

Impacts of Snow Distribution and Temperature Regimes on Seedlings in a Diffuse Treeline on
Pikes Peak, CO

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Abstract

Treelines are an ecotone structured by the interactions of exogenous gradients and endogenous feedbacks. Endogenous feedbacks operate through adult trees that modify their microclimates and impact seedling dynamics. These impacts are assumed to be positive, but the mechanisms remain poorly understood. This study investigated (1) how the distribution of adult trees impacted snowmelt and in turn how snowmelt impacted seedling distribution, survivorship and growth. (2) how adult trees modify thermal regimes and how these regimes influence seedling distribution. The study was conducted at a 60x150m area of interest of a diffuse treeline on Pikes Peak, CO from 2019-2021. 419 seedlings were mapped in 2019 and their survivorship and growth was measured in 2021. Aerial images of snowmelt and thermal regimes were collected in May and August 2021, respectively. A qualitative analysis was used to determine snow distribution and temperature regimes. The relationship between seedling establishment and snow distribution was measured with a chi-squared test and an R analysis calculated seedling density in relation to thermal regimes.

Snowpack was heterogeneously distributed throughout the field site, with complete cover in the densely forested area initially and patches of snow cover in the tundra. The snow in the forest melted quickly, and the last patches of snow were distributed on the leeward side of adult trees. There was a significant relationship between seedling establishment and snowpack, indicating that seedlings preferentially established in snow. There was no significant relationship between snowpack and survivorship or between snowpack and the most recent year of growth (mm). In the predawn aerial images of temperature, the trees were the warmest areas, the tundra was the coldest and the interstitial spaces of the forest were intermediate temperatures. Seedlings were absent in the areas of extreme high (2.5-3.5°C) and minimal in areas of low temperatures (-

4.5°C) in the predawn thermal imaging and seedling density was bimodal within the middle of the temperature range. The midday aerial images showed that the treetops had the coldest temperatures and the interstitial spaces of the densely forest zones were often the warmest. Seedling density was also bimodal and seedlings were absent in the areas of the highest temperatures (27.5°C-31.5°C). The bimodal aspect of seedling density in both the predawn and midday datasets suggests that seedling density is influenced by temperature through multiple pathways. These results indicate a significant impact of adult trees on seedling microclimates that influence seedling distribution and establishment.

Introduction

Altitudinal treelines mark the spatial transition from a closed-canopy forest to alpine tundra. Treeline ecotones are the upper physiological limits of a tree species and the lower boundary for alpine herbaceous species, resulting in a strong decline in tree height and density (Malanson et al., 2011; Harsch & Bader, 2011). These ecotones occur at high altitudes and are impacted by not only underlying plant physiology and external abiotic conditions, but also internal feedbacks (Körner, 1998; Körner & Paulsen, 2014; Hartshorn, 2020). Treelines vary spatially due to endogenous and exogenous factors and there are four globally reoccurring forms of altitudinal treelines: diffuse, abrupt, krummholz, and island (Harsch & Bader, 2011). Diffuse treelines are characterized by a gradual decrease in height of trees and tree density along the ecotone and will be the main focus of this study. Abrupt treelines are categorized as a continuous forest bordering an alpine tundra. Island treelines are patches of trees above a continuous forest, and lastly, krummholz are composed of severely stunted or deformed trees (Harsch & Bader, 2011). These differing spatial patterns are formed by the interaction of short-range and long-range internal feedbacks over underlying external stress and harshness gradients.

The most important exogenous gradient impacting tree growth and survival at treeline is decreasing temperature in relation to increasing elevation (Harsch & Bader, 2011). Tree growth is climatically constrained by low temperatures which occur more frequently and severely at higher elevations due to the adiabatic lapse rate (Körner, 1998). Another exogenous gradient at elevation is the decreasing partial pressure of CO₂ at increasing altitudes. However, many studies of leaf gas exchange at treeline show no strong disadvantages of decreasing pressure of CO₂ on tree growth (Körner, 1998). Other external factors include increasing stresses of UV radiation and changes in snowpack with increasing elevations (Sheldon, 2021; Russell, 2019).

Decreasing temperatures have a strong impact on tree growth, establishment, and survivorship. The growth-limitation hypothesis (GLH) suggests that annual mean temperatures are the limiting factor that form treelines. This hypothesis suggests that treelines form not because of a lack of carbon, but because conifers are unable to use the carbon gained from photosynthesis because of low soil and air temperatures (Smith et al., 2003; Grace et al, 2002). There is a minimum temperature necessary for sufficient production of new plant cells and the development and differentiation of functional tissues of plants, causing a lack of growth above a certain elevation (Körner, 1998). Körner and Paulsen (2014) studied 376 naturally-occurring treelines and found that tree growth requires a minimum length of 94 days in a growing season. The season is defined as all days with a daily mean temperature greater than 0.9 °C. In a study on dendrochronology of trees on Pikes Peak (Colorado, USA), Kummel et al. (2021) found strong correlations between tree ring width index and increasing monthly growing season temperatures in the past century. Where there are higher average temperatures, there is not only more tree growth but likely stronger survivorship. Tree growth helps replace frequent biomass loss at high elevations. Wind abrasion of needle cuticles, apical bud damage, snow loading and frost heaving result in biomass loss (Smith et al., 2003). Trees that can regenerate this tissue loss should have increased survivorship.

At treeline, seedlings experience a high degree of mortality. Over 90% of seedlings die within their first year of growth, indicating that conifers experience the strongest pressures in their early stages of life (Germino & Smith, 1999). Places where seedlings prosper is indicative of where there will be adult trees in the future. Understanding seedling mortality at treeline is crucial to understanding the future dynamics of the ecotone.

Endogenous feedback structures work with exogenous gradients to impact and shape treeline structures. Neighboring interactions impact seedling establishment and growth in multiple ways (Hartshorn, 2020). Trees create microsites that have enhanced or degraded environments for survivorship and growth through facilitation, competition, and inhibition. A positive feedback system occurs when a plant modifies the environment it occupies, improving the site for itself (Resler et al., 2005). This can be coupled with facilitation to not only help itself, but the other plants nearby. However, plants also modify conditions and resources by competition for available water and nutrients. Because of competition for resources, plants can inhibit others nearby from seedling establishment. Plants can also inhibit the growth and survivorship of others through changes in conditions such as temperature and wind speed. These positive and negative neighboring interactions can occur simultaneously and at different spatial scales, such that short-range facilitation can result in long-range inhibition, impacting the spatial distribution of seedling establishment, growth, and survivorship of treelines (Hartshorn, 2020).

Numerous studies on facilitation at treeline indicate that biomass growth and seedling establishment are found to be higher when other plants are nearby. In a study conducted by Callaway et al. (2002) on 115 species over 11 mountain ranges, it was found that competition generally dominated interactions at lower elevations, whereas facilitation dominated interactions at higher elevations. The phenomenon is known as the Stress Gradient Hypothesis (SGH). At lower elevations, stressors, such as winds and temperature, are benign, and therefore plant populations can grow to a density where competition for limited resources becomes significant. At higher elevations, where abiotic stressors are harsh, the physiological limits of plants inhibit growth more than limiting resources (Callaway et al., 2002). The SGH suggests that neighboring

interactions should be more positive and beneficial at higher elevations, where stressors are severe.

Trees at treeline modify their surroundings through sheltering to form microclimates. The spatial distribution of adult trees has been found to alter seedling microclimates such that there is a greater survivorship of young seedlings (< 5 cm height) closer to adult tree islands (Germino et al., 2002). These tree islands alter multiple micrometeorological parameters for young seedlings including solar and longwave radiation, temperatures during the day and night, and snowdrift accumulation (Germino et al., 2002). These factors further modify the environment including by enhancing soil moisture, sheltering from severe weather, and therefore altering the growing season length (Germino et al., 2002).

Seedlings adjacent to tree islands receive protection from the open sky during the day and at night. In a study conducted by Germino and Smith (1999), it was found that leaves exposed to the night sky, further away from islands of adult trees, experienced temperatures well below air temperature (up to 7 °C below). This resulted in dew formation and/or frost, causing leaf abrasion and biomass loss. Furthermore, the low nighttime temperatures under an open sky can result in cold-induced photoinhibition, limiting growth and regeneration. Low temperatures are known to induce light-dependence loss in photosynthetic capacity and can directly damage photosystem reaction centers (Ball et al., 1991). Species near physiological limits, such as at treeline, are more vulnerable to photoinhibition, and facilitation with nearby neighbors can prevent such damage (Ball et al., 1991; Smith et al., 2003). Low-temperature induced photoinhibition results in reduced carbon gain and higher mortality in conifer seedlings (Germino and Smith, 1999; Smith et al., 2003). However, this cold-induced inhibition can be prevented through microclimate modification. At night, canopy tops are warmer than ground

temperatures because they are coupled with the warmer atmosphere (Sheldon, 2021). At night, radiative cooling decreases ground temperatures and atmospheric temperatures are warmer (M. Kummel; 2021). Longwave radiation from trees create “halos” of infrared radiation and warm up the ground and seedlings below (Sheldon, 2021; M. Kummel, 2021; M. Kummel, personal communication, February 2022). This heating can be favorable to seedlings, preventing photoinhibition and encouraging growth and establishment. However, this warm radiation at night can also melt snow below trees, creating shallower snowpack and altering conditions to which seedlings are sensitive. During the day, excessive solar radiation can be destructive to seedling growth, due to increased UV exposure (Resler et al., 2005). Neighboring trees create shadows that modify the surrounding environment and reduce solar radiation for sensitive seedlings. In general, studies have shown that warmer air and soil temperatures in both summer and winter are associated with high rates of seedling recruitment and establishment (Sheldon, 2021).

Although seedlings prefer warm temperatures, they have higher mortality rates in too high of temperatures. High temperatures are paired with high levels of UV radiation that can cause damage to plant cells. In a study by Sheldon (2021), in areas of high daytime temperatures (>18.94 °C), seedling density is lower than in areas of average to warm seedling temperatures. The majority of these areas were in downwind tree eddies and received direct insolation. Seedling densities are strongest in areas of warm temperatures without extreme insolation at the ecotone.

Neighboring interactions also create microclimates by forming shelters that modify wind. Wind moves with high velocity on the tundra because of a lack of terrain roughness (Oke, 1987). The diffuse treeline creates aerodynamic resistance that increases sheer stress against the wind

and decreases the velocity of the wind. Each tree creates a low-pressure, turbulent eddy on the leeward side (Sheldon, 2021; Oke, 1987). The high-speed winds carry snow towards the forest, creating drift pockets of snow behind trees at the top of the ecotone. As the forest becomes denser, the high velocity wind from the tundra slows down, depositing snow in the forest.

Snow burial provides insulation, sun protection, and decreases desiccation (Malanson, 2007). Sufficient snow cover can prevent freezing in soil and stems because in deeper snowpack, temperatures remain near 0°C (Frey, 1983). In the spring and summer, melting snow provides seedlings with moisture, but can also potentially limit seedlings' growing season and lead to damage from snow fungus (Russell, 2019). Deep snow can also lead to waterlogging in poorly drained places, hurting seedling survivorship (Malanson et al, 2011). Seedling establishment is correlated with both higher amounts of snow and sheltering, which both occur closer to tree islands, despite higher levels of competition. Seedlings prefer snowpack, but not too deep of snowpack, for establishment and growth.

Sheltering can have important impacts on temperature regimes of the treeline. At night, the trees decrease the exchange rate of air between the atmosphere and the pockets of space between trees, therefore these interstitial spaces are much colder than areas immediately below the canopies. At night, the air temperatures typically experience an inversion with warmer temperatures aloft and cooler near the ground (Oke, 1984). The cold air is much denser than the atmosphere, which inhibits mixing and perpetuates the cold night-time microclimates in the interstitial spaces (M. Kummel, personal communication, February 2022). During the day, this eddy effect is still present, but air temperatures typically decrease with height, the ground is warmed by the sun, and convective processes cool the ground (Sheldon, 2021). Hence the

inhibition of convection by sheltering decreases heat removal and makes these microclimates warmer.

Access to the open sky work together with high wind speeds to impact snow and temperature regimes at treeline. Sheltering can also have important effects on desiccation of seedlings. In the winter when the ground is frozen and water availability is sparse, strong winds further desiccate trees (M. Kummel, personal communication, February 2022). Seedling establishment and survivorship is associated with the sheltering of nearby trees specifically in the alpine tundra, where strong wind and blowing snow is the harshest (Russell, 2019). Within 2-3 days after snowfall, snow is already redistributed to the sheltered zones by wind (Russell, 2019). High wind speeds pile snowpack on the leeward shelter zones such as trees, but nighttime infrared radiation melts snow to create tree wells below canopies (Resler et al, 2005; Russell, 2019). Sheltering aids to slow down wind, modifying the climate for strengthened seedling growth, establishment and survivorship.

This study is concerned with seedling distribution, growth, and mortality in relation to snowpack and temperature regimes. I hypothesized that the diffuse treeline on Pikes Peak would exhibit neighboring interactions to create microclimates to promote seedling establishment, growth and survivorship, and that presence of snowpack would also increase seedling development and survivorship. In this study, the research questions included: (1) Would seedling distribution and mortality correlate with snowpack? (2) How do trees modify surrounding climates, and does this impact seedling growth, establishment, and mortality?

Methods

Site Description

The study site is a diffuse treeline with a gradual decrease of tree density from an old growth monodominant forest of *Picea engelmannii* (Engelman Spruce) to alpine tundra and was originally established by Elwood in 2012. The site is located on the west slope of Pikes Peak, a 14,115 foot mountain on the Colorado Front Range near Woodland Park, Colorado. The rectangular area of interest (AOI) is 150 meters long and 60 meters wide and runs parallel to the elevation gradient with a northwestern aspect. The elevation of the site ranges from 3609 m above sea level (a.s.l.) to 3719 m a.s.l. The upper boundary of the AOI represents the tree species' maximum elevation, meaning no trees were present above upper boundary. The center of the site is located at 105°5'25" W and 38°51'35" N. This site was chosen because the treeline is known to be significantly advancing (Hartshorn 2020; Elwood 2012). The treeline prior to 1957 was an abrupt treeline at 3651.5m a.s.l. according to aerial images and dendrochronological records (Elwood, 2012). Furthermore, Kummel et al. (2021) found that this treeline was moving significantly upslope at an average rate of 0.253m in elevation/year and that the rate of advancement accelerated through time. Not only did the treeline migrate, it also underwent a transformation into a diffuse treeline. This movement and transformation coincided with significant patterns of local warming, specifically in the last 40-50 years (Kummel et al., 2021).

The space between spruce trees is occupied by tundra vegetation and no other tree or shrub species are present. The majority of the trees were upright and very few krummholz mats were present. There is a small rockslide towards the bottom of the transect near the old growth forest, and a significant number of granite boulders were found throughout. Snow typically covers the site from late September to late May.

Field Methods

Elwood (2012) created the first tree and seedling survey of this site. In 2019, Hartshorn revisited the site and retagged every Engelmann spruce greater than 10 cm in height within the transect and geolocated each tree. In this study, I revisited the tagged trees and collected data for the most recent year of growth (2021) and for mortality. Engelmann spruce shorter than 10 cm were not included in this study. The Engelmann spruce were divided into three classes based on visible signs of mortality: (0) = dead (no living needles present); (0.5) = half dead (more than 50% of the canopy dead); (1) = alive. Each spruce that was either alive or half dead was measured for 2021 year of growth by measuring from the top of the leader scar to the closest bud scare with a caliper. 419 seedlings and 648 total trees were measured in total in fall of 2021.

Drone Data Collection and Analysis

In May of 2021, Kummel and Ceckanowicz took drone imaging of the field site with a Phantom 4 drone during the snow melt season. For this study, four flights were processed and analyzed. The first flight was on May 19th 2021 and the last flight on June 5th 2021, with two intermedial flights (May 22nd, 2021 and May 29th, 2021). All the flights were taken in the middle of the day from 11 am to 12 pm MT. The flights were at 40m above surface level and taken with an 80% sideways and forwards overlap of images. I processed these flights in the photogrammetric software Drone2Map. The processing included 14 ground control points (GCP) that were extracted from Hartshorn's 2019 orthomosaic and referenced in Drone2Map. I also georeferenced the orthomosaics to Hartshorn's 2019 orthomosaic in ArcGIS Pro in order to produce a more precise map. The error in alignment to Hartshorn's 2019 orthomosaic was in the range of 10-20cm.

In June 2021, Kummel and Ceckanowicz collected drone images with an Inspire 2 drone with an Altum, six-band sensor. One flight was taken before dawn, 45 minutes before direct sun exposure, after civil twilight. The other was taken midday at 12pm MT. I processed these flights in Agisoft Metashape by referencing them to the same 14 GCPs from Hartshorn's 2019 orthomosaic. I further georeferenced these orthomosaics in ArcGIS Pro Hartshorn's 2019 orthomosaic to increase precision.

GIS Analysis

Analysis of the Relationship between Seedling Distribution and Snow

The location of the trees, seedlings, and saplings and associated attribute data including height, mortality classification, and growth in the past year were imported to ArcGIS Pro. I created an individual layer for only seedlings less than 0.5 m (n= 419) and a layer for smaller seedlings less than 0.25 m. To analyze seedling distribution in relation to presence of snow, I performed a supervised classification using maximum likelihood algorithm in ArcGIS Pro to create binary (snow vs. no snow) raster layers for each of the 4 orthomosaics that contained snow. I extracted the values of the snow raster to each seedling location, classifying it as 1 (snow) or 2 (no snow). To estimate the proportion of area covered by snow, I generated 1000 random points on each raster and extracted the values of the snow to each point.

A chi-squared analysis was used to determine whether seedlings (<0.5m) preferentially established inside or outside of snow patches for each of the four drone flights with snow. I ran this analysis by determining the number of seedlings expected and actually observed inside and outside of snow patches. I determined the expected number of seedlings by calculating what the distribution of seedlings would be if their distribution was proportional to the snow coverage. For example, if 70% of the area was covered by snow, I would expect 70% of seedlings to be

located in snow. An additional chi-square analysis was used for only small seedlings (<0.25m) in order to determine whether snow had a more pronounced impact on smaller seedlings. Both analyses were run for all four drone flights in order to account for changes in snowpack.

To determine the impact of snowpack on seedling mortality, I used MedCalc's online Relative Risk Calculator and compared the mortality rate of the exposed group (the seedlings in snow) to the mortality rate of the control group (not in snow). This analysis was run for all four flights. To determine the relation between snow patches and growth rate, I used an independent sample t-test in SPSS to compare the residual growth rate of the seedlings to the presence of snow. I calculated residual growth rate by calculating the residual from the growth rate by size regression analysis. This corrected the growth rate for the effect of seedling size because larger seedlings grow faster in general.

Analysis of the Relationship between Seedling Distribution and Temperature

I imported the orthomosaics of the predawn and midday flights into ArcGIS Pro and extracted the thermal band (band 6) from each. I digitized all adult trees and tree clusters from Hartshorn's 2019 orthomosaic and removed them from the 2 thermal orthomosaics. This removed the tree temperatures and allowed me to focus on the relationship between seedling distribution, mortality and growth, and ground temperatures. I clipped each raster to the AOI. Then, I extracted temperatures for each seedling by using the "extract values to points" tool in ArcGIS. Pro.

To analyze the relationship between seedling distribution and density and temperature, I used a RStudio code written by Sheldon and Kummel in 2021. The function divides the temperature distribution into temperature ranges and calculates temperature density within each temperature band.

Results and Discussion

The goal of this research was to identify how seedlings respond to endogenous feedbacks at a diffuse treeline in terms of mortality, distribution, and growth, as well as the impacts of these endogenous feedbacks on snow distribution and temperature regimes. To examine this, I analyzed snowpack distribution, diurnal regimes and seedling distribution at a diffuse treeline on Pikes Peak, CO. In the ecotone, short-range feedbacks pair with long-range exogenous gradients to influence microsites and seedling dynamics. To study these complicated treeline dynamics, my research was guided by two main questions: (1) How do trees modify snowpack and the spatial structure of snow melt, and does seedling distribution and mortality correlate with snowpack? (2) How do trees modify surrounding temperature regimes, and does this impact seedling growth, establishment, and mortality?

Snow Distribution

The four drone orthomosaics depicted snow melt in the spring of 2021 (Figure 2). A qualitative analysis of these rasters showed the progression of snow melt at my site from May 19th (~ 90% snow cover) to June 5th 2021 (~10% snow cover). The observed snow distribution patterns are shaped by interactions among atmospheric conditions, snow, topography, and vegetation (Heimstra, 2006). On May 19th 2021, most of the ground was covered in snow heterogeneously (Figure 2a). The snow coverage was continuous in the dense forest interstitial spaces but absent under tree canopies. This indicates that the tree canopies are substantially heating the ground beneath them and melting the snow (Oke, 1987; Russell 2019). High velocity winds carried snow from the tundra into the forest where eventually, a high density of trees slows down the wind and deposits the snow. The result of this process is snow accumulation in the interstitial spaces of the high-density forest (Heimstra, 2006). In the tundra, there are large

patches of bare ground, suggesting that the wind has carried some snow away, decreasing the snow depth; these spaces are the first areas of melting snow in the spring (Heimstra, 2006). There are distinct snow drifts behind adult trees in the upper, low-density forest and tundra towards the NNE direction. These snow drifts are indicative of strong wind patterns that create high pressures on the windward side of trees and push snow to the leeward side of the trees. The snow is deposited on the leeward side because of the low-pressure eddy that forms on the leeward side in response to the high velocity winds. This is consistent with the findings of Heimstra (2006).

In the aerial images from May 22nd and May 29th 2021, the snow melted significantly in the high-density forest, with mostly bare ground existing in the interstitial spaces between tree clusters (Figure 2b & 2c). More snow also melted in the tundra, expanding the existing patches of bare ground, but less significantly than in the dense forest. This indicates that the interstitial patches are warmer than the open tundra due to radiation from tree canopies and inhibition of mixing with the atmosphere. The patches in the tundra and the less-densely forested transition zone are mostly on the leeward side of the adult trees and tree clumps and snow drifts are still present. This indicates that the snow has accumulated on the leeward sides and the higher depths of snow are decreasing the rate of snowmelt. Areas with higher snow depth are the last areas to become snow-free (Heimstra, 2006). By June 5th 2020, almost all of the snow had melted (Figure 2d). Only a few patches of snow still existed, again on the leeward sides of adult trees. There is also snow present in the rockslide, indicating that topographic features impact snow distribution by impacting the accumulation of snow.

Snow Distribution and Seedling Establishment, Growth and Survival

The chi-squared test determined whether seedlings preferentially established in snow. At the beginning of snow melt (May 19th) and at mid snow melt (May 22nd and May 29th), the chi-squared analysis indicated that the observed seedlings did establish in snow more than expected ($\chi^2 = 315.837$, $p < 0.0001$; $\chi^2 = 36.817$, $p < 0.0001$; $\chi^2 = 13.275$, $p = 0.0003$, respectively) over the entire AOI. These results were statistically significant. The chi-squared results for the small seedlings (<0.25m) on May 19th and May 22nd also indicated that these seedlings preferentially established in areas of snow ($\chi^2 = 315.837$, $p < 0.0001$; $\chi^2 = 36.817$, $p < 0.0001$, respectively). The results of the chi-squared analyses from aerial images on May 19th, May 22nd, and May 29th 2021 were expected and congruent with the findings of Russell (2019) and Hättenschwiler and Smith (1999). Seedlings preferentially established where snow is present during the late Spring because seedlings rely on snow for moisture, insulation, increased microbial activity, and decrease the potential for small roots to freeze (Russell, 2019).

Too much snow may be detrimental to seedlings and can impact seedling establishment. The chi-squared analyses of the data from June 5th 2021 indicated that seedlings do not preferentially establish in snow patches that last into the early summer ($\chi^2 = 0.169$, $p = 0.6809$). The snow that persists into the early summer is mostly deeper compared to other areas that are now snow-free. This result is statistically insignificant, indicating that seedlings do not prefer nor avoid areas of long-lasting, deeper snow. The seedlings may preferentially establish in areas where snow is not too shallow nor too deep. These results align with the results found by Hättenschwiler & Smith (1999) who saw that there is an optimal snow depth necessary for maximum seedling establishment of Engelmann spruce seedlings (between 0.5m and 1.5m). Too much snow accumulation is detrimental to a seedling's carbon balance and can inhibit growth, as

well as waterlog the seedling and increase the presence of snow fungus (Hättenschwiler & Smith, 1999; Russell, 2019; Malanson et al., 2011).

The Relative Risk Calculator indicated that seedling mortality does not correlate with presence of snow in the aerial images of May 19th and May 22nd 2021 for all seedlings (5/19/21 relative risk = 0.7230, $p = 0.2817$; 5/22/21 relative risk = 1.2022, $p = 0.4846$). Similar results were found with the relative risk calculations with just the small seedlings (<0.25m) from May 22nd 2021 (relative risk = 1.0196, $p = 0.9461$). These results contradicted those found in a previous study by Russell (2019) on the abrupt treeline on Pikes Peak, where findings showed that seedling mortality was significantly greater when there was less than 80cm of snow and that seedling survival was higher in snow patches overall. Russell (2019) suggested that seedling survival was highest in areas of intermediate snow depths and found a high correlation between survivorship and snow. My results do not indicate a high correlation between survival and snow. This contrast in results could be due to differences in snow distribution at the two field sites. The field site that Russell analyzed was an abrupt treeline and there was minimal to no snow presence in the upper tundra, but a distinct band of snow directly above treeline, whereas at the diffuse field site, the snow was distributed differentially throughout the tundra. This difference could account for our contrasting findings on mortality and snow presence. Furthermore, Russell collected data on about 2,000 seedlings at the abrupt field site and at the diffuse site I collected data on about 419 seedlings. This difference in sample size could have also impacted my results.

The independent sample t-test in SPSS of the earliest flight did not indicate a significant correlation between seedling growth and snow distribution ($t = -1.135$, $p = 0.257$). This result is unexpected since seedlings tend to prefer establishing in snow and therefore should also have the means to have accelerated growth in snow patches. In a study of planted tree in a subalpine zone,

Frey (1983) found that snow covered seedlings showed markedly greater growth in vertical height for all tree species studied. Snow protects seedlings from winter stresses such as desiccation, freezing, and strong winds, and therefore should promote seedling growth. My results are similar to Hoffman's (2019) analyses of snow cover and seedling growth. Hoffman studied the abrupt field site on Pikes Peak, and also did not find a significant relationship between snow cover and seedling growth.

Temperature Distribution

The predawn thermal orthomosaic (Figure 3a) indicated that trees were significantly warmer than the tundra. A qualitative analysis of this raster indicates that the coldest region occurs in the dispersed forest and the tundra. The adult trees and tree clusters are the warmest and the areas surrounding the trees were also warmer than the coldest regions. The trees are warmer because of coupling with the warm atmosphere at night. At night, the ground cools significantly through radiative cooling, but the atmosphere stays warm. The cold ground cools the layer of air right above it, creating an inversion. The dense cool air on the ground does not mix with the warm air in the atmosphere, but the trees interact with the atmosphere and remain warm (Grace et al., 2002; Sheldon, 2021; Kummel, 2021). Because of the warm temperature of the trees, they radiated a significant amount of heat to the ground and makes the interstitial spaces warmer than in the tundra.

During the day regime (Figure 3b), treetops were colder than surrounding areas. Treetops are coupled with the cooler atmosphere during the day and therefore have lower temperatures than surrounding areas (Grace et al., 2002). Some topographical regions, such as crevices and the distinct rockslide, were also cooler. Interstitial spaces in the lower forest were much warmer than open spaces in the tundra. This indicates that warm air was trapped in these spaces and unable to

mix with the atmosphere (Grace et al., 2002; Sheldon, 2021). There are also areas of significant warmth in the tundra. This could be due to differential sun exposure and topographical changes. These regimes are as expected and align with past literature of day regimes and nightly inversions (Grace et al., 2002; Sheldon, 2021; Oke, 1987).

Temperature Distribution and Seedling Establishment, Growth and Survivorship

The R analysis of temperature distributions from the aerial images before dawn (Figure 4a) indicated that seedling density is highest at two temperatures: -1.5°C and 0.5°C . The seedling density decreases between these two temperatures at -0.5°C . Congruent with previous literature, seedling density was lowest at the extreme low (-4.5°C) and extreme high (above 1.5°C) temperature regimes. In particular, seedlings were absent at 2.5°C and 3.5°C at night. These temperatures occurred in the close proximity of adult trees. This finding is surprising because at night seedlings should prefer warmer temperatures because colder temperatures cause photoinhibition (Germino and Smith, 1999; Smith et al., 2003). These regimes should aid to prevent photoinhibition, but this absence of seedlings may be a result of competition from the adjacent adult trees. This finding contrasts with Sheldon's findings (2021) of seedling density on the abrupt treeline on Pikes Peak. Sheldon (2021) found that at night there were seedlings present in sites that were warmer than 6°C . Another surprising finding was that the distribution was bimodal with two maximums at -1.5°C and 0.5°C . This contrasts with Sheldon's findings who found a single maximum from 2.5 - 4.4°C during the nighttime regime. This result may indicate that there are several pathways through which temperature is impacting seedlings. This may also indicate that there are other factors, such as competition and facilitation, that influence seedling establishment in these areas.

The analysis of the midday aerial images (Figure 4b) also indicated an absence of seedlings at extreme high (27.5°C - 31.5°C, the maximum temperature measured) and low temperatures (below 1.5°C). This is congruent with other studies that found seedlings did not prefer extreme thermal environments. Sheldon (2021) found low seedling densities above 19.9°C and below 5°C. Hellmers et al. (1970) found thermal inhibition of growth and survivorship of Engelmann spruce seedlings above 35°C in growth chambers. Although my maximum temperature of 31.5°C is below the threshold of 35°C, my temperatures reflect a single day towards the end of the growing season, and these high temperature areas most likely reach this threshold earlier in the growing season. Interestingly, my data from the daytime regimes also contained multiple peaks for seedling density at 5.5°C and 17.5°C. Similar to the nighttime regime, this may indicate that temperatures impact seedlings in multiple ways, directly or indirectly.

There are a few limitations of this study, primarily in the sample size of both seedlings and thermal images. First, the sampling size of seedlings is only 419 within the field site and a larger sample size could have provided more significant results. There also were some discrepancies tree tags when the site was revisited in 2021 from the retagging completed in 2019 that may have led to some error. Furthermore, some seedlings that's were marked dead (0) in 2019, appeared to be half-dead (0.5) or alive (1) when revisited in 2021, creating more discrepancies. Additionally, there may have been human error when measuring year of growth for each seedling.

The number of thermal images that were collected and analyzed also limited this study. Each aerial image (predawn or midday) was from a singular day and did not provide data on the variability of temperatures. Analyzing aerial images from multiple days during the growing

season would allow for a clearer understanding of the variability and range of temperatures on the field site. Furthermore, there were small errors (10-30 cm) in the referencing and geolocating of the aerial images to the 2019 orthomosaic.

Conclusion

At the treeline ecotone, long-range gradients and short-range feedbacks interact to establish and modify treeline and seedling dynamics. The most important exogenous gradients at treeline are variability in snowpack and decreasing temperature with increasing elevation (Körner, 1998; Hättenschwiler & Smith, 1999). These exogenous gradients should make it more difficult for spruce seedlings to establish, grow, and survive at higher elevation, but the presence of neighboring trees can help mitigate these impacts through endogenous feedbacks which are assumed to be positive (Smith et al., 2003) Adult trees and their spatial distribution modify microclimates including snowpack dynamics, and seedlings respond to these dynamics and establish, grow and survive accordingly.

My study showed strong endogenous feedbacks from tree distribution to seedling dynamics via the impact of adult trees on snow melt. Snow distribution in the alpine ecotone was influenced by wind, radiation from treetops, and sheltering. At this field site, wind had transported snow from the tundra into the forest. Therefore, during the early melt season, there was a full snow cover in the forest and patchy snow cover in the tundra. As the snow melted, the snowpack in the forest was significantly reduced, likely due to longwave radiation from tree canopies. In the tundra, the snow patches lasted longer and were particularly present on the leeward sides of trees. Snowpack influenced seedling distribution and our results indicated that seedlings preferentially established in places of snow. The seedlings however did not prefer the deepest areas of snowpack, indicating that too much snow could be detrimental to seedling

establishment. Surprisingly, the data in this study did not show correlation between neither seedling mortality nor seedling growth and the presence of snow. Trees in the dense forest modified the environment in ways that were hostile to seedling establishment because the trees facilitated earlier snowmelt and seedlings prefer areas with longer snow persistence.

There were strong endogenous feedbacks from adult trees on the ground temperature which influenced seedling dynamics. The thermal image showed that trees distinctly modified their thermal surroundings. During the night regime, due to coupling with the warm atmosphere, the trees were much warmer than the tundra and significantly warmed the interstitial spaces in the forest. Seedling density was greatest in intermediate temperatures and lowest in areas that were particularly warm at night. During the day regime, the trees were cooler than their surroundings and interstitial spaces trapped the warm air. On this field site, there was an absence of seedlings in the areas with the warmest daytime temperatures. Adult trees structure the treeline's thermal regimes in such a way that both facilitates and creates hostile environments to seedling establishment.

In summary, the most significant finding was that seedlings preferentially established further from trees due to the trees impact on both snowpack and thermal regimes. This is surprising because much of treeline literature suggests that sheltering has a positive impact on seedling dynamics (Smith et al., 2003; Germino, 2002; Harsch & Bader, 2011) whereas in this study, I found that endogenous feedbacks were the primary drivers in inhibiting seedling establishment.

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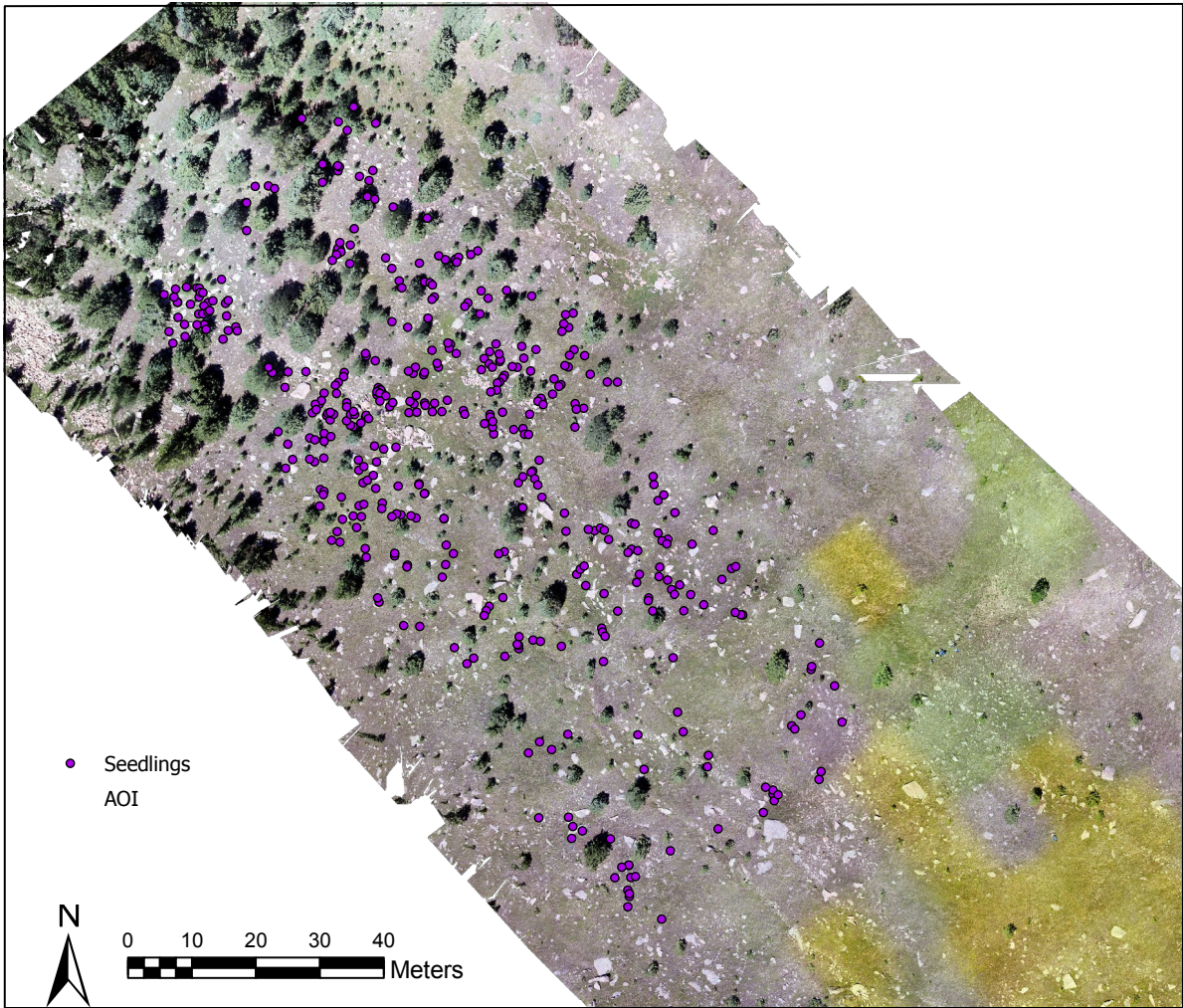
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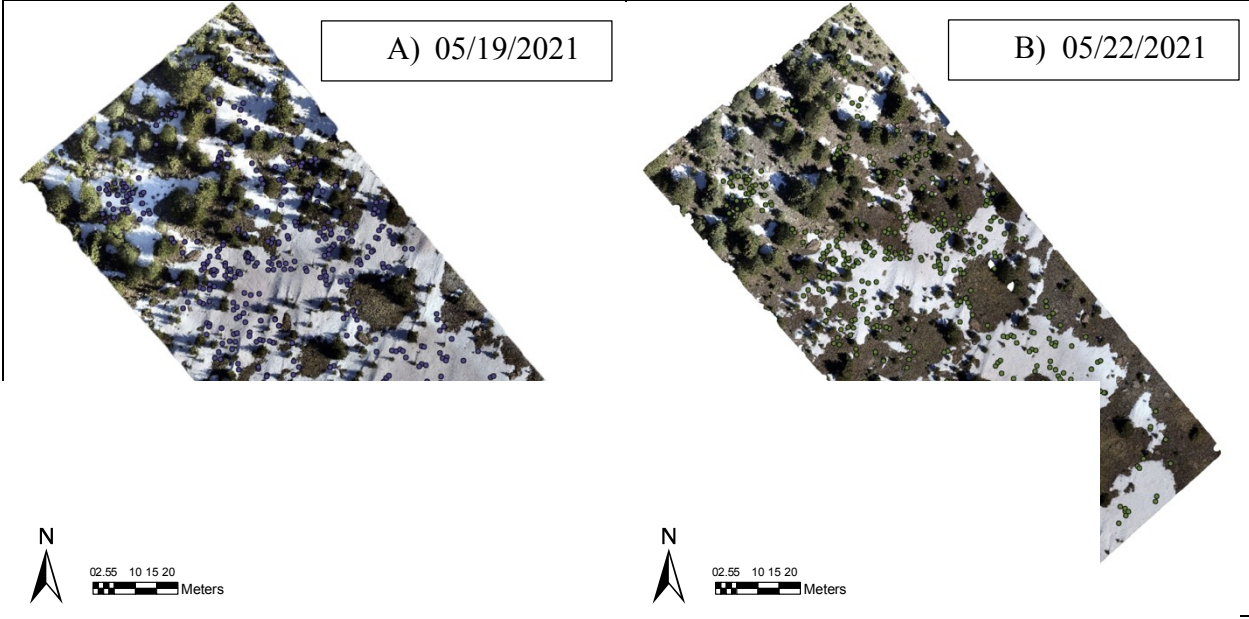
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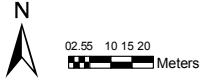
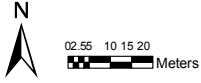
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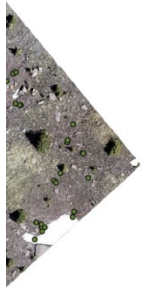


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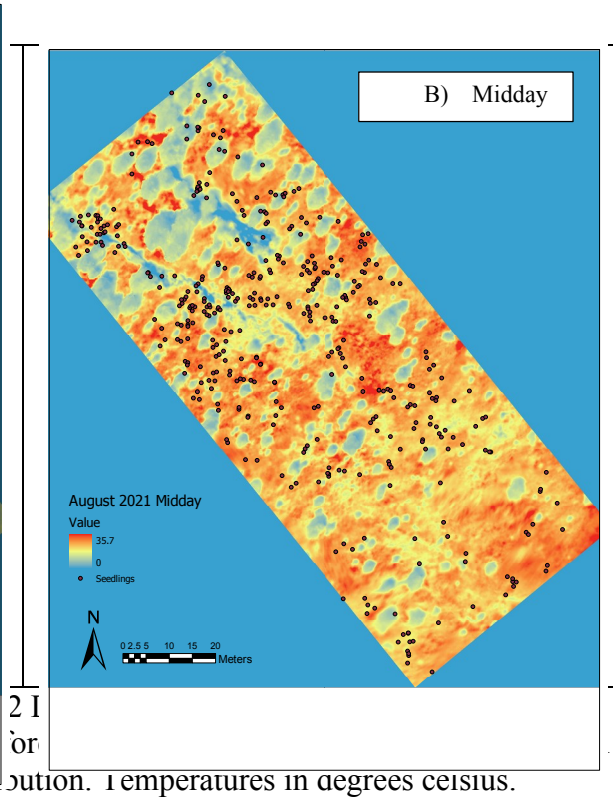
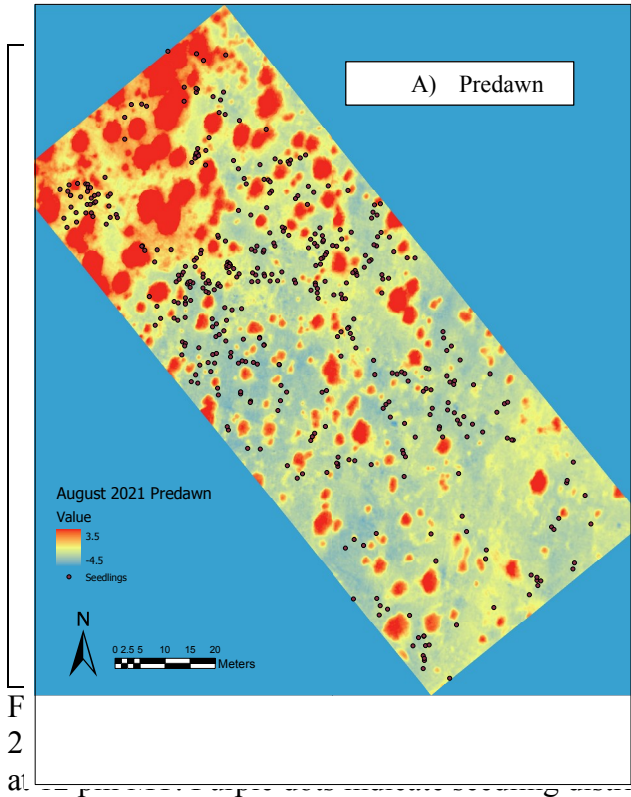


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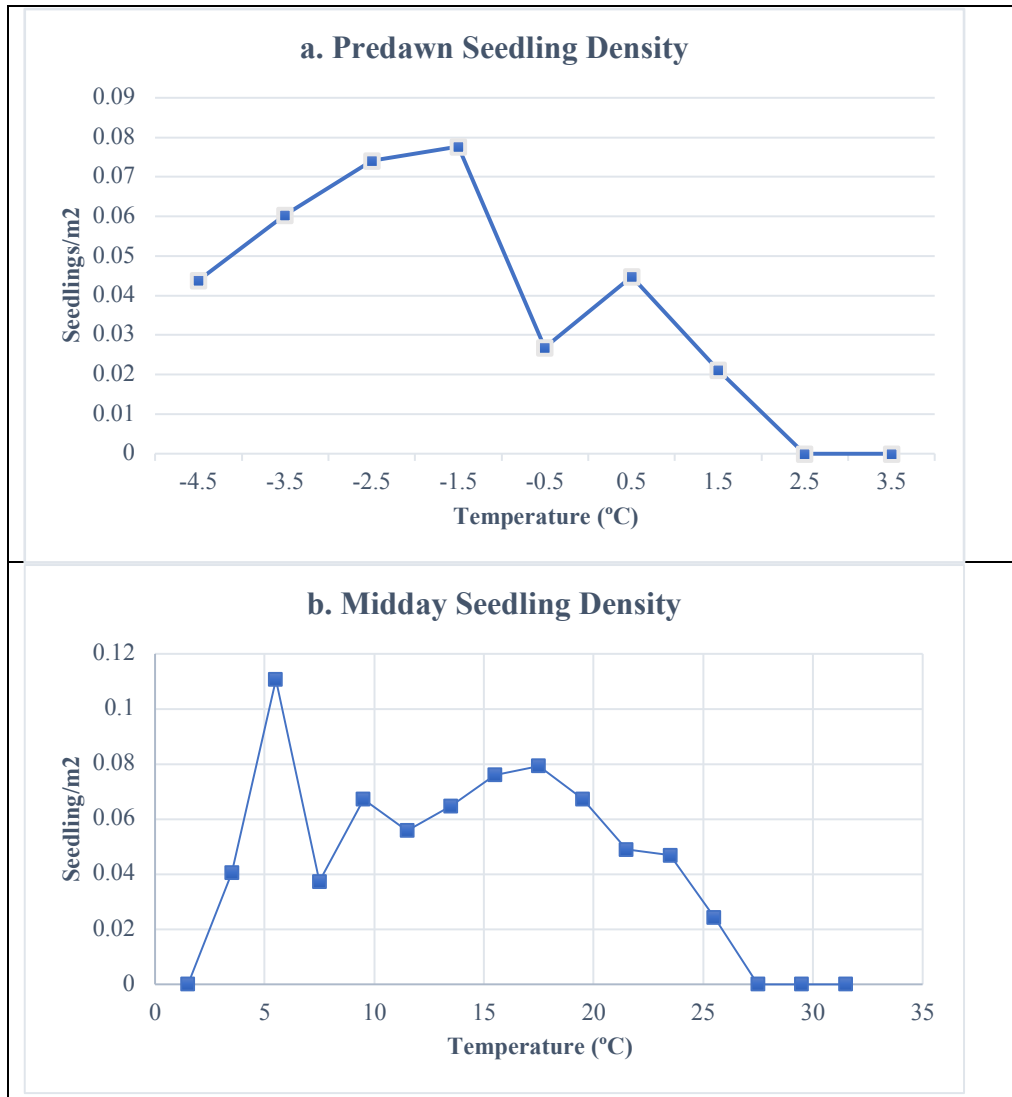


Figure 4. a) Seedling density in relation to nighttime ground temperatures ranging from -4.5°C to 3.5°C. Data collected from aerial imaging before dawn. b) Seedling density in relation to daytime ground temperatures ranging from 1.5°C to 31.5°C. Data collected from aerial imaging taken around 12 pm MT.