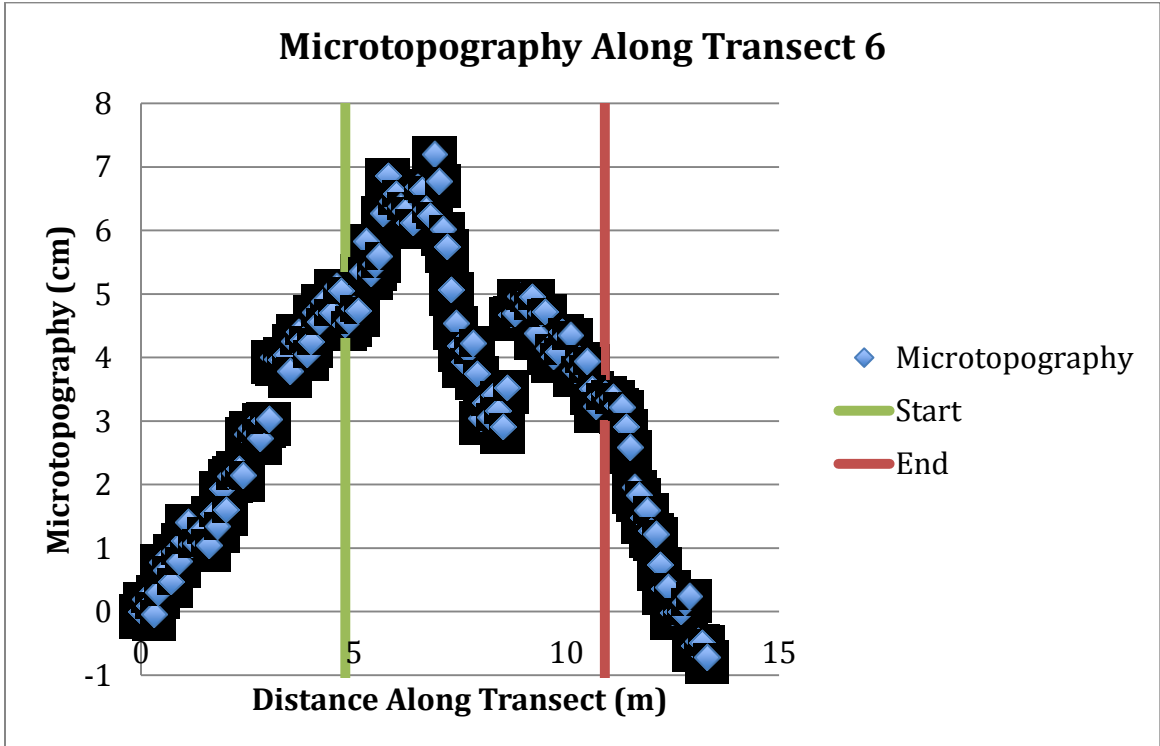
Figure 3f: Micro-topography Along Transect 6.

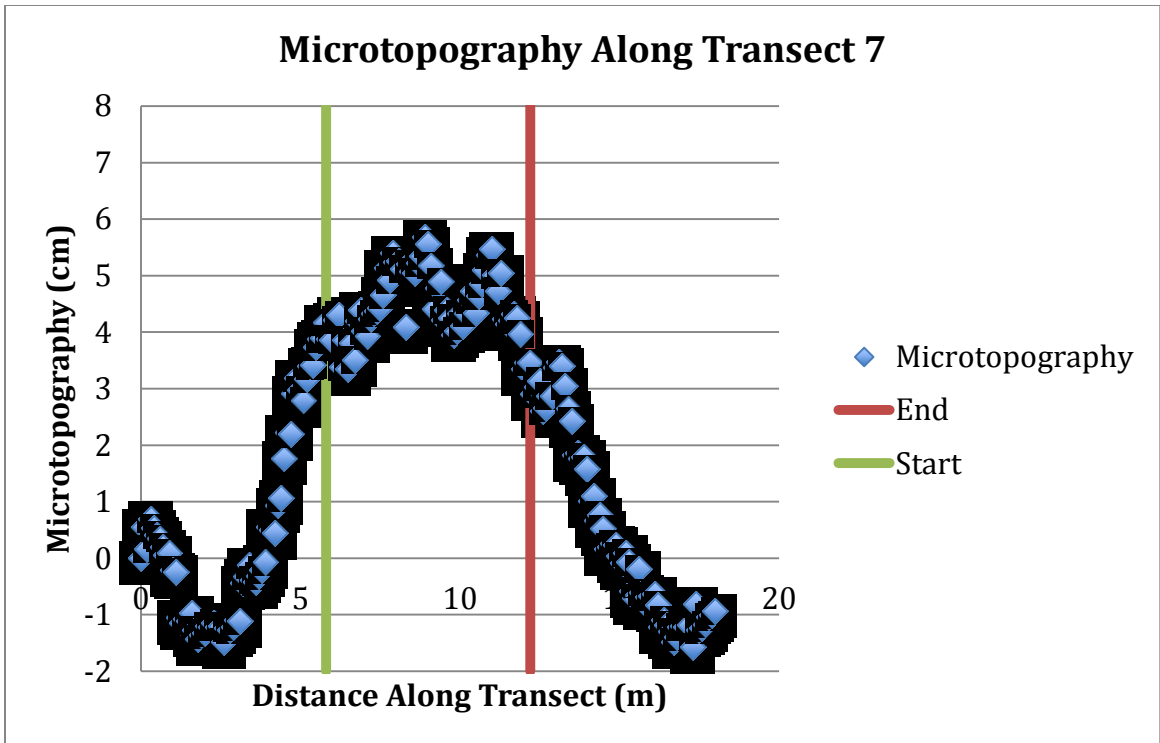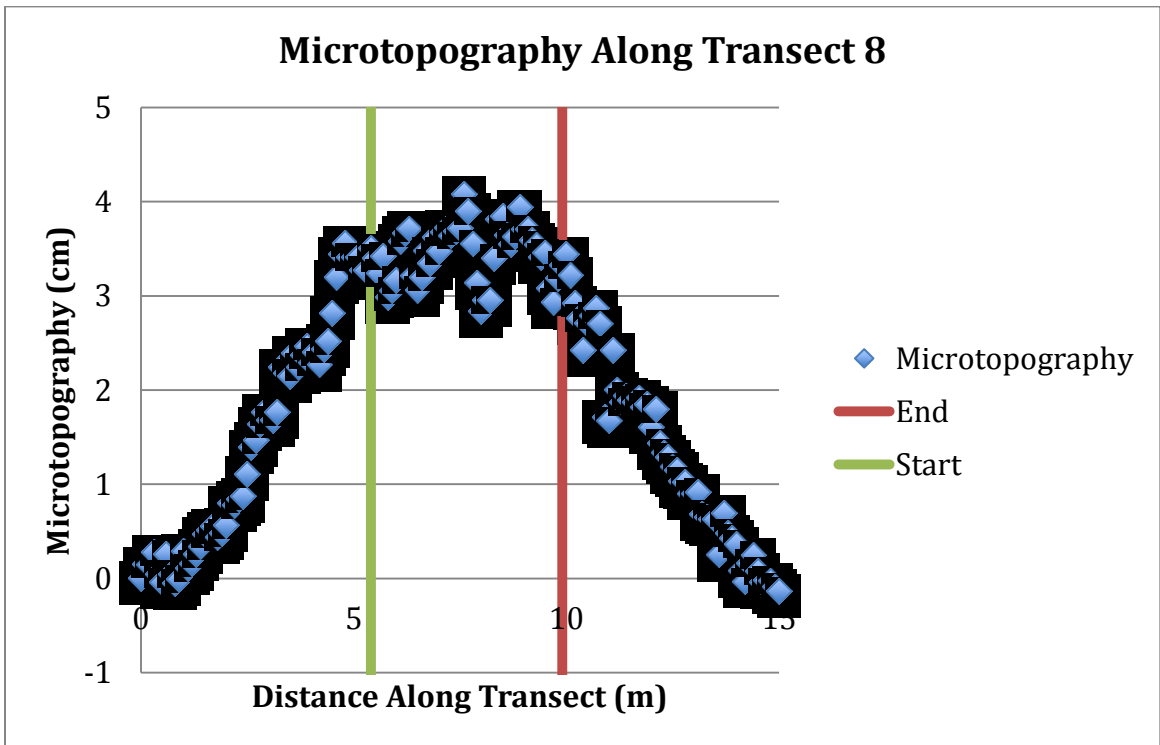Figure 3g: Micro-topography Along Transect 7.
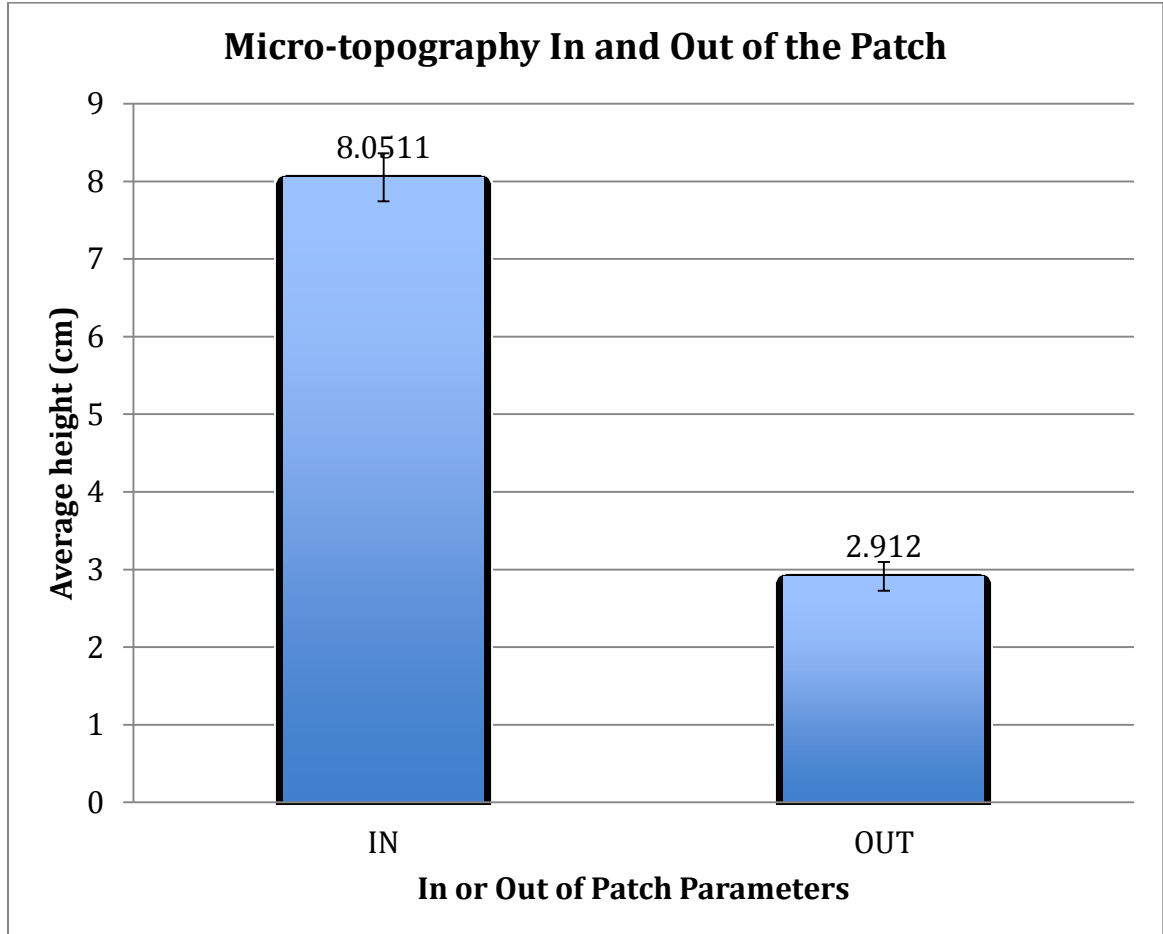

Figure 3h: Micro-topography Along Transect 8.

Figure 3: Micro-topography In and Out of the Patch. The micro-topography inside the patch was significantly larger than that outside of the patch (~2.75 times larger in patch) (t = 14.256; df = 693.156; p < 0.0005).
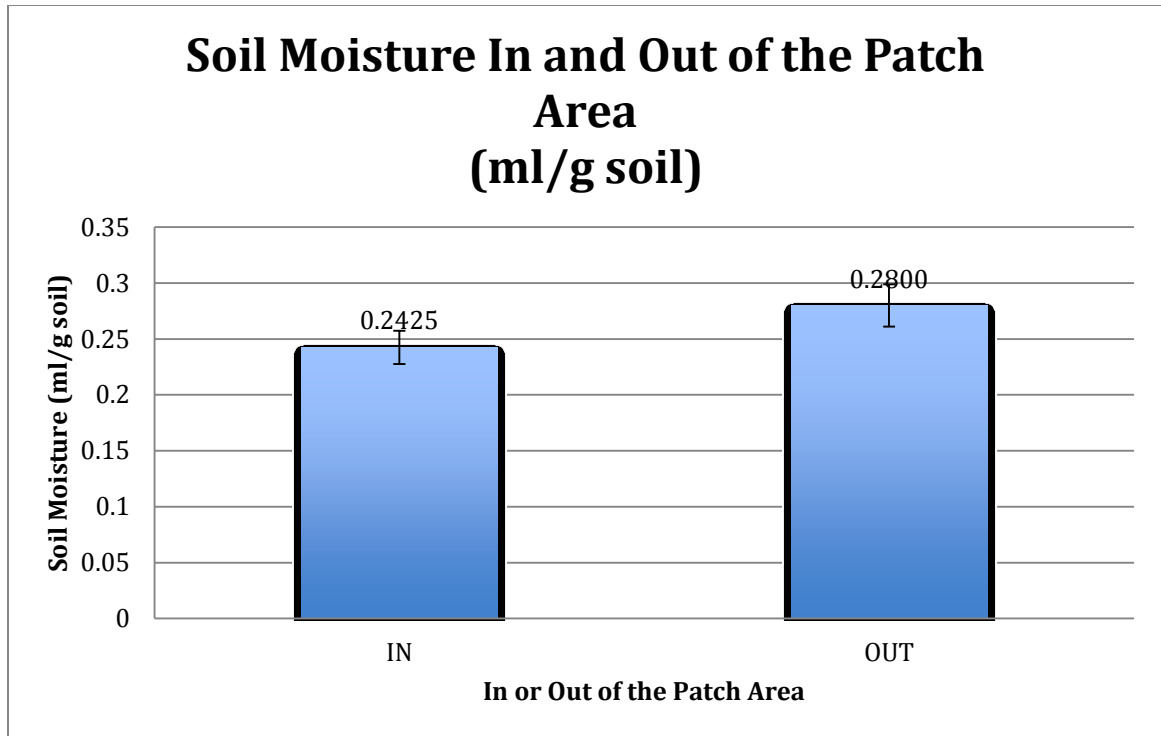
Figure 4: Soil Moisture In and Out of the Patch in ml/g of soil. Overall, the patch was drier than the surrounding tundra (t = -4160; df = 7; p =0.004) but this result was variable from transect to transect.
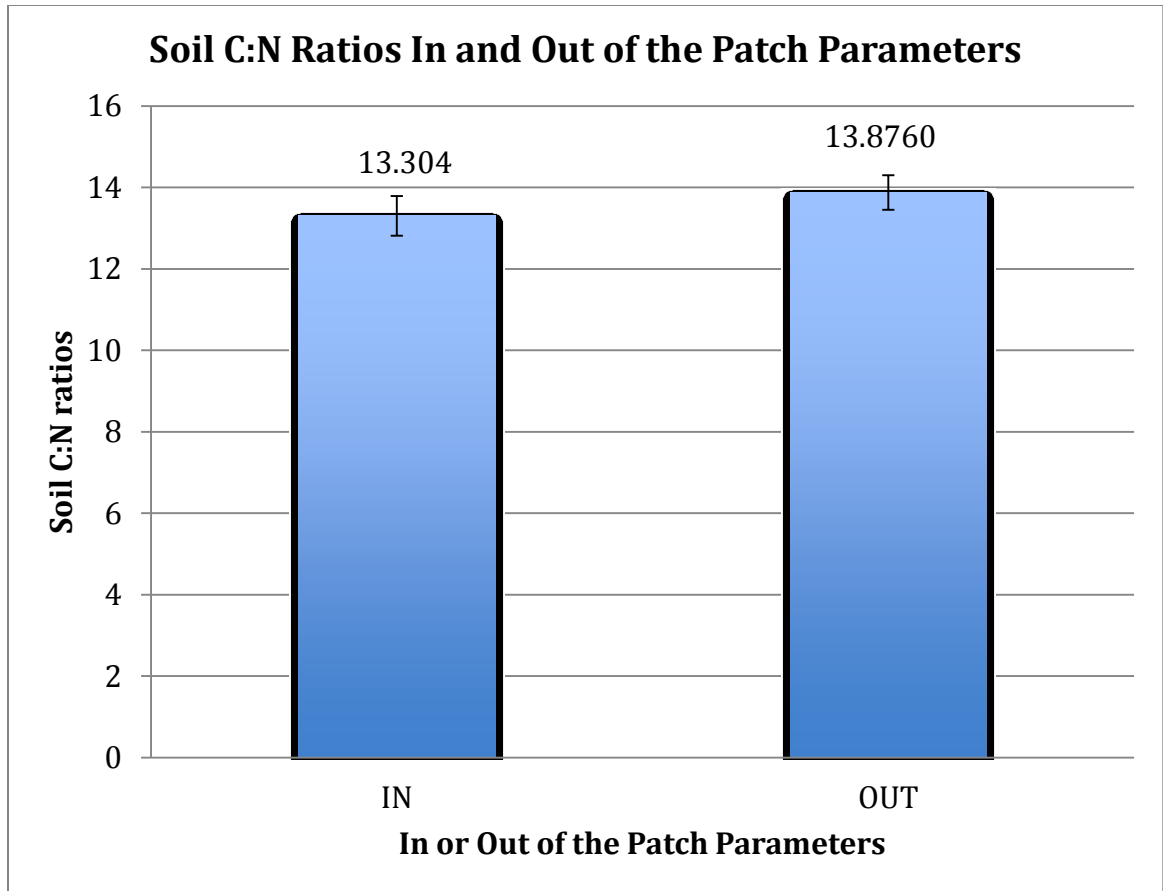
Figure 5: Soil C:N Ratios In and Out of the Patch Parameters. The soil inside of the patch is slightly more fertile than soil in the open tundra (t = -3.04; df = 4; p = 0.038).
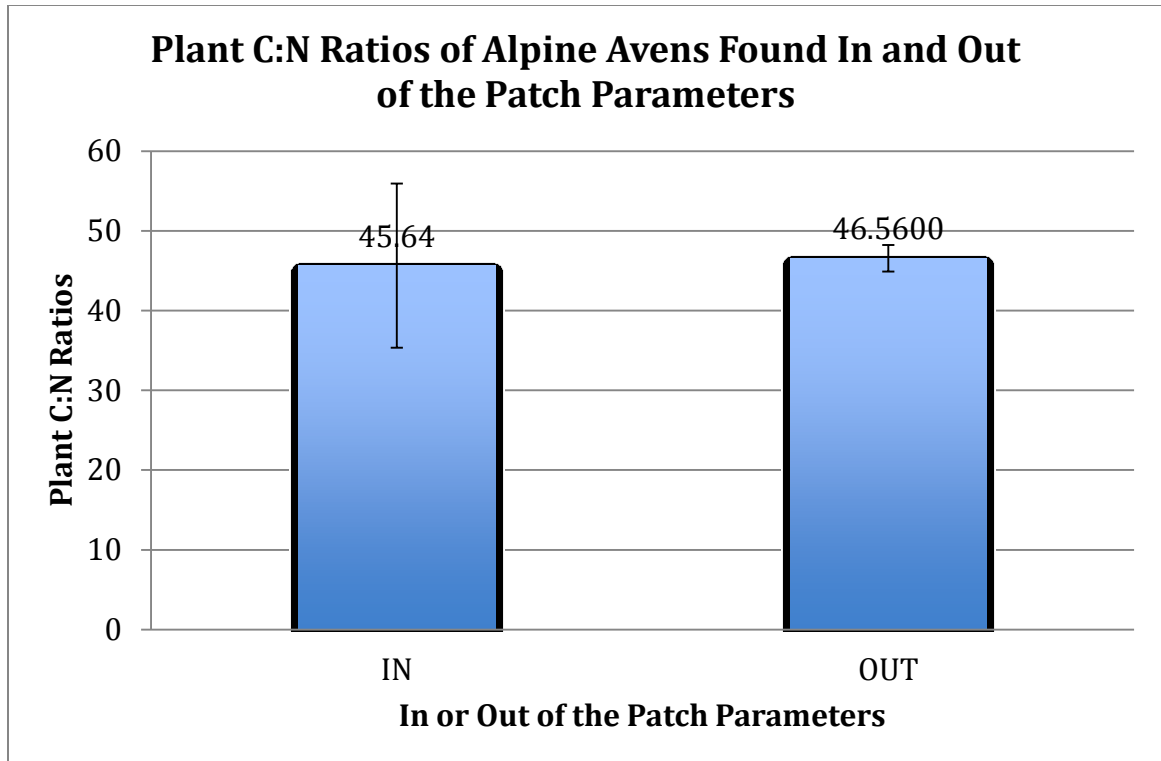
Figure 6: Plant C:N Ratios of Alpine Avens Found In and Out of the Patch Parameters. The plant C:N ratios inside the patch were not significantly different than plant C:N ratios of individuals found outside of the patch (t = -0.159; df = 2; p = 0.888). *These C:N ratios are larger than expected, probably because the rhizomes of Alpine avens plants were analyzed. The Alpine avens found inside the patch also had a more variable plant C:N ratio than those found outside.
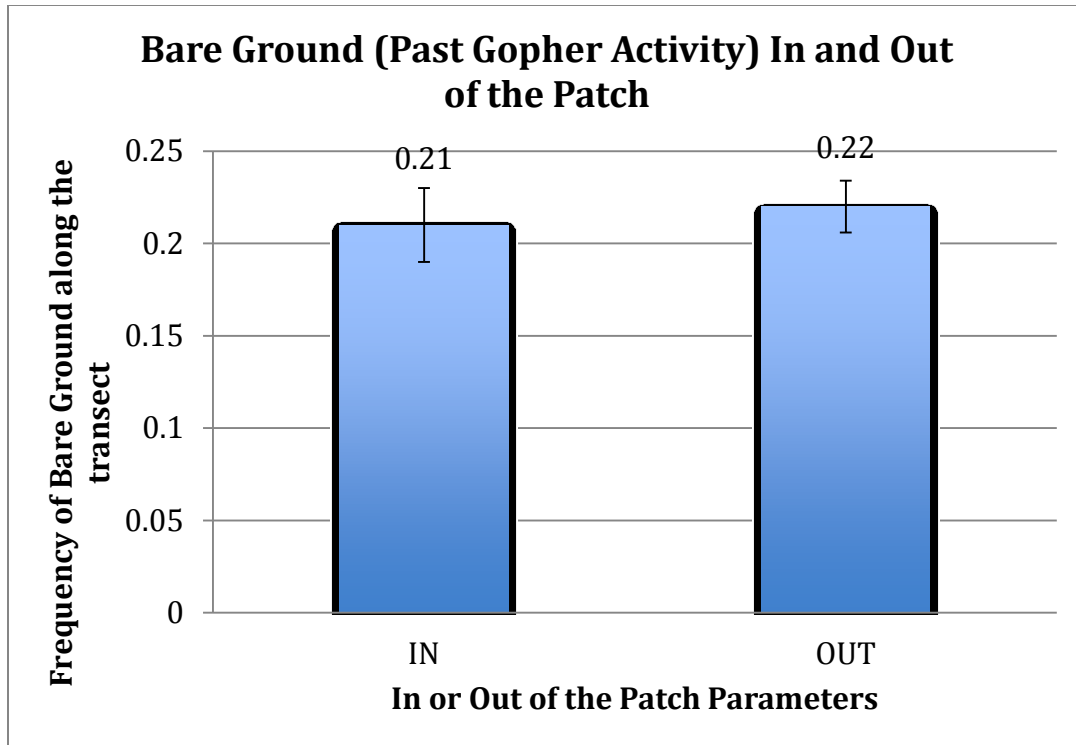
Figure 7: The frequency of bare ground found inside and outside of the patch. There was no significant difference between the frequency of bare ground inside and outside of the patch (t = -0.502; df = 1236; p = 0.616). This indicates that older gopher activity is equal within 5m around the patch.
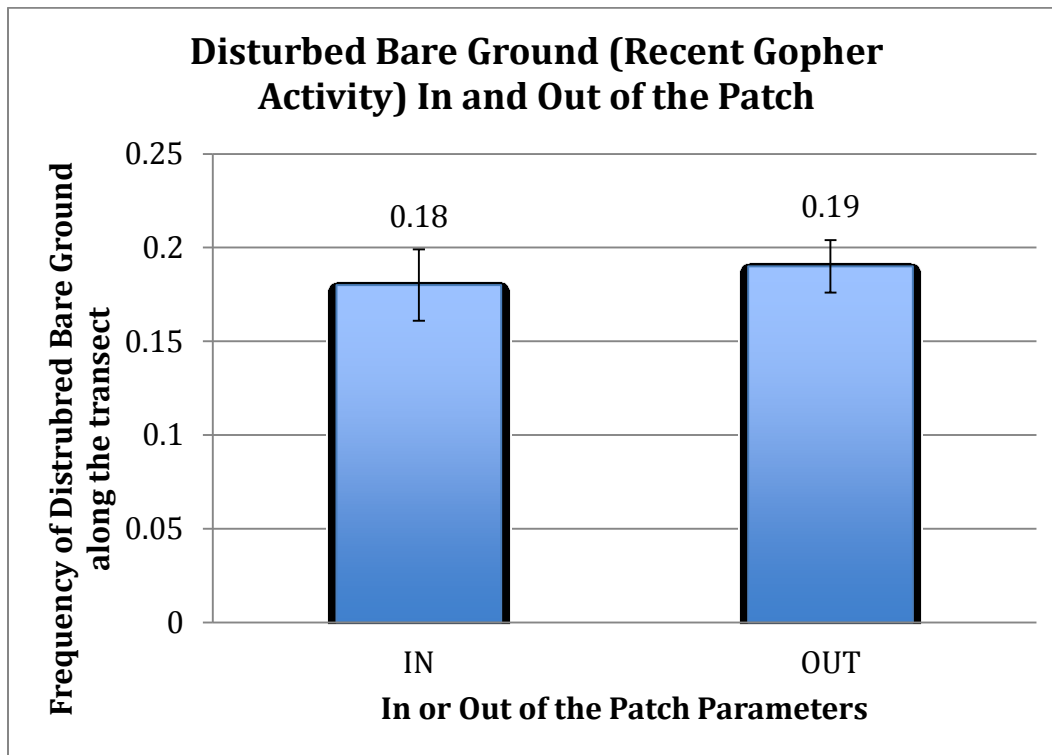
Figure 8: The frequency of disturbed bare ground found inside and outside of the patch. There was no significant difference between the frequency of disturbed bare ground inside and outside of the patch (t = -0.588; df = 1236; p = 0.556). This indicates that recent gopher activity is equal within 5m around the patch.

Bi-stable Dynamical Structure Lotka-Volterra

k_1

Population Number of Species 1
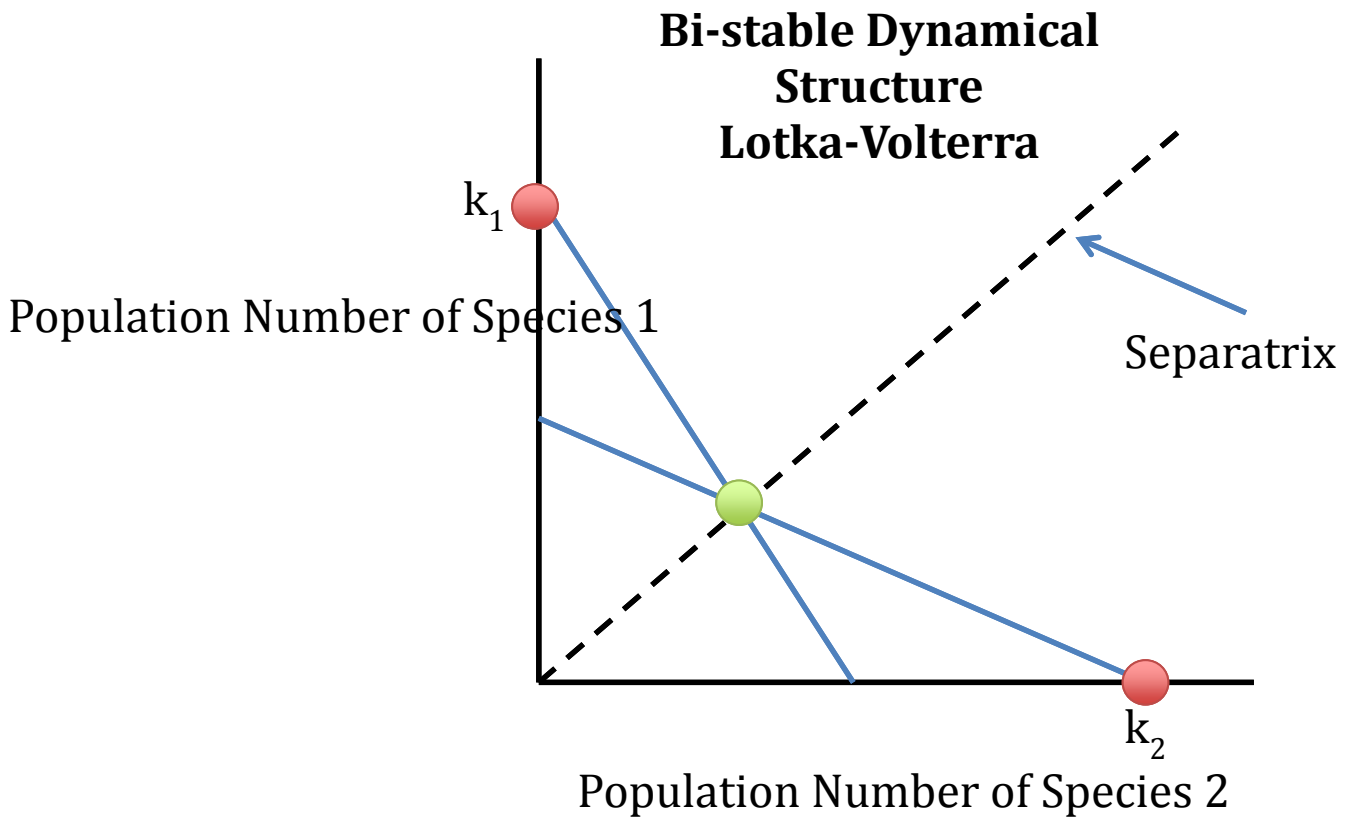
Separatrix

k_2

Population Number of Species 2

Diagram 3: Graph of the bi-stable dynamical structure in the Lotka-Volterra systems. The populations of two species and their carrying capacities (k_1 or k_2) in an ecosystem are compared. The two stable equilibria are located designated by red dots. The separatrix is a threshold line that separates the basins of attraction to the two alternate stable equilibria. The saddle point is located the intersection of k_1, k_2 and the separatrix and is identified by a green dot.