A SPATIAL ANALYSIS OF MICROCLIMATES AND SEEDLING GROWTH AT AN
ABRUPT TREELINE ON PIKE'S PEAK

A THESIS

Presented to

The faculty of the Environmental Program

Colorado College

In Partial Fulfillment for the Requirements for the Degree

Bachelor of Arts in Environmental Science

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May 2017

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Introduction

Treelines are frequently defined as temperature sensitive transition zones that demarcate the boundary between forested landscapes and treeless, alpine environments (Harsch et al. 2009). In areas where geography does not obstruct growth, this climatically constrained ecological boundary represents the uppermost physiological limit of trees, as most trees have a growth threshold for temperatures between 5.5-7.5˚C (Körner and Paulsen 2004). Current literature reveals that, photosynthesis and acquisition of carbon is not necessarily limited by lower temperatures, but allocation and utilization of that stored carbon for physical growth is restricted by the previously mentioned temperature threshold (Grace et al. 2002, Körner and Paulsen 2004). In other words, trees should not be able to establish and grow anywhere that exceeds the 5.5-7.5ºC temperature threshold. As a result, treelines are found at elevations and latitudes that coincide with mean growing season air temperatures in a similar range as the aforementioned growth threshold (Körner and Paulsen 2004). Therefore, on a global scale, treeline elevation and movement are externally, or exogenously, controlled by temperature patterns.

For the past century, many treelines have been seeing tree recruitment and growth beyond historical elevations in conjunction with warming climate trends, yet not all are moving at the same rate (Harsch et al. 2009). Harsch (2009) found that diffuse treelines, characterized by decreasing tree density and height with increasing elevation, are moving at significantly faster rates than abrupt treelines that sharply end with no apparent decrease in density. Harsh and others have concluded that treeline shape and structure may be responsible for discrepancies in rate of movement despite global, widespread temperature warming trends.

While overall temperature and increases in temperature due to climate change are external determinants and drivers of treeline movement on a broad scale, a focus on smaller, endogenous factors may help elucidate why certain treelines are responding differently to climatic changes (Malanson et al. 2011). On smaller, more localized scales, tree to tree interactions, treeline structure influence on microclimates and the resulting feedbacks are relevant and important (Malanson et al. 2011, Case et al. 2014). Specific studies on endogenous factors aim to understand small scale abiotic and biotic factors (wind, snow, sun exposure, water availability) that may be influencing seedling establishment above treeline and how specific treeline structures can promote or interfere with growth and further establishment (Malanson et al. 2011, Case et al. 2014). These small-scale factors may interact in conjunction with larger-scale temperature trends to either create positive or negative feedbacks that could affect the future treeline positions.

Our study at an abrupt treeline on Pike's Peak focuses on these feedback mechanisms that might be influencing overall movement of treelines. As mentioned previously, treeline movement is influenced by both large-scale factors, such as temperature, and smaller-scale influences, such as microclimate facilitation and feedbacks. We would like to understand these feedback mechanisms and whether they are interconnected or separate mechanisms. In other words, we want to know whether the feedback that influences movement also impacts spatial structure of treelines and vice versa.

Large scale factors

The predominant large-scale factor determining treeline location is temperature. While it is widely acknowledged that tree growth is temperature-limited, there is some disagreement in

the literature on which season is the main driver and by which specific mechanisms growth is being affected.

Körner and Paulsen's (2004) study suggests that warming summer temperatures, during the growing season, could allow growth to occur in previously inhospitable conditions and allow treelines to advance upwards due to a longer growing season and milder temperature minimums. Since temperature and elevation are inversely correlated, then widespread increases in temperatures could allow growth at higher elevations.

On the other hand, Harsch's (2009) study shows that milder and warmer winter temperatures are the main drivers in treeline advance through mechanism of seedling survivorship. Milder, warmer winters could result in less freeze events as well as the likelihood snow fungi and overall temperature extremes that frequently cause seedling mortality when the trees are dormant. Freeze events can kill new growth and cold temperatures, allowing for the persistence of snow, make trees more susceptible to snow fungi (Harsch et al. 2011, Renard et al. 2016). Thus, having warmer, shorter winters could reduce the chance of freeze events or susceptibility to snow fungi from persisting snow and allow more trees to survive into the summer growing season. On the other hand, exposure to warm air while roots are still frozen in the ground could lead to desiccation and increased mortality (Marchand 1987). In this respect, warmer winters might have a negative effect on seedling survivability. Therefore, the effects of warmer winter temperatures are still unknown and need to be researched further.

Additionally, studies have been conducted on the effects of snowpack on seedling survivability. Since snowpack is directly related to temperature, it is important to discuss here. Several studies have revealed that snowpack insulates trees from temperature extremes, prevents

surrounding temperatures from dropping below freezing and protects seedlings from ice crystal

blasting (Renard et al. 2016, Greenwood et al. 2015, Kroiss et al. 2015, Hagedorn et al. 2014,

Malanson et al. 2011). Alternatively, persistence of snow can also make trees more susceptible to

snow fungi and cause mortality. Therefore, warmer winters which could result in less snow,

might negate the positive effects of snowpack and cause greater seedling mortality. Warmer

winters might also mean shorter winters and a lower likelihood of snow fungi. Thus, the effects

of snowpack are twofold and so are the effects of an overall warmer climate.

Warmer temperatures in conjunction with other factors could help advance the treeline

or hamper its movement depending on how and during which season these temperature changes

are the most pronounced. As a result, changing temperatures are likely to affect individual

treelines differently depending on how these changes interact with microclimates and small-scale

factors present at each treeline. Large-scale changes in temperature are likely linked to

smaller-localized phenomena and interactions occurring at treeline and thus, a smaller scale

focus is required to understand these unique, endogenous interactions.

Localized factors and feedbacks

While temperature is the main external factor affecting treeline location, it cannot be used

solely to explain treeline movement, structure and location (Malanson et al. 2011). In fact,

localized factors are likely the drivers of discrepancies in treeline elevations, shapes and

movement. Smaller-scale interactions encompass how individual trees and entire treeline

structures interact with local climates to create microclimates that in turn, promote or inhibit

growth and establishment of other trees. If microclimates and endogenous factors did not have

any effect on growth and distribution of trees, we would not see discrepancies in treeline shape that currently exist ranging from abrupt to diffuse and island to krummholz in shape (Malanson et al. 2011, Harsch et al 2009). Therefore, endogenous factors and microsite facilitation must be playing a role in determining treeline structures, as these distinct shapes can create favorable microclimates for growth in areas that are otherwise disadvantageous. Once these favorable microsites exist, they can be amplified through positive feedback mechanisms, allowing widespread growth in areas that have historically hampered growth. The main focus of many current studies examines how these microclimates impact localized factors such as, snowpack depth and persistence, wind and sheltering and open sky exposure.

While snowpack can be affected by large-scale temperature shifts, snowpack distribution and persistence is also influenced by microclimates. Vegetation and microtopography can slow wind speeds on their leeward sides, allowing snow drifts to accumulate just downwind of them. This presence of snow can insulate young seedlings and their roots from extremely cold temperatures and protect them from winter snow blasting that can damage needles (Renard et al. 2016, Greenwood et al. 2015, Kroiss et al. 2015, Hagedorn et al. 2014, Malanson et al. 2011). Alternatively, the persistent shadows cast by these trees could also allow snow to remain for long periods of time, which creates a conducive environment for snow fungus that kills trees. Therefore, the microclimates created by trees can influence snowpack at treelines, which can be favorable and create more available microsites for growth (a positive feedback) or kill trees and remain stagnant (a negative feedback).

Neighboring vegetation can also impact open sky exposure for nearby trees. Trees exposed to more open sky at night experience much colder temperatures, due to radiative losses

that are not captured by nearby canopies, and much warmer temperatures during the day due to

lack of shading (Smith and Germino 2003). During the day, trees are susceptible to

photoinhibition from exposure to high solar radiation after experiencing extremely cold

temperatures. Therefore, canopy cover might be beneficial in these respects, as it moderates

temperature and potential photoinhibition (Kroiss et al. 2015, Greenwood et al. 2015, Pyatt et al.

2016 and Smith et al. 2003). At the same time, shading from trees can produce extremely cold

shadows that may persist throughout the day inhibiting growth by maintaining temperatures

below the growth threshold. Therefore, sky exposure also mediates temperature and creates

feedbacks that can inhibit or promote growth. Overall, research has found that increased canopy

cover is overwhelmingly conducive for growth, and that the benefits of sheltering and

moderating temperature offset the impact of the cold shadows (Malanson et al 2011). As a result,

the beneficial effects of increased canopy cover are likely to promote growth, thereby increasing

overall canopy cover and encourage further growth.

     Vegetation as well as microtopography is likely to influence the effect that wind has on

growth rates and establishment. Extremely harsh winds, present at many treelines, can result in

desiccation of trees by increasing evapotranspiration rates and abrasion. As a result, there are

many stunted and misshapen trees at treeline coupling to the ground to avoid these high wind

speeds (Körner and Paulsen 2004). Growing on the leeward side of already-established trees may

reduce the amount of wind that seedlings are exposed to. The already-established trees can break

wind and provide a warmer, more stagnant microclimate for trees to establish downwind

(Malanson et al. 2011, 2013, Renard et al. 2016, Greenwood et al. 2015, Smith and Germino

2003 and Case et al. 2014). Thus, tree-to-tree interactions can facilitate growth in otherwise

inhospitable conditions and allow for establishment and growth above historical limits regardless of temperature.

Each of these localized, endogenous factors work in conjunction with larger-scale exogenous factors such as temperature (Case et al. 2014). The question is: how these microclimates created by existing treeline structures and individual trees impact growth and establishment, and how they will result in positive or negative feedbacks that determine the future structure and position of treelines.

Microclimates present at abrupt treelines

Our study on abrupt treelines aims to understand and examine how the specific shape of entire treelines can create microclimates and feedbacks that either facilitate establishment or hinder it. To understand the influence of these feedbacks, it is important to have a grasp of the microclimates that could arise on a mountain as a result of an abrupt treeline structure.

During the day there are two potential microclimate scenarios. At daytime, heating of the lower air layer from solar radiation causes upslope anabatic winds to arise by creating a temperature gradient in the atmosphere (Oke pp.176). If this upslope flow is perpendicular to the treeline, the abrupt treeline is likely to act as a shelterbelt. Due to decreased resistance moving rapidly from a thick forest to sparse tundra, air will accelerate over the upslope edge of the treeline, creating a low pressure zone on the leeward side of the treeline. This pressure gradient beneath the accelerating air creates an eddy structure and the accelerating air itself forms a boundary between the eddy and the upper atmosphere. The accelerating air acts as a barrier that prevents mixing of air between the eddy and the upper atmosphere. With constant solar radiation

input throughout the day, the ground heats up consistently at the field site. Because the air temperature above the ground is cooler than the ground itself some heat will dissipate from the ground to warm the surrounding air. The air that warms up within the eddy zone remains warm due to its inability mix with the upper atmosphere. As a result, the gradient between the air and the ground in the sheltered zone is low, which allows the ground to continually warm from solar radiation. Ultimately, this eddy structure will result in a pocket of warm air and ground temperatures just upslope of the old growth treeline.

 If the flow is not perpendicular and instead parallel, the moving air meets resistance and friction with the treeline and slows down. This slower air, which mixes less with the atmosphere, also has time to heat up from the warm ground. Like in perpendicular flow, sensible heat flux will be low and both the ground and air will remain warm. Thus, in either daytime scenario, a warm pocket of air and ground temperatures forms directly upslope of the treeline. This slow, warm pocket could augment growth during the summer growing season and promote snow drift build up that could insulate the trees during the winter.

During the night, when solar input in no longer present, the ground cools due to radiative cooling. Because the ground is colder than the surrounding air the sensible heat flux goes down into the ground, resulting in the cooling of the lower air layer. Because the air atop a mountain is much thinner, it cools quicker, becomes more dense and flows downhill towards the valley floor (Oke 1987, pp. 178). Without trees, the air would flow continuously to the valley floor with little resistance, but with the presence of an abrupt treeline, the cold air gets "dammed" up against the abrupt and dense barrier. The air pools upslope of the dam creating a thick, stagnant pocket of cold air. Because this pool is so stagnant and cold, no mixing with the warmer upper atmosphere

occurs and the ground will cool rapidly due to radiative cooling and remain cold due to a absence of warm air mixing in reducing the amount of sensible heat flux.

Research Focus

With an understanding of potential microclimates created by an abrupt treeline and how they might influence seedling mortality and establishment, we can predict feedback mechanisms that could impact the future of the abrupt treeline at our field site on Pike's Peak. As trees, prefer warm ground temperatures for growth and survival, they might recruit into the sheltered eddy zone that remains warm during the day. At the same time, the same eddy zone during the night might become extremely cold due to the cold air dam. Thus, one of our major questions is whether the night or day has a greater impact on seedling growth and distribution. Ultimately, if trees are able to recruit in front of the treeline, evolving into another abrupt treeline, this process will continue to repeat itself. If the microclimate created by this current abrupt treeline is not conducive for seedling growth and establishment, then the treeline will remain stagnant through a negative feedback mechanism. Therefore, our research aims to understand the microclimates at this abrupt treeline and how they impact seedling growth and establishment that will in turn affect the shape and movement of a future treeline through feedbacks.

Methods

Field Site

The field site for this study is located on the northwest slope of Pike's Peak in Southern Colorado at approximately 12,000ft. The site is almost exclusively composed of Engelmann

Spruce and characteristic of an abrupt treeline with a sharp and defined old growth boundary and minimal tree-island or krumholtz formations above the existing treeline. The transition between forest and tundra is particularly abrupt, approximately 20m wide, with no presence of a shrub belt between these two regions. There is a section of approximately 2-5m in width of tall saplings in front of the old growth treeline and several seedlings below 2m in height in the tundra. Within 60m of the old growth treeline, seedlings and trees completely disappear. Within this larger field site, an area of interest (AOI) of 30 by 60 meters was created to narrow the focus area. The AOI location was specifically chosen in a region of the treeline that appeared the most uniform, containing no holes or tree-islands, and spanned from inside the treeline to the tundra to capture the entire ecotone (Fig. 1). The AOI was then divided into three distinct regions: old growth forest, sheltered eddy zone and the tundra. The boundary between the old growth forest and eddy zone was distinguished by using a GPS and walking a line between the tallest (oldest) trees at the treeline and the younger, smaller trees slightly above the dense forest. The subsequent line dividing the eddy zone and tundra was created by walking a line between the lowest wind blasted trees present at the field site. Tree trunks visibly blasted by ice crystals in the winter indicate that they are no longer in the eddy zone and thus, mark the end of the sheltered area. All trees within the sheltered, eddy zone show no sign of winter snow abrasion. The sheltered zone itself was then divided into an upper and lower eddy zone at about halfway between the old growth treeline and the tundra. This was done because we noticed two distinct patterns in distribution within the eddy zone and wanted more specific regions to discuss trends.In 2016, the AOI was studied for the entirety of the month of September with intermittent data collection into October.

Data Collection

Within the AOI, all seedlings (live and dead) under 30 cm were GPS-ed and surveyed (Fig.1). For each seedling found in the transect, the age, height, top and side bud growth and canopy cover was recorded. Age was approximated by counting bud scars on the trunks. The surveyor collecting age remained consistent throughout the study to prevent any discrepancies in aging techniques. The height (cm) was obtained by measuring from ground to highest needle, and the top and side growth measurements (mm) were measured from start of the current year's bud growth to the longest needle. Canopy cover was measured using a spherical densiometer and counting the number of intersections on the grid of the spherical mirror that were filled with trees. Four canopy cover measurements were taken at each tree and averaged afterwards.

A temperature grid was also created to obtain an estimation of ground temperatures throughout the AOI (Fig. 2). A 110-point grid was created within the transect with ten rows spanning from the tundra into the old growth forest, each containing 11 points that were approximately 3m apart. For each of these points, a GPS location was recorded and ground temperature measurements using a FLIR infrared camera were taken. Ground temperature measurements were taken before sunrise, which is representative of night time temperatures and in the early afternoon, which is more representative of the daytime regime. Each temperature reading was taken by the same person at the same height and distance from the point to minimize variation in measurements. Each image was then averaged to obtain a mean ground temperature reading for each point.

Data Analysis

Upon completing data collection, all seedling and temperature grid data were entered into

ArcGIS 10.0.4 to visually and statistically analyze. To examine ground temperature patterns

within the AOI, the day and night grid values were used to interpolate the temperature as a

surface. Utilizing the X,Y coordinates as the point location and the temperature as the Z value, a

spatial analysis tool in ArcGIS can create a surface to visually represent the temperature values.

Two different interpolation methods were considered when attempting to interpolate temperature

surface and yielded somewhat different results. Spline interpolation, which passes the surface

through every data point value, did not provide a reasonable or logical surface that was

representative of what temperatures were observed in the field ("Interpolating Surfaces in

ArcGIS Spatial Analyst"). Because the tool cannot interpolate within a certain polygon (our AOI

in this instance), artifacts outside of the AOI were likely driving the interpolation. Instead,

kriging, which uses a weighted average between nearby points to predict the surface, provided a

more representative image of the temperature regimes. Though kriging did provide a better

interpolation for our research purposes, some caution was taken when using kriging for analysis.

Since kriging takes weighted averages and then predicts, instead of creating a surface that runs

through actual values like spline does, kriging runs the risk of homogenizing rather heterogenous

surfaces. In the case of the daytime temperatures in the lower eddy zone, which is quite

heterogeneous due to shadows cast by trees, the kriged interpolation shows a far more

homogenous AOI than is actually present. While initially troubled with this fact, the realization

that shadows would shift throughout the day as the sun moved, made it more appropriate for the

kriging to represent an average. From the kriged raster, each temperature class was converted

into a polygon with an integer representing a temperature range. For nightime temperatures the polygon values range from 1-5 with one representing the coldest recorded temperatures around -6 to -7˚C and five representing the warmest temperatures around -1 to -2˚C (Fig. 4). For daytime temperatures the polygon values range from 1-6 with one again representing the coldest recorded temperature range from 4 to 6˚C and six representing the warmest temperature range from 14 -16˚C (Fig. 5).

The growth of trees was represented in a similar way using interpolation. Growth residuals of each tree were calculated by plotting top growth versus height. Using the regression to predict growth, given height, actual growth was subtracted from expected growth to obtain the growth residuals. These residual values were then interpolated using the spline method. The spline raster was also converted into polygons with integers representing a range of growth residuals (1 representing the worst growth and 5 showing the best growth).

For both the temperature and growth residual interpolation, the number of seedlings per temperature or growth class was summed up to determine whether seedling distributions were overrepresented or underrepresented in certain regions based on temperature or growth residuals. A chi-square statistical analysis helped determine whether distributions were random or not in relation to ground temperatures and growth residuals.

Results and discussion

Seedling distribution

Based on an understanding of growth and temperature limitations for seedlings and microclimates, potentially created by an abrupt treeline structure, we would not expect to see

seedlings establishing in the tundra. This is likely due to harsh climatic extremes such as high winds and extremely low temperatures during the winter due to lack of insulating snow. With respect to the eddy zone, we would expect seedlings to establish within this region because it likely stays warm during the day with the sheltering from the eddy and insulated with the snow drifts during the winter. The effects that the extremely cold night regime should also be taken into consideration when predicting these seedling distributions. We expected to see few trees establishing in the old growth forest due to competition and shading.

When mapped (Fig. 1), live and dead seedling distributions appear to be non-random. Using a chi-square analysis, live seedlings are significantly underrepresented in the tundra with a X^2 of 33.032, df=1 and a p-value of 0.0001 and significantly overrepresented in the sheltered eddy zone with an X^2 of 75.596, df=1, and a p-value of 0.0001. Within the closed canopy forest the seedlings are again underrepresented with X^2 of 14.947, df= 1 and a p-value of 0.0001. Therefore, distribution appears to be nonrandom and results support our predictions.

Live seedlings appear to cluster in distinct bands or pods that run perpendicular to existing treeline within the upper eddy zone. We predict that this is due to the sheltering provided by the eddy zone during the day. With knowledge of the shelterbelt mechanism, this eddy should protect seedlings from harsh winds, moderate temperature and result in the accumulation snow during the winter, which all assist in seedling growth. The band of seedlings to the skier's left continues to extend past the eddy zone and into the tundra mirroring the existing shape of the old growth and asymmetrical lines. In the lower eddy zone, adjacent to the old growth treeline, there is an absence of seedlings and an overabundance of dead trees, which is potentially due to the pooling of cold air at night or resource competition as the treeline moves

upwards. Thus, it appears as though there are preferential areas to establish and specific regions where tree mortality is likely to occur. Moreover, it appears as though and these regions of seedling survivorship are at distinct, separate elevations.

A logistic regression (Fig. 3) based on elevation and survivability reveals that mean elevation for living trees differs from mean elevation of dead trees. For the region above the treeline, the regression predicts a switching elevation between dead and live trees at approximately 3507 m with an r^2 value of 0.301. This regression indicates that there is a significant correlation between elevation and survivability and that trees are surviving at a higher elevation above treeline than dead trees. This distinct pattern of live seedlings establishing in an abrupt, distinct band in the upper eddy zone might indicate a feedback in which mature, abrupt treelines facilitate the growth subsequent abrupt treelines in the sheltered zones they create upslope. In other words, abrupt treelines structures create more abrupt treelines that are likely to advance at very slow rates.

Temperature regimes

In order to understand the spatial structure of seedling recruitment, we examined temperature distributions within the AOI at night just before sunrise and during the day at solar noon. Interpolation of the temperature grid reveals distinct temperature patterns within the transect during the night (fig. 4) and day (fig. 5). At night, the old growth forest exhibits the warmest temperatures (~ -1.5˚C) as illustrated by the red and white bands in (fig. 4). These warm

temperatures can be attributed to the large quantity of trees in the forest radiating heat and warming up the entire region around them. Tree temperatures average in at approximately 3˚C and the ground temperature around 0 ± 2˚C. The coldest region (~ -6.5˚C), shown by the green band in fig. 4, exists in the upper eddy zone. This cold (green) band is likely the signature of the cold pool of air that dams up against the treeline at night. The extremely cold ground temperatures result from a lack of mixing between the dense and cold pool of air and warmer air from the upper atmosphere. Although this band of cold ground temperatures was expected, we anticipated its existence closer to the old growth treeline instead of in the upper eddy zone. This could be because the forest is radiating so much heat that the effects cold air pool are offset by the radiative heating effects from the forest. Fig. 6 , which is a image taken looking downslope, shows these temperature discrepancies between the forest and the ground temperatures during the early morning and aids in understanding how the the heat radiation from the forest could offset the effects of the cold air pool. The tundra overall exhibits warmer temperatures than the cold pool directly below it, likely due to cold air flowing freely over the tundra allowing for mixing of warmer air from the upper atmosphere.

The daytime interpolation (fig. 5) reveals that temperature patterns are almost entirely reversed from the nighttime regime. The lower forested old growth zone has now become the coldest region due to a dense canopy that inhibits any solar radiation from reaching the forest floor. As a result, this area remains the coldest (~4.5˚C) throughout the course of the day. In the upper eddy zone, the coldest region at night becomes the warmest area (~15.5˚C) during the day. This is likely due to a combination of a high exposure to solar radiation and wind sheltering provided by the treeline. Because the air is more stagnant within the eddy zone, it has more time

to warm up from the ground and remain warm due to lack of mixing with cooler air from the upper atmosphere. The kriged interpolation of the lower eddy zone illustrates some temperature variability in the region with pockets of ground temperatures ranging between 6 and 14˚C. While the interpolation does not capture the extent of this variability created by the cold shadows cast by trees, as shown by the FLIR image (Fig. 7), it does still successfully demonstrate that this region is not as homogenous as the other zones. These shadows and greater canopy cover likely have an effect on seedling growth as ground temperatures within shadows remain in the 1˚C range all day.

Upon noticing somewhat of a reversal of temperatures between the night and day regimes, the temperatures were plotted against each other to see if there was any significant correlation. The regression (Fig. 8) reveals little to no relationship between night and day temperatures within the entire AOI with an r^2 value of 0.023. This regression of the entire AOI indicates that night and day temperatures are not as strongly correlated as they appear when visually comparing the night and day kriged temperature maps. Though the regression of the entire AOI indicates little to no relationship, when qualitatively looking at figure 4 and 5, the coldest region during the night significantly overlaps with the warmest region during the day. Therefore, although the regression does not show a reversal of day and night temperatures within the AOI, it is important to note that the upper eddy zone does have the greatest temperature extremes.

Temperature and seedling distribution

When seedling locations are overlaid on the kriged temperature maps, they do not appear

to be randomly distributed in relation to temperature. To quantify and analyze whether

distribution is in-fact related to temperature, a chi-squared statistical test was conducted. The null

hypothesis in every case assumed that seedlings are randomly distributed and that their

distribution is proportional to the size of the temperature class polygon created by the

interpolation. The alternate hypothesis states that seedlings are not randomly distributed in

proportion to each of the temperature classes. To find actual counts of seedlings present in each

temperature class polygon, the points within each polygon were summed up. To calculate the

number of expected seedlings in each polygon, the area of each polygon temperature class was

summed up and then divided by the total area of interest. Using this proportion, we multiplied

the total number of seedlings in the entire AOI by these proportions to find the expected count

for each polygon temperature class. Using the chi-squared analysis, we were able to differentiate

and analyze whether the distribution of seedlings within these temperature classes was random or

not. Because we calculated each temperature class individually against the entire AOI, a

Bonferroni adjustment for the p-value was necessary. Instead of comparing against the standard

p-value of 0.05, we compared our p-values against a more stringent value of 0.01.

Placed on top of the map of night temperatures, seedlings cluster densely directly on top

of the coldest band (green) of ground temperatures in fig. 4. A lower-than-expected quantity of

seedlings appear in the other temperature regions, especially in the warmer tundra zone and the

much warmer lower eddy zone, which is predominantly composed of dead seedlings. The

chi-square test (Table 1) revealed that the seedlings were significantly overrepresented in the

coldest region (green) or gridcode 1 (upper eddy zone). The expected count, based on the size of

that temperature class, was around 52.67 seedlings, yet the actual count was 131 seedlings. The resulting X^2 value was 52.67, df=1 and p-value was 0.0001, which is statistically significant and indicates that seedlings are not randomly establishing in this area based on temperature. This is surprising, as we would expect seedlings to avoid the coldest temperatures based on temperature thresholds for growth. Other statistically significant findings were found in gridcodes 2 (tundra and mid eddy zone) and 3 (lower eddy zone), which correspond to the yellow and orange regions respectively. In these two regions, seedlings were found to be underrepresented (gridcode 2: X^2=30.98, df=1, p-value=0.0001 and gridcode 3: X^2=11.80, df=1, p-value= 0.0006) indicating that seedlings are avoiding this lower eddy zone. The concept of growing degree days is widely recognized and best understood as a minimum development threshold that growing season temperatures must exceed for growth. In this case, gridcode regions 2 and 3 could be cold enough during both the night and day that the degree day threshold might not be reached. When a chi-square test was conducted for dead seedlings (Table 2), no statistically significant findings were discovered. This indicates that dead seedlings are randomly distributed throughout the AOI with respect to recorded nighttime temperatures.

Considering that extremely low temperatures are not conducive to growth and survival, it was surprising to see such a high concentration of seedlings established in the coldest and most exposed region during the night. Despite being characterized by the worst growing conditions with the cold air pool and a high percentage of open sky, the upper eddy zone is seeing the highest seedling recruitment. Because the nighttime conditions cannot logically explain the presence of seedlings in this zone, daytime conditions could be having an overwhelming influence on seedling establishment and distribution. Additionally, it is surprising to see less

seedlings and significantly more dead trees establishing in the lower eddy zone which is relatively warm during both the night and day due to radiative heat from trees and sheltering. One potential explanation is that this inhospitable environment during the night, could be very conducive to growth during the day and vice versa.

During the day, when seedlings are placed on top of the temperature map, seedlings tend to distribute in the warmer regions of the map. The coldest zone during the night becomes the warmest region during the day. Interestingly, the seedlings cluster densely in the second warmest temperature zone between 12.3-14.3˚C, yet tend to avoid the hottest region that ranges between 14.4-16.4˚C. This is likely because too much heat will result in desiccation of the seedlings (Harsch et al. 2011). Additionally, a study conducted on physiological limits of Engelmann spruce shows that spruces prefer moderated microclimates that are neither too hot nor too sheltered. Therefore, they are likely avoiding the extremely warm zone because they are not physiologically adapted to those conditions (Bansal et al. 2011). The seedlings tend to overall avoid the lower eddy zone, which during the day has the most heterogenous temperatures. This is somewhat surprising because this area likely receives the highest seed input, yet the lack of seedlings indicates that there are negative effects of the extremely cold shadows cast by the saplings in this zone. These findings rival all other conclusions (Smith et al. 2003) about canopy cover and shading being beneficial to seedling growth. Under the current circumstances on Pike's Peak, the sheltered eddy zone created by the abrupt treeline is likely providing the sheltering that neighboring vegetation would otherwise provide and therefore, the neighboring vegetation is only heavily shading seedlings in this zone, likely discouraging growth.

For the daytime regime, the temperature class ranging from 10.2-12.2˚C appeared in the lower eddy zone as well in the tundra. To distinguish between those two zones, which are very different microclimates due to the shadow heterogeneity of the lower eddy zone, these two polygons were separated for the chi-square test into "gridcode 4 tundra" and "gridcode 4 eddy". The chi-square test for the daytime regime (Table 3) revealed that seedlings were significantly underrepresented (X^2=20.80, df=1, p-value=0.0001) in gridcode 4, the cool tundra zone (coded orange in fig. 5) with an expected count of 28.92 and an actual count of 6 seedlings. The test also showed that seedlings were significantly overrepresented (X^2=35.21, df=1, p-value=0.0001) in in gridcode 5(upper eddy zone, coded pink in fig. 5) with almost twice the seedlings found than expected. Lastly, the test found that dead seedlings were significantly overrepresented in gridcode 4 eddy in the lower eddy zone (X^2=19.97, df=1, p-value=0.0001). These chi-square results show that daytime temperature has a larger impact on seedling distribution (dead and live) than the nighttime regime.

These temperature and distribution results overall indicate that seedlings are preferentially distributing into areas that appear to be the warmest during the day and coldest at night, which happens to be in the upper eddy zone. The distribution of dead trees in the lower eddy zone is overwhelmingly impacted by the daytime temperature regime. Overall, daytime temperatures and how they interact with microclimates are likely having a greater effect on seedling distribution than the nighttime temperatures.

Growth and distribution

The growth and distribution relationship was analyzed in a similar manner to the temperature and seedling distribution by interpolating growth residuals (Fig. 9). The preferred interpolation for this analysis was spline instead of kriging, because spline managed to maintain a high resolution image of the variability in growth residuals throughout the AOI. On the map, the red and white colors are the only growth classes that represent positive growth residuals, or more growth than expected based on a linear relationship between height and top bud growth. The remaining color classes (orange, yellow and green) represent growth that was worse than expected. From a purely qualitative analysis, seedlings appear to cluster and distribute in areas that of good growth in the upper eddy zone. This qualitative analysis is confirmed by a chi-square test (Table 5) revealing that seedlings are distributing in areas of good growth and are significantly overrepresented in gridcodes 4 (X^2=25.88, df=1, p-value=0.0001) and 5 (X^2=2.26, df=1, p-value=0.0001) which correspond to the red and white regions respectively. They are also surprisingly overrepresented in gridcode 3 (X^2=80.38, df=1, p-value=0.0074) which does represent negative growth residuals. This may be due to the nature of the spline interpolation and how it interpolated between point values. Not surprisingly, seedlings are significantly underrepresented (X^2=63.98, df=1, p-value=0.0001) in regions of poor growth. Dead seedling calculations (Table 6) reveal that they are overrepresented in the region that represents the worst growth, which appears to be around the lower eddy zone. As predicted, their distribution is likely driven by mortality. In contrast, not only is the upper eddy zone a preferential area to establish, but also an area of good growth. The microclimate in this upper eddy zone created by the eddy and the absence of shadows appears to create an area that is conducive to growth. In contrast, the

regions that represent the worst growth also appear to have the highest concentration of dead seedlings. Therefore, mortality is likely tied to distributions of lower than expected growth.

Overall, this analysis shows that seedlings are recruiting into areas and near other seedlings that are growing well. This is likely indicator that a certain microclimate exists where these seedlings are recruiting and is also conducive to growth.

Temperature and growth

To understand whether growth is tied directly to ground temperature, growth residual values and ground temperature values, obtained by extracting the temperature raster data to each to each of the seedling points, were plotted against each other. As growth and meristem activity is limited by temperature (Körner and Paulsen 2004), we would expect to see a positive relationship between temperature and growth - the warmer the temperatures at both night and day, the better the growth. Our results, surprisingly, did not show this strong positive relationship between temperature and growth.

Night ground temperatures versus growth (Fig. 10) showed an inverse relationship where growth residuals increased with decreasing temperatures. The reported r^2 value was 0.098 indicating that very little of the variation in this graph could truly be predicted by the linear regression. Therefore, there are other unmeasured factors or covariates that are affecting growth at treeline other than ground temperature. In contrast, day temperatures plotted against growth residuals (Fig. 11) revealed a positive relationship between temperature growth, as expected. The warmer daytime temperatures were also associated with the best growth. While this relationship exists, the r^2 value, again, was very low at 0.109. As with the night temperatures, there are likely

other missing factors that are affecting growth other than just temperature. Existing literature points to snow cover and duration, canopy cover and air temperature as other likely factors influencing growth at treeline.

While the individual night and day vs. temperature graphs revealed weak relationships, we wanted to see whether seedlings were growing well with a certain combination of night and day temperatures. When the day and night temperatures of the seedlings, obtained by extracting kriged raster data from the seedlings points, were plotted against each other (Fig. 12), a strong relationship arose. The regression, with an r^2 value of 0.77, shows that seedling are preferring areas that are either warm during the day and cold at night or warm at night and cold during the day. They are entirely avoiding regions that are both cold during the night and day, and warm during the night and day. It is reasonable that seedlings would completely avoid areas that are both cold during the night and day due to an inability to accumulate degree days, yet the lack of data points in the warm day and night region is surprising. While this microclimate might be theoretically favorable, it may not exist in reality at this abrupt treeline. The areas that are warm at night are cold during the day due to the dense canopy of the old growth forest and the extremely cold shadows of the saplings in the lower eddy zone. Therefore, the seedlings may have no other option than to seek out areas that are at warm during at least one portion of the 24hr period. Considering the carbon sink theory in which seedlings are able to photosynthesize at low temperatures, but unable to utilize that stored carbon for growth, seedlings may be able to acquire carbon under cold or warm conditions, but must be in a warm region during either the day or night to at least grow (Smith et al. 2003). Additionally, degree growing day theories support this data and could explain why warm temperatures during a portion of the 24-hour

period could be sufficient for growth. Therefore, it is reasonable to see seedlings establishing in areas that are warm during the day and cold at night or vice versa.

Conclusion

The 2016 study of the microclimate and seedling distribution at an abrupt treeline on Pike's Peak reveals several feedbacks involved in facilitating and inhibiting upwards movement of abrupt treelines. Our results show that seedlings are significantly distributing into the second warmest region during the day and the coldest region at night. This indicates that seedlings prefer to distribute in areas that see warm ground temperatures during the day (~12-14ºC) and cooler temperatures (~-7--6ºC) at night. Existing literature points to root growth of other conifer species being limited below 5-8ºC and rapidly increasing within the 10-20ºC range (Vapaavuori et al. 1992, Korner 2004, Lopushinsky et al. 1990). If seedlings have a difficult time growing below ~4-8˚C range and the seedlings are still distributing into regions at night that drop far below the temperature threshold, the daytime regime, which reaches the perfect temperature range for growth, is likely responsible for the presence of seedlings in this zone. In addition to literature on the temperature thresholds for growth, many studies that focus on plant growth for agricultural purposes have focused on the concept of growing degree days. The theory of degree days stems from the fact that plant development depends on temperature and that, plants need to accumulate a specific amount of heat to continue developing (Miller et al. 2001). If we apply the idea of degree days to seedlings at treeline, this could indicate that seedlings only need to accumulate a certain amount of heat throughout the growing season. Therefore, the warm daytime

temperatures present in the upper eddy zone might be sufficient for continued growth, despite the

fact that the same zone frequently drops far below the growth threshold at night.

Since seedlings are practically underrepresented (some areas more significant than

others) in all other regions, which shows that there is a significant pattern in distribution with

respect to ground temperature, the upper eddy zone must be an extremely conducive

microclimate for growth, likely created by the sheltering of the eddy. The other areas of

underrepresentation (lower eddy zone and tundra) are somewhat expected. The lower eddy zone

is likely a poor microsite for growth due to the cold shadows cast by the trees (which remain in

the 1ºC range during the day and are even colder at night) or due to the heavy accumulation of

snow from the eddy structure, which leads to a higher susceptibility to snow fungus and

mortality. The tundra was also expected to have a lower quantity of trees as the area is not

protected or moderated by the eddy leading to exposure to temperature extremes and high winds.

The findings of under representation in the lower eddy zone disagree with existing literature on

microsite facilitation and the benefits of growing on the leeward side of other vegetation (Pyatt et

al. 2016, Greenwood et al. 2015, Renard et al. 2016, Harsch et al. 2011). The saplings in this

lower eddy zone may provide some warmth during the night by capturing radiating heat, but the

ground in this region still remains below freezing at night. During the day, the shading is so

intense, that the ground temperatures barely rise above the aforementioned temperature

threshold. In the case of our abrupt treeline, there is already sheltering from the eddy and

therefore, the climate mediating effects of neighboring vegetation are negated by the larger

shelter structure and the cold shadows. Additionally, due to the nature of the eddy created by the

abrupt treeline, snow drifts are likely to accumulate and persist for too long in the lower eddy

zone, which could also be causing mortality during the winter season. Thus, in these other regions, besides the upper eddy zone, seedlings are likely underrepresented due to a combination of factors mentioned above and potentially other factors that have not been explored yet. In an abrupt treeline setting, where there is a larger sheltered microclimate, microsite facilitation from neighboring vegetation may not be as important as it was previously thought (Renard 2016, Pyatt 2016, Smith 2003).

Seedling growth and distribution analysis reveals that seedlings are preferentially distributing into regions and zones of observed good growth or areas where terminal buds grew the most during the growing season. Coincidentally, this zone of good growth coincides with the same region that is warm during the day and cold at night. Therefore, there might be some ties to how these fluctuations in temperature might lead to better growth observed through terminal bud lengths. Existing literature on the temperature effects on growth and development of Engelmann spruce states that night temperature was the most important factor in promoting all aspects of growth, except for terminal bud formation, which was controlled by day temperatures (Hellmers et al. 1970). Since the regions of good growth overlap with the warmer day temperatures, our data matches and is supported by previous findings. Therefore, the daytime temperatures may be responsible for the observed good growth in the upper eddy zone.

Seedling growth and distribution analysis also reveals that distribution is tied to mortality, or that there is an absence of trees in areas where growth is bad. In other words, this means that trees are likely dying from experiencing consistently poor growth year after year. High mortality of trees in this region could be linked to a number of factors. As literature has previously pointed to, persistence of snow into the growing season can make seedlings more

susceptible to snow fungi (Harsch et al. 2011). During the summer, desiccation, overheating and photodamage are cited causes of seedling mortality (Harsch et al. 2011). Desiccation and photodamage are unlikely in the lower eddy zone, as saplings provide adequate shading from intense sunlight and slower moving air within the eddy zone would reduce mixing resulting in lower transpiration rates. Therefore, there are likely multiple variables at play and for future research, it will be valuable to establish and find out which season is likely causing the majority of the poor growth and resulting seedling mortality.

Upon comparing temperature and growth, analysis shows that temperature is not the sole factor in influencing growth, and thus, some unmeasured covariate is likely impacting growth of the seedlings. Regressions between growth residuals and day or night temperatures shows no strong correlations. This means that solely temperature cannot predict how well seedlings will grow, but does not mean that temperature doesn't play a role. It is likely a combination of endogenous and exogenous factors that need to be further explored.

These results point to the most prevalent and important conclusion of this study that, this abrupt treeline structure on Pike's Peak is creating a microclimate that is facilitating the establishment of another abrupt treeline several meters above the existing one. Once this new treeline, currently composed of young seedlings matures, it is likely to perpetuate the current pattern and create another abrupt treeline just upslope of itself. Thus, the slow advance of abrupt treelines can be explained by this feedback process that requires the growth and maturity of seedlings in order to continue advancing.

The shape, location and movement of this treeline is therefore determined by both exogenous and endogenous factors. The warming climate in conjunction with the eddy may have

enabled initial establishment above the current treeline, but the current microclimates and small scale factors are likely to perpetuate and facilitate this upwards movement in the future. Therefore, for future studies of treeline dynamics, it will be important to consider these internal and external factors working on multiple scales to fully understand all the mechanisms at play.

The next steps in this research will be to quantitatively understand the effects of canopy cover on seedling distribution and how the microclimates at this abrupt treeline are influencing snowpack and snow accumulation. Quantitatively analyzing canopy cover using the spherical densiometer measurements will elucidate and confirm conclusions about the effect that canopy cover has on seedlings. Analyzing snowpack can further clarify other feedback mechanisms for growth and whether snow accumulation at this field site is promoting or inhibiting growth.

Overall, this research has added to the knowledge and discussion about treeline dynamics and formation by specifically focusing on the micrometeorology and feedback mechanisms present at an abrupt treeline. The insensitivity of abrupt treeline structures to climate change and global warming trends is now somewhat understood and similar research can be applied to study other treelines. Ultimately, this research aids in understanding how abrupt treelines may respond to warming global temperatures and how future treelines may look as a result.

Appendix A: Figures

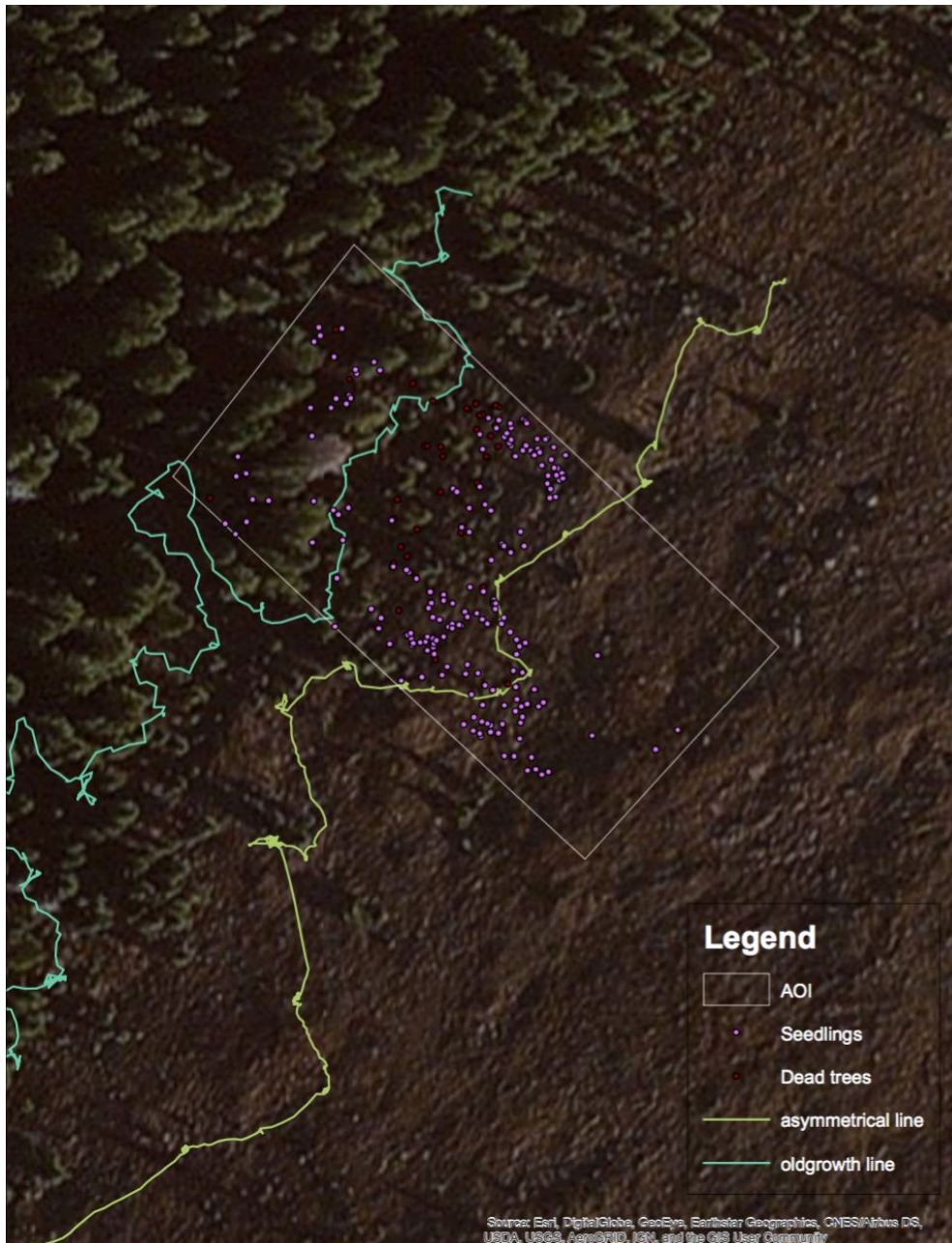Figure 1: Map of AOI with live and dead seedlings

Fig. 1 shows the AOI overlaid on an aerial image of the field site. GPS locations of live seedlings (<30 cm) are shown in light purple and the dead seedling locations are shown in dark red. The old growth treeline is represented by the teal line and the end of the "eddy zone" is shown by the light green line.

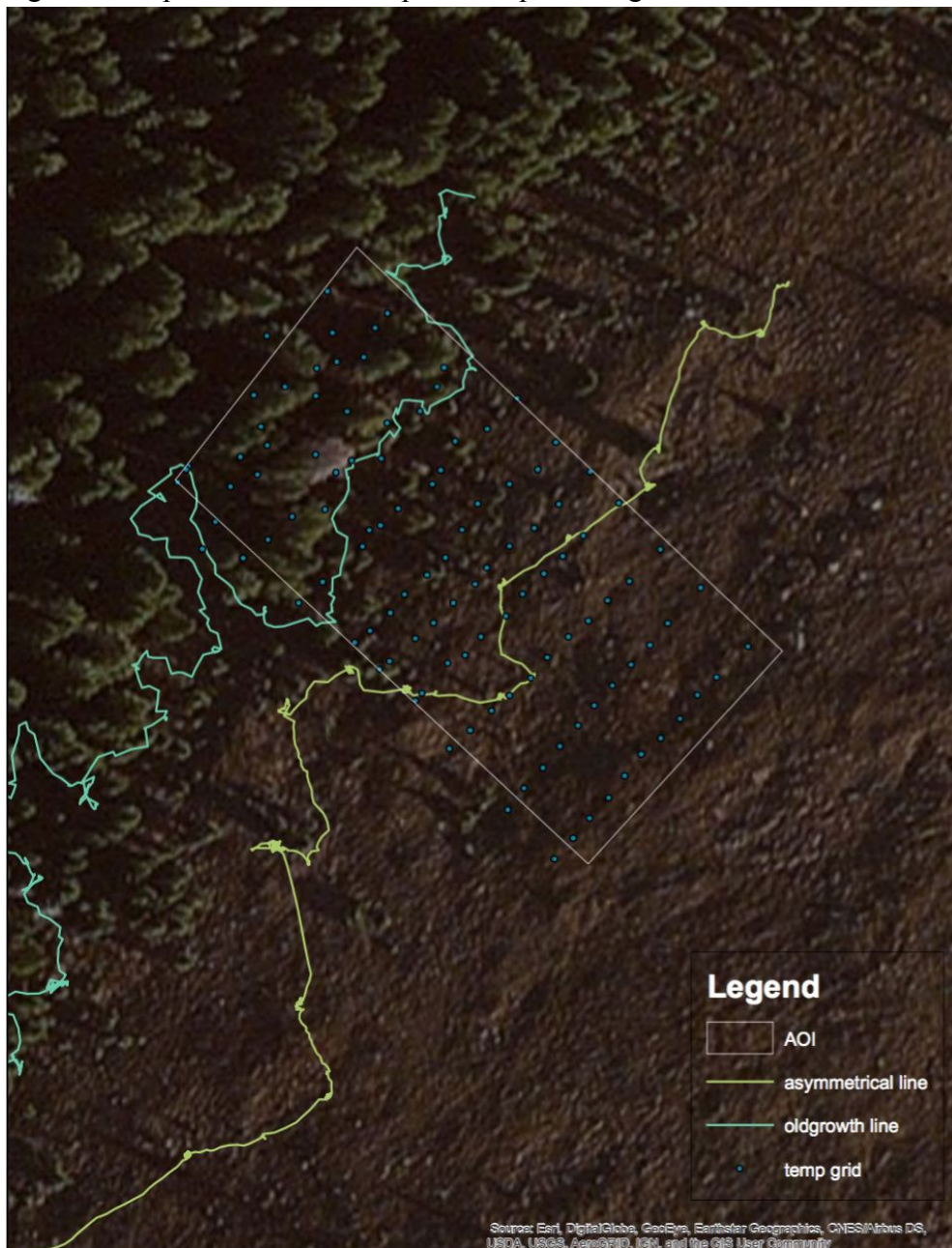Figure 2: Map of AOI with 110-point temperature grid

Fig. 2 shows a similar image to fig. 1 with locations of the temperature grid shown by the blue dots instead of seedling locations. The temperature grid consists of 10 rows of 11 points. The distortion in the grid closer to the old growth forest is likely due to satellite obstruction from large trees.

Figure 3: Logistic regression
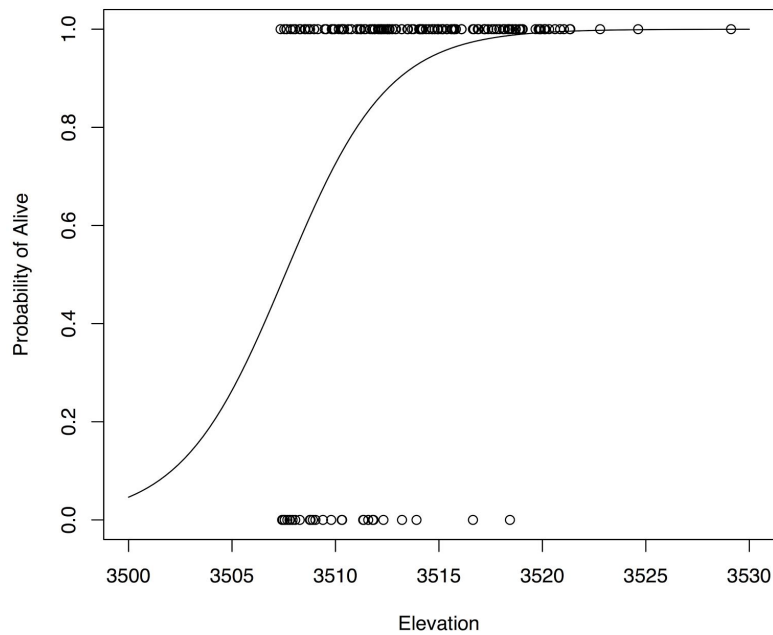
This logistic regression shows that there is a distinct elevation at which we can predict whether or not seedlings will be alive. Conducted for seedlings above the old growth treeline and within the AOI, this logistic regression shows trees above approximately 3507 m will survive.

Figure 4: Kriged nighttime temperature map with seedling distribution
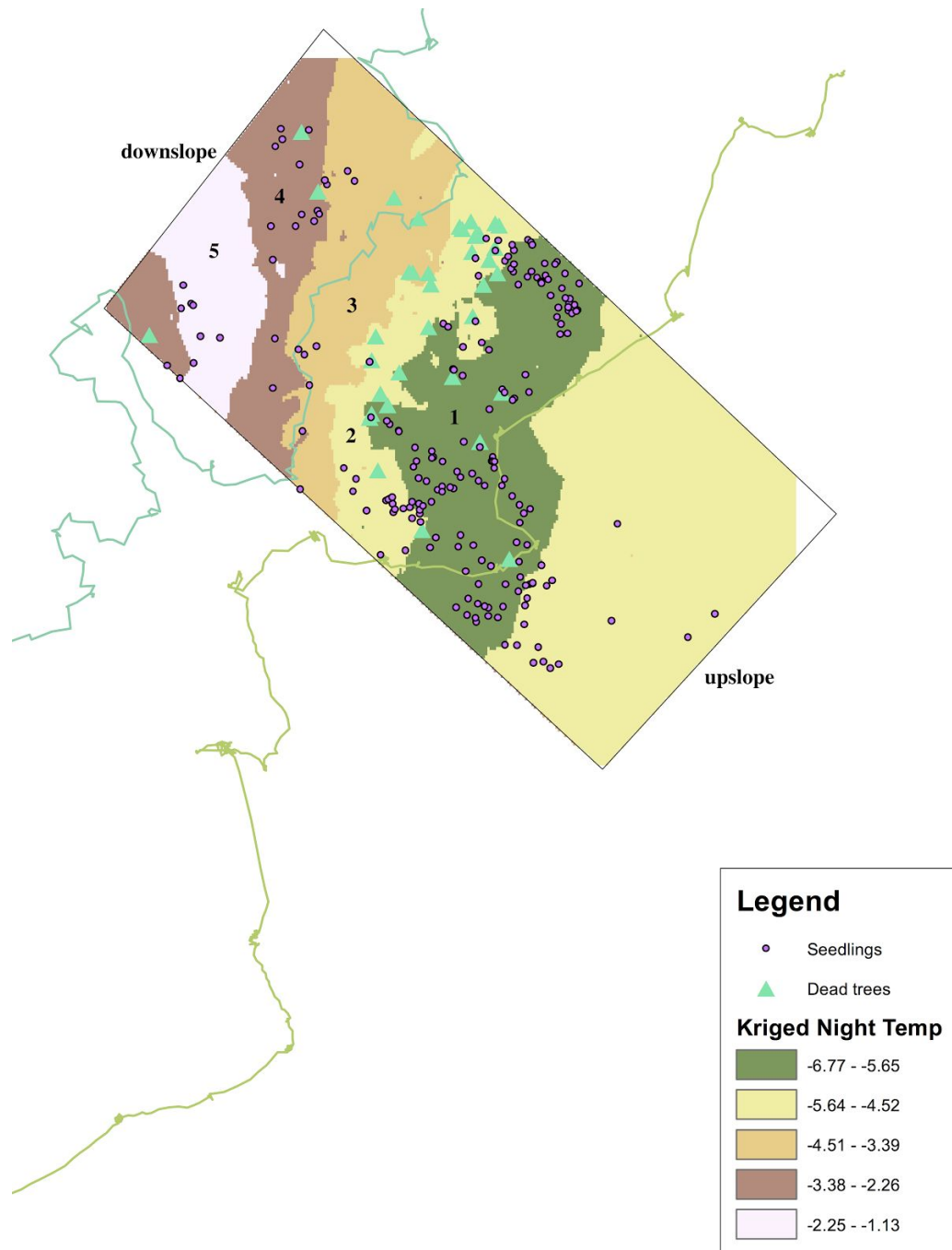

Fig. 4 shows the kriged nighttime temperature map with seedling distributions overlaid. Coldest temperatures are represented by the green and the warmest temperatures are shown by the light pink. Live seedlings (purple dots) appear to cluster in the green band, whereas dead seedlings are predominantly found in the yellow zone closer to the old growth treeline.

Figure 5: Kriged daytime temperature map with seedling distribution
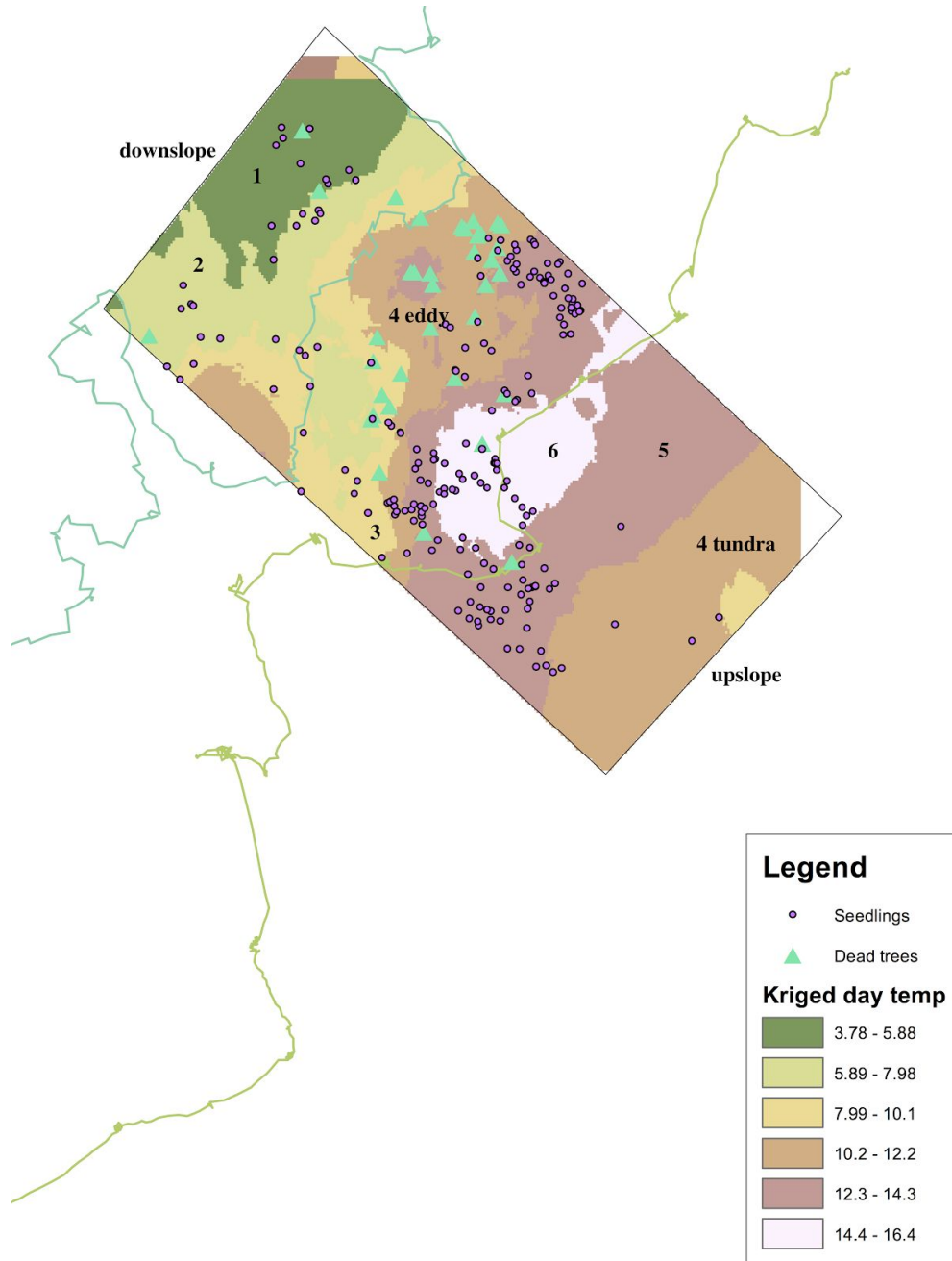
Fig. 5 shows the daytime kriged temperature map with seedling distribution overlaid. The coldest temperatures are still represented by the green and the warmest shown by the light pink. In contrast to fig. 4, the coldest region is now in the old growth forest and the warmest region is in the upper eddy zone. Seedlings appear to cluster, not in the warmest region, but in the second-warmest temperature class (salmon color). The lower orange region (next to the old growth forest) is distinct from the upper orange region (in the tundra) as they are two very different microclimates with similar interpolated temperatures.

Figure 6: Early morning downslope FLIR IR image
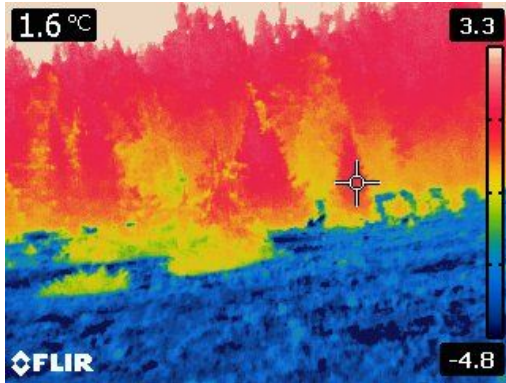
Taken early in the morning, this image shows that trees are around 3.3ºC during the coldest time of the day and the ground is significantly colder around -4.8ºC.

Figure 7: Afternoon FLIR IR image of shadows
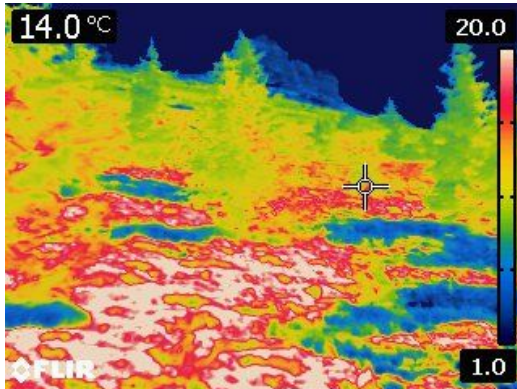
This image shows the heterogeneity in the lower eddy zone where the ground remains shadowed by trees. The ground with direct sun exposure shows temperature readings around 20ºC+, whereas the shadows remain in the 1ºC range.

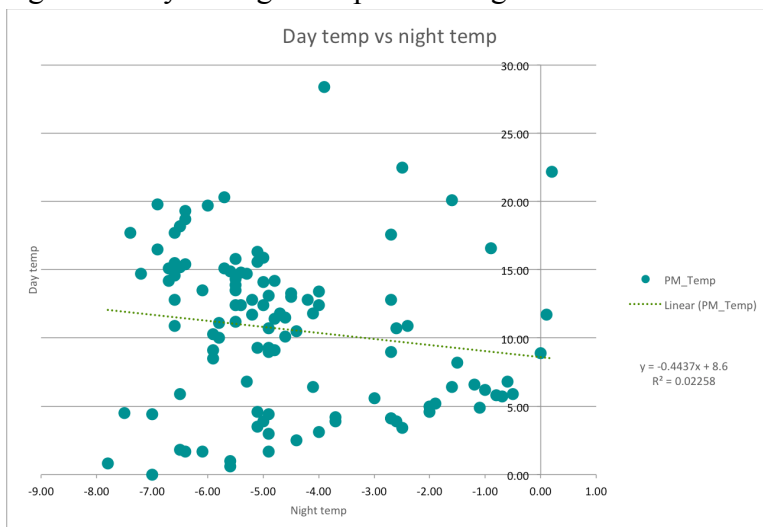Figure 8: Day vs. night temperature regression

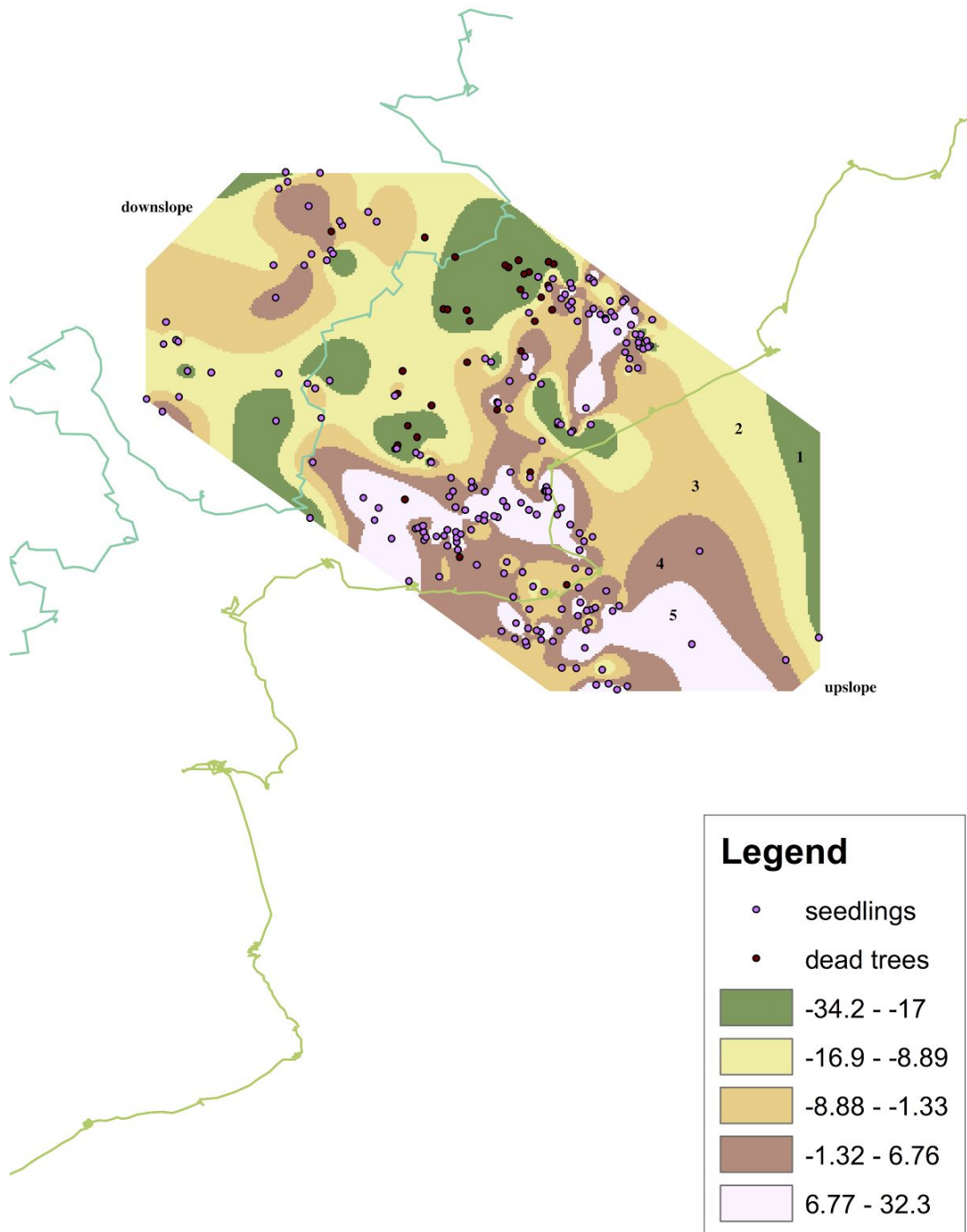Figure 9: Growth residual spline interpolation map

Fig. 9 shows a spline interpolation of the growth residuals. Light pink represents zones of positive growth residuals (ie. good growth) and green represents zones of the worst growth. Seedlings appear to cluster in zones of good growth and dead seedlings appear to be concentrated in the zones of worst growth (green and yellow).
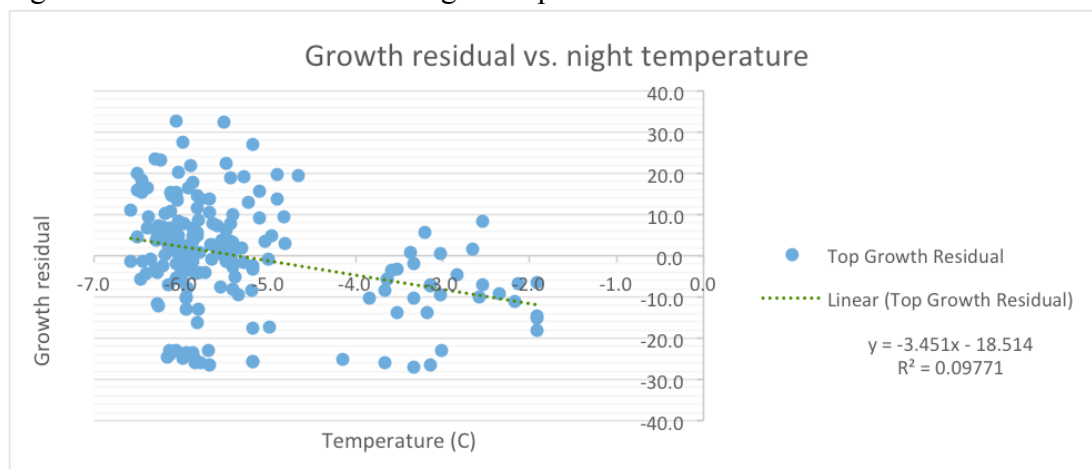
Figure 10: Growth residuals vs. night temperature

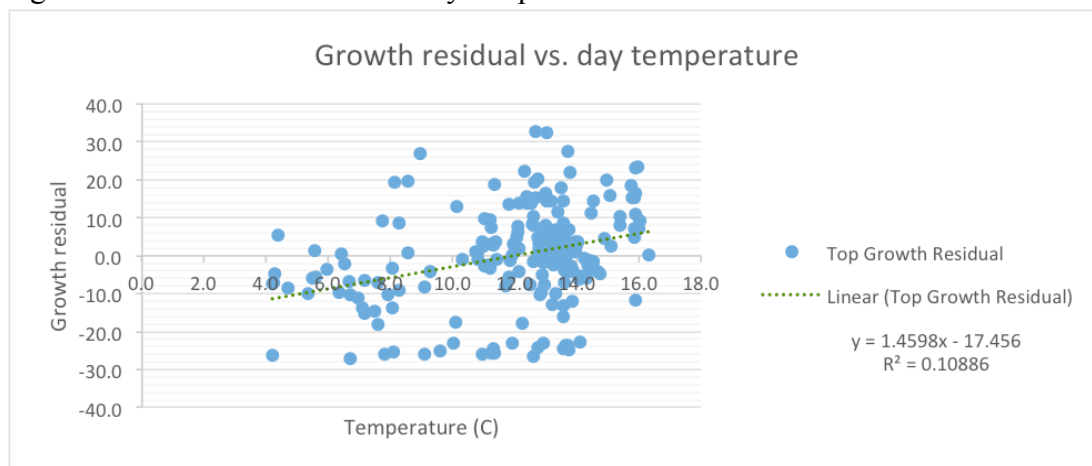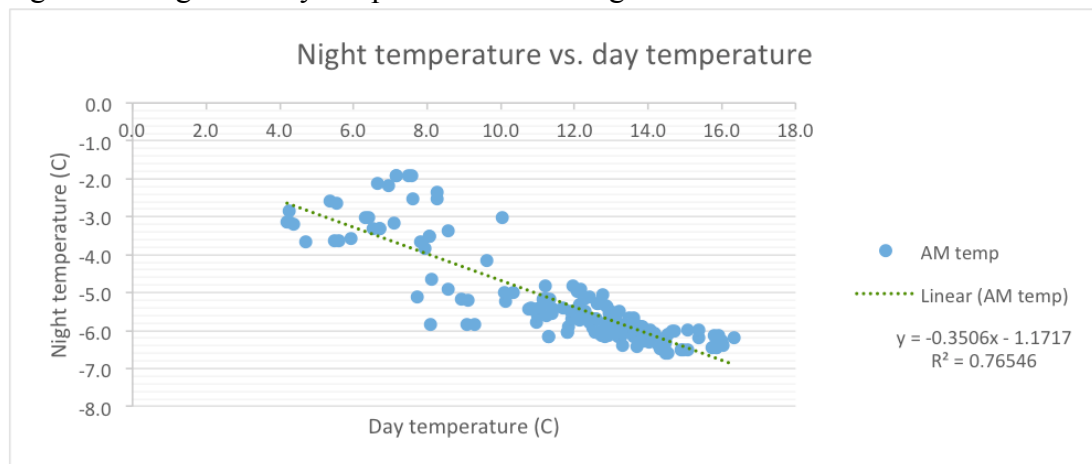Figure 11: Growth residuals vs. day temperature

Figure 12: Night vs. day temperature of seedlings

Appendix B: Tables

Table 1: Chi-square test for nighttime distribution (alive)

GRIDCODE	TEMP VALUES (ºC)	COUNT	EXPECTED COUNT	X^2	df	PVAL	REPRESENTATION
1	-6.77 to -5.65	131	52.67254313	151.091	1	0.0001	Overrepresented
2	-5.64 to -4.52	54	95.60217822	30.976	1	0.0001	Underrepresented
3	-4.51 to -3.39	18	37.17697611	11.802	1	0.0006	Underrepresented
4	-3.38 to -2.26	18	29.33967346	5.024	1	0.025	Underrepresented
5	-2.25 to -1.13	9	15.33723845	2.808	1	0.0938	Underrepresented

Table 2: Chi-square test for nighttime distribution (dead)

GRIDCODE	TEMP VALUES (ºC)	COUNT	EXPECTED COUNT	X^2	df	PVAL	REPRESENTATION
1	-6.77 to -5.65	10	8.208708021	0.405	1	0.5247	Overrepresented
2	-5.64 to -4.52	18	14.89904076	0.69	1	0.4063	Overrepresented
3	-4.51 to -3.39	5	5.793814459	0.111	1	0.7395	Underrepresented
4	-3.38 to -2.26	3	4.572416643	0.55	1	0.4582	Overrepresented
5	-2.25 to -1.13	0	2.39021898	2.415	1	0.1202	Underrepresented

Table 3: Chi-square test for daytime distribution (alive)

GRIDCODE	TEMP VALUE (ºC)	COUNT	EXPECTED COUNT	X^2	df	PVAL	REPRESENTATION
1	3.78 to 5.88	13	23.04111648	4.867	1	0.0274	Underrepresented
2	5.89 to 7.98	24	32.92093497	2.825	1	0.0928	Underrepresented
3	7.99 to 10.1	16	25.59287207	4.048	1	0.0442	Underrepresented
4 eddy	10.2 to 12.2	34	32.47500966	0.083	1	0.7733	Overrepresented
4 tundra	10.2 to 12.2	6	28.9205011	20.804	1	0.0001	Underrepresented
5	12.3 to 14.3	105	64.62155261	35.213	1	0.0001	Overrepresented
6	14.4 to 16.4	30	20.56037029	4.764	1	0.0291	Overrepresented

Table 4: Chi-square test for daytime distribution (dead)

GRIDCODE	TEMP VALUE (°C)	COUNT	EXPECTED COUNT	X²	df	PVAL	REPRESENTATION
1	3.78 to 5.88	1	3.590823348	1.898	1	0.1683	Underrepresented
2	5.89 to 7.98	3	5.13053532	0.905	1	0.3415	Underrepresented
3	7.99 to 10.1	7	3.988499544	2.311	1	0.1284	Overrepresented
4 eddy	10.2 to 12.2	15	5.061040467	19.97	1	0.0001	Overrepresented
4 tundra	10.2 to 12.2	0	4.507091081	4.601	1	0.032	Underrepresented
5	12.3 to 14.3	9	10.07089132	0.119	1	0.7302	Underrepresented
6	14.4 to 16.4	1	3.204213552	1.534	1	0.2155	Underrepresented

Table 5: Chi-square test for growth residual distribution (alive)

GRIDCODE	COUNT	EXPECTED COUNT	X²	df	PVAL	REPRESENTATION
1 (worst growth)	19	12.79433055	3.219	1.000	0.0728	overrepresented
2	25	80.68375891	63.981	1.000	0.0001	underrepresented
3	99	80.38197682	7.164	1.000	0.0074	overrepresented
4	50	25.88088783	25.783	1.000	0.0001	overrepresented
5 (best growth)	9	2.25904589	20.328	1.000	0.0001	overrepresented

Table 6: Chi-square test for growth residual distribution (dead)

GRIDCODE	COUNT	EXPECTED COUNT	X²	df	PVAL	REPRESENTATION
1 (worst growth)	12	2.153501182	48.1730	1.0000	0.0001	overrepresented
2	12	13.58043467	0.3060	1.0000	0.5801	underrepresented
3	9	13.52963966	2.5190	1.0000	0.1125	underrepresented
4	1	4.356189041	2.9700	1.0000	0.0848	underrepresented
5 (best growth)	0	0.380235447	0.3840	1.0000	0.5353	underrepresented

References Cited

"Interpolating Surfaces in ArcGIS Spatial Analyst" Colin Childs, *ESRI Education Services*

Bansal, S., Reinhardt, K and Germino, M. (2011) "Linking carbon balance to establishment patterns: comparison of whitebark pine and Engelmann Spruce seedlings along an herb cover exposure gradient at treeline." *Plant Ecology,* 212: 219-228.

Case, B and Duncan, R. (2014) "A novel framework for disentangling the scale-dependent influences of abiotic factors on alpine treeline positions." *Ecography,* 37: 838-851.

Grace, J., Berninger, F and Nagy, L. (2002) "Impacts of climate change on treeline." *Annals of Botany,* 90: 537-544.

Greenwood, S., Chen, J., Chen, C. and Jump, A. (2015) "Temperature and sheltering determine patterns of seedling establishment in an advancing subtropical treeline." *Journal of Vegetation Science,* 26(4): 711-721.

Hagedorn, F., Shiyatov, S., Mazepa, V., Devi, N., Grigor'ev, A., Bartysh, A., Fomin, V., Karpalov, D., Terent'ev, M., Bugman, H., Rigling, A and Moiseev, P. (2014). "Treeline advances along the Urals mountain range - driven by improved winter conditions?" *Global Chang Biology,* 20: 3530-3543.

Harsch, M., Hulme, P., McGlone, M and Duncan, R. (2009) "Are treelines advancing? A global meta-analysis of treeline response to climate warming." *Ecology Letters*, 12: 1040-1049.

Harsch, M and Bader, M. (2011) "Treeline form - a potential key to understanding treeline dynamics." *Global Ecology and Biogeography,* 20: 582-596.

Hellmers, H., Genthe, M., Ronco, F. (1970) "Temperature affects growth and development of Engelmann Spruce." *Forest science,* 16(4):447-452.

Körner, C and Paulsen, J. (2004) "A world-wide study of high altitude treeline temperatures." *Journal of Biogeography,* 31: 713-732.

Kroiss, S. and HilleRisLambers, J. (2015) "Recruitment limitation of long-lived conifers: implications for climate change responses." *Ecology,* 96(5):1286-1297.

Lopushinsky, W., Max, T.A. (1990) "Effect of soil temperature on root and shoot growth and on budburst timing in conifer seedling transplants." *New Forests,* 4(2): 107-124.

Malanson, G. et. al. (2013) " Alpine treeline of western North America: linking organism-to-landscape dynamics." *Physical Geography,* 28(5): 378-396.

Malanson, G., Resler, L., Bader, M., Holtmeier, F., Butler, D., Weiss, D., Daniels, L and Fagre, D. (2011) "Mountain Treelines: a Roadmap for Research Orientation." *Arctic, Antarctic, and Alpine Research,* 43(2): 167-177.

Marchand, P. (1987). *Life in the cold: an introduction to winter ecology.* University Press of New England.

Miller, P., Lanier, W., Brandt, S. (2001) "Using growth degree days to predict plant stages." *MSU Extension Service.*

Pyatt, J., Tomback, D., Blakeslee, S., Wunder, M., Resler, L., Boggs, L and Bevency, H. (2016). "The importance of conifers for facilitation at treeline: comparing biophysical characteristics of leeward microsites in Whitebark pine communities." *Arctic, Antarctic and Alpine Research,* 48(2):427-444.

Renard, S., McIntire, E and Fajardo, A. (2016) "Winter conditions - not summer temperature - influence establishment of seedlings at white spruce alpine treeline in Eastern Quebec." *Journal of Vegetation Science,* 27(1): 29-39.

Smith, W., Germino, M., Hancock, T and Johnson, D. (2003) "Another perspective on altitudinal limits of alpine timberlines." *Tree Physiology,* 23: 1101-1112.

Vapaavuori, E.M., Rikala, R., Ryyppö, A. (1992). "Effects of root temperature on growth and photosynthesis in conifer seedlings during shoot elongation." *Tree Physiology,* 10(3): 217-230.