DIURNAL TEMPERATURE REGIMES DRIVE SEEDLING DISTRIBUTION AT AN ABRUPT TREELINE

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By

Jessie Sheldon

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Dr. Miroslav Kummel, Associate Professor

Dr. Howard Drossman, Professor

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Abstract

While it is generally accepted that temperature determines the approximate altitude of treeline, drivers of fine-scale treeline dynamics are poorly understood. A dominant driver of fine-scale dynamics is sheltering of seedling by adult trees. Within the treeline literature, there is an underlying assumption that sheltering from trees is beneficial for seedlings, initiating a positive feedback loop. However, sheltering can potentially create both hospitable and hostile microclimates. In this study, we examined the relationship between microclimate and seedling distribution at an abrupt treeline on Pikes Peak, Colorado and ask two main questions: (1) how do trees modify their surrounding microclimate, and (2) how do these microclimates impact seedling establishment? To explore these questions, we analyzed 2017 daytime and nighttime thermal images of treeline, and 2017 seedling data mapped with 20 cm precision. We first analyzed the spatial distribution of surface temperature with respect to the treeline spatial structure, followed by seedling density with respect to ground temperatures.

Overall, we found that variations within the microclimates surrounding adult trees are determined by three primary factors: (1) the obstruction of boundary layer airflow, which results in the formation of eddy-like isolated pockets of air that exhibit exaggerated diurnal temperatures (2) long wave radiation from trees, a nighttime phenomenon that warms a certain radius of the ground beneath a tree, and (3) shade, which accounts for the majority of low daytime temperatures. These three competing mechanisms interact, resulting in a mosaic of variable ground temperatures adjacent to trees. Between these variable microclimates, seedlings exhibited distinct temperature preferences, with the highest density at both moderate daytime and nighttime temperatures, and an explicit avoidance of both daytime and nighttime high and low temperatures. When temperature is divided into 12 equal classes and seedling density is

compared between the classes, the best fit for both the daytime and nighttime datasets were third degree polynomials (Daytime: adjusted R^2= 0.70, F(3,8)= 9.458, p=0.005, Nighttime: adjusted R^2=0.58, F(3,8)=6.043, p=0.019). An analysis using a relative distribution estimate function (Rhohat) in spatstats package in R corroborated these findings.

Introduction

Altitudinal treelines mark a stark transition between two different ecological zones: forest and tundra. This remarkably consistent and visible boundary is a defining feature of mountainous landscapes across the globe. Temperature is regarded as the primary factor determining the location of this particular boundary. During the growing season, treelines across the globe largely possess mean root-zone temperatures between 6.4 and 7.8C (Korner & Paulsen, 2004). Ecosystems framed by climatic boundaries, such as altitudinal treelines, are beginning to undergo significant shifts as the pace of global climate change accelerates (Walther et al., 2002). Increased temperatures will fundamentally alter the climatic constraints that determine the location of treeline, resulting in significant implications for alpine environments and global carbon cycling (Malanson et al., 2011; Grace et al., 2002). Within their approximate boundary, global treelines vary significantly in their internal spatial distribution, that is, how the tree "line" actually appears (Korner, 2012). In reality, this transition is rarely as abrupt as the term tree-*line* would suggest. The entire transitional zone, from the fully mature forest to the upper limits of seedling establishment, is known as an ecotone. While growing season root-temperatures determine treeline approximate altitude (±50 meters), the exact altitude of treeline and the internal distribution of trees within the ecotone are areas of active research (Korner & Paulsen, 2004, Malanson et al., 2011).

Overall, fine-scale terrain irregularities and local tree population dynamics, rather than large-scale climatic trends, shape the distribution of trees within the ecotone (Holtmeier & Broll, 2012; Elliot, 2011). While these fine scale patterns do not diminish the importance of the bigger picture, these many small factors capture the true dynamism of the ecotone (Malanson et al., 2011; Holtmeier & Broll, 2012). The ecotone and tundra above the forest edge reveals topography composed of hostile and habitable microsites (Korner, 2012). These microsites are primarily defined by differences in heat gain and loss, which are largely modulated by wind, shade, and snowpack. Each of these modulators are, in turn, strongly affected by fine-scale topography, the location of outpost trees and krumholtz islands, and treeline structure (Malanson et al., 2011). Additional modulators indirectly related to heat include water (e.g., Brodersen et al., 2006), geomorphology (e.g., Resler et. al, 2005; Resler 2006), and biotic factors such as pathogens (e.g., Resler & Tomback, 2008). Within the ecotone, outpost trees and tree islands have the potential to modify the surrounding microsite to conditions advantageous to seedlings, resulting in a positive feedback loop (Malanson et al., 2011). While studies that focus on large-scale temperature patterns have primarily described thermal impacts on the growth of mature trees, fine-scale patterns appear to drive the complex dynamics of seedling distribution and growth (Malanson et al., 2011).

While many studies of global treeline drivers focus on mature trees, the key to treeline dynamics is seedling germination, establishment, survivorship, and growth (Smith et al., 2003). Seedlings are generally defined as trees 10 years old or younger (Smith et al., 2003). Seedling distribution is critical in understanding how treeline structures will change, yet their vital role in treeline movement and the spatial distribution of trees is often overlooked, as there often appears to be no shortage of seedlings at treeline (Korner & Paulsen, 2004). However, successful seedling growth is dependent on microsite facilitation in the early stages of germination and establishment (Smith et al., 2003). In a 2015 study, younger seedlings were found to be more sensitive to several microsite conditions, such as soil temperatures and exposure, than older seedlings, highlighting the importance of the early stages of seedling development (Greenwood et al. 2015). While seedling spatial distribution is important at all treelines, it is particularly critical when considering abrupt treelines, including the abrupt treeline examined in this study (Harsch & Bader, 2011). In abrupt treelines, tall, mature trees grow right up to the lower edge of the tundra, indicating that the system is not growth-limited (Harsch & Bader, 2011). Rather, the system is seedling-limited, as abrupt treelines are characterized by a significant decrease in seedling abundance and increase in seedling mortality just above the forest edge (Harsch & Bader, 2011).

Within the existing body of treeline literature, there is an underlying assumption that sheltering from trees, boulders, and other topographic features creates beneficial conditions for seedlings (Resler et. al, 2005; Resler, 2006). Holtmeier & Broll (1992) found that the mechanisms of this facilitation can be observed when comparing ground temperatures inside and outside of tree islands within the ecotone. Within tree islands, ground temperatures are relatively constant while temperatures in the open fluctuate significantly between night and day, with considerably warmer soil temperatures during the day (Holtmeier & Broll 1992). The low, constant temperatures in treed areas can be attributed to the reduction of ground heat flux by forest canopy screening (Aulitzky, 1961; Korner & Paulsen, 2004). Many studies show that seedling germination and survivorship depends greatly on favorable microsite conditions; such conditions are often facilitated by neighboring trees and boulders, where large temperature swings can be mediated through reduced sky exposure and sheltering from high winds and direct insolation (Germino & Smith, 1999; Germino & Smith, 2001; Germino et al., 2002; Resler et al., 2005; Resler 2006). However, while the positive effects of sheltering and neighbor-facilitation on seedlings dominate treeline literature, sheltering is actually a complex phenomenon that intersects with both ecology and atmospheric physics.

Microsite conditions are dependent on heat exchange within the atmospheric boundary layer. The atmospheric boundary layer is the bottom 10% of the troposphere, characterized by turbulent mixing and heated air parcels rising from the surface (Oke, 1987). Of particular relevance to this study is the roughness layer, the portion of the atmospheric boundary layer characterized by complex eddies and vortices that develop as air flows around and through objects, such as trees. The roughness layer generally extends 1-3x over the height of these objects (Oke, 1987). As is obvious to anyone who has walked along a windy ridgetop, topography and tree structures greatly modify wind speed and direction. Just as a stone creates a downstream eddy in a river, atmospheric eddies develop on the leeward side of trees, creating semi-stationary pockets of air that are isolated from the rest of the atmosphere (Oke, 1987). Within the low pressure "wake" that develops downwind of an object, wind speed and force decrease, resulting in a sheltering effect (Oke, 1987). The semi-stationary nature of the air in these eddies has significant ramifications for the site's thermal balance, as both latent and sensible heat flux are driven by turbulence (Oke, 1987). Increased residence time of the air in an eddy reduces heat exchange between the isolated air mass and the rest of the atmosphere (for both sensible and latent heat), resulting in reduced heat flux and causing nighttime and daytime temperatures in sheltered pockets to become respectively colder and hotter than the surrounding ambient air (Germino et al., 2002).

This diurnal cycling of radiative balance greatly affects microsite conditions. At night, the atmosphere is a *source* of heat and moisture for the surface. The surface cools more rapidly than the air, resulting in a negative surface radiation budget and the downward transfer of heat as well as the cooling of the atmospheric layer directly above the surface (Oke, 1987). This cold, dense air at the surface then forms a ground-based radiation inversion (Oke, 1987). With a large temperature gradient and low winds, this inversion becomes difficult to disrupt (Jordan & Smith, 1994). Of particular importance to this study site and mountainous environments in general, this cold, dense inversion layer slides downhill, generating a pattern of nighttime downslope winds (Oke, 1987). These nighttime winds are generally slow due to poor coupling between the surface and the boundary layer of air (Oke, 1987). At a small scale, isolated eddies forming on the leeward sides of trees prevent convection with the ambient air, making it difficult for heat and moisture from the surrounding atmosphere to enter the isolated pocket.

During the day, the surface is heated by solar radiation, causing an energy surplus. The boundary layer of the atmosphere subsequently becomes a *sink* of heat and moisture, rather than a source (Oke, 1987). At a larger scale, a positive surface radiation budget develops as surface temperatures increase from insolation, resulting in an upward heat flux and the dismantling of the nighttime inversion layer (Oke, 1987). As the sun rises, the dominant mechanism of heat transfer shifts from conduction to convection, and surface heat is primarily transferred to the atmosphere by turbulence as sensible or latent heat, depending on the availability of water for evaporation (Oke, 1987). Air closest to the surface becomes rapidly heated and subsequently rises, causing a trend of daytime upslope winds (Oke, 1987). Strong vertical coupling between the surface and the boundary layer results in generally higher daytime wind speeds (Oke, 1987). At a small scale, heat increases in leeward eddies, potentially also increasing moisture levels. This is because the air in the eddies is relatively stationary and the successful transfer of heat away from the site's surface into the ambient air is dependent on turbulence (Oke, 1987).

Through these modifications of radiative balance and wind speed, the boundary layer interactions with the active surface drive microclimate temperature variations within sheltered areas (Holtmeier & Broll, 2012). Isolated air pockets that form downwind of trees can cause extreme microsite temperatures (Oke, 1987), perhaps complicating the theory of neighbor facilitation as a beneficial interaction. Whatever their root cause, temperature extremes can have detrimental effects on the physiology of trees (Jordan & Smith, 1994; Germino & Smith, 1999; Germino et al., 2002; Wieser et al. 2010; Davis & Gedalof, 2018). In the summer, cold nighttime temperatures (exacerbated by decreased wind speeds and nighttime inversions) combined with high insolation the following day, can result in photoinhibition, often proving fatal for seedlings and saplings (Jordan & Smith, 1994; Germino et al., 2002). Cold ground temperatures can also inhibit growth, as photosynthesis is positively correlated with root-zone temperatures (Wieser, 2010). Though perhaps not as strongly documented as their aversion to cold, trees can also be detrimentally impacted by unusually high temperatures (Alexander, 1987). Heat increases transpiration as the vapor pressure within needles increases. Temperature highs during winter months can be particularly detrimental to trees, as water is not in an available state in the soil to replenish the losses from evaporation in the needles (M. Kummel, personal communication, February, 2021). Combined with drought conditions, increased transpiration can increase tree mortality and even preclude seedling establishment (Holtmeier & Broll, 2012). Additionally, extreme heat can cause girdling in seedlings (Alexander, 1987). Overall, the literature suggests that within environments—such as treeline—that harbor both high and low temperature extremes, establishment and growth is best at intermediate temperatures, as both extremes can damage plant physiology. However, for optimal seedling performance, there appears to be a bias towards slightly warmer temperatures. Several studies have found that warmer-than-average growing seasons, soil temperatures, and artificially-warmed site conditions are all positively correlated with seedling establishment and growth, though this has mostly been explored on temporal rather than spatial scales, and primarily within daytime temperature regimes (Danby & Hik, 2007; Holtmeier & Broll, 2007; Eliott, 2011; Greenwood et. al., 2015).

The feedback cycles that occur within an ecotone drive treeline dynamics. As trees interact with wind and the surrounding atmosphere, they create variable microclimates, which impact seedling distribution, and in turn determine the location of a new treeline. In light of potential climatic boundary shifts, it is critical to understand the specific fine-scale drivers of microclimate variation and seedling establishment above treeline (Greenwood et al., 2015). However, as previously addressed, the sheltering effects seen at treeline can be helpful or harmful. In this study we aim to explore the synergies and contradictions within sheltering and facilitation—whether these microsite modifications are burdens or benefits to seedling establishment—to reach a more nuanced understanding of the ecotone. Given the complexity of these dynamics, we explore a two-part question: (1) How do trees modify their surrounding microclimate, and in turn (2) how do these microclimates impact seedling establishment?

Methods

Site Description

The study site is located on the northwest side of Pikes Peak, a 14,115 ft. mountain that sits due west of Colorado Springs, Colorado. The mountain is composed of 1.1-billion-year-old Pikes Peak granite that is felsic in composition, which in turn produces acidic, coarse soils (H. Fricke, personal communication, October, 2020). The approximately 10,000 square meter study area sits at approximately 3,500 meters in elevation and consists entirely of Engelmann spruce. The treeline within the area of interest is an abrupt treeline, characterized by a stark border between a forest canopy and low-stature vegetation in a sparsely populated tundra (Harsch &

Bader, 2011). Trees below the forest edge in the study area have a maximum height of 15 meters, while trees in the ecotone and tundra maximum heights of approximately 5 meters (Russell, 2019). Historic aerial imagery reveals that the spatial distribution of trees within the study area used to be closer to a tree island structure. However, in the 1950s, seedlings began establishing between the tree islands, steadily filling in the gaps to eventually produce the abrupt treeline structure we see today (Neumeyer, 2016).

The study site was divided into three main zones: forest, sheltered zone, and tundra. The sheltered zone and the tundra are demarcated by a windswept line, above which trees exhibit signs of wind damage (Warner, 2018). Within the study area, the vast majority of seedlings are within the sheltered zone, as compared to the forest or tundra (Russell, 2019). Additionally, the study area has had minimal anthropogenic disturbances, unlike many treelines in the Rocky Mountains in which the upslope tundra was commonly grazed by domestic livestock in the 19th through early 20th centuries.

Data Collection (Drone Images & Seedling Data)

Thermal images were collected on August 18th, 2017, over the course of two drone flights. The first flight to capture the nighttime thermal regime occurred early in the morning before any sunlight directly reached the area of interest, with clear skies and winds blowing 2 m/s downslope (Fig. 1A). The flight lasted 23 minutes. The second flight was taken at noon, with clear skies and upslope winds of <0.5 m/s, and lasted 18 minutes (Fig. 1B). Both images were generated using an Infrared Cameras Inc. Series 8640 Broadband thermal camera, with a resolution of 0.1C, and mounted on an octocopter custom-built drone. The drone was flown perpendicular to treeline to account for temperature changes withing the flight time, and in tight, parallel lines to allow for 75% image overlap. To accommodate for the atmospheric temperature distortion between the surface and the drone, the exact temperatures of 30 recognizable surface objects were recorded to calibrate the temperature readings from the drone. The raw thermal readings were processed in Agisoft to produce orthomosaic images. The nighttime and noon thermal image have pixel sizes of 9.37 cm^2 and 10.12 cm^2, respectively. Neither of the two thermal images generated were georeferenced. The reference visible spectrum orthomosaic image was collected via drone flight in 2018 (McGarigal, 2019). Seedling data was also collected in the summer of 2017, in which the coordinates of approximately 2,000 seedlings were recorded. The methodology for seedling data field collection was previously described by Russell (2019).

GIS Processing

To begin processing the thermal images in ArcPro, both thermal images were georeferenced to the ortho target layer using identifiable surface features such as stones as control points. All layers that were not already in 1983 UTM 13N were converted to ensure uniformity between layers. However, even with this initial georeferencing using 16 control points, the thermal images still showed significant warping when compared to the orthomosaic layer. To reduce this warping, the area of interest was split into six strips running perpendicular to treeline, each 23 meters across with a 1-meter buffer, using the “buffer” and “clip raster” tools. Each strip was then individually georeferenced using 10-30 control points, once again tied to identifiable surface objects. The “spline” transformation function was used to rubber sheet the thermal images to the target orthomosaic layer for each strip. Once georeferenced, the strips were merged back together using the “mosaic to raster” tool.

To analyze seedling distribution in relation to daytime and nighttime temperature regimes, a new area of interest shapefile was generated that excluded trees. Without such removal of trees, seedlings located directly under forest canopy would be associated with canopy top temperatures rather than ground temperatures. This new area was constructed using canopy polygons drawn from a 2018 orthomosaic illustrating the perimeter of trees. The polygons were cut out of the study area using the “erase” tool. The “raster calculator” tool was then used to convert the pixel values of the thermal rasters to exact temperatures, based on field temperature measurements. Next, each thermal raster was “reclassified” to divide temperatures into 12 even classes. For the daytime raster, each of the 12 temperature classes represented a range of 1.7C, from 5.0C to 25.9C. For the nighttime raster, each of the 12 classes represented a range of 0.4C, from 1.7C to 6.4C. This intentionally excluded temperatures above 6.4 degrees because nighttime temperatures above 6.4C were only present in canopy tops instead of ground temperatures; therefore, their presence in the new area of interest was likely due to error that occurred when creating the raster. “Extract Value to Points” was then used to assign a temperature class to each of the seedlings that fell within the refined area of interest (1,882 seedlings). Seedling data was exported into Microsoft Excel for further analysis.

To analyze ground temperatures with respect to elevation and proximity to trees, the treeless area of interest was divided into two similarly sized zones above and below a windswept line. The windswept line was generated from field observations on site and marks the approximate boundary of the sheltered zone within the area of interest (Warner, 2018). This split allows for the separate analysis of temperature patterns in both the ecotone and the tundra. Within each zone, 5,000 random points were generated. Using “buffer” and “zonal statistics” tools, a half-meter buffer was generated around each of the 10,000 points, and the mean temperature within each buffer was calculated. Additionally, the “near” tool was used to calculate the distance from each point to the closest canopy polygon to analyze the relationship between ground temperature and proximity to trees. Using “extract multi values to points,” mean buffer temp, distance to canopy polygon, and elevation values were all added to the attribute tables of each of the 5,000 random points in both the ecotone and the tundra. Attribute tables were then exported into Microsoft Excel for further analysis.

Statistical Analysis

All statistics generated from these datasets were calculated in Microsoft Excel or R.

Results

Treeline Microclimate

Night Regime

Before sunrise, the highest temperatures recorded were on the tops of trees in the forest, sheltered area, and the tundra. Tree top temperatures ranged from 6.4C to 9.3C (visible in Figure 1A as green to rust colors). In many instances, the visible warmth of the trees extended beyond their perimeter, as seen with the purple/pink halo of ground temperatures surrounding canopy islands (Fig. 1A). Low temperatures were primarily located directly downhill and downwind (2 m/s straight downslope winds) of canopy clusters in the forest and isolated trees in the ecotone and tundra. The lowest temperature recorded was 1.7C, which was observed in ground temperatures just downhill of trees. Moving downhill from the tundra to the sheltered area, the overall temperature pattern within the area of interest showed a consistent temperature drop of approximately 4.8C to 3.6C over the course of about 50 meters.

Using the area of interest with the canopy polygons removed, ground temperatures with respect to elevation were analyzed both above and below the windswept line (Fig. 2). In the sheltered zone, from the forest up to the windswept line, temperature variability steadily decreased from a range of approximately 5 degrees ($\sigma=1.06$ for the lowest elevation range of 3505-3510 meters) down to a range of 1 degree ($\sigma=0.19$ for the highest elevation range of the sheltered zone of 3525-3530 meters) (Fig. 2A). Nighttime temperatures in the sheltered zone with respect to elevation had a slightly negative slope -0.03C per meter of elevation increase.

From the windswept line uphill through the tundra, temperature instead increased with elevation, at an approximate rate of 0.027 degrees Celsius per meter (Fig. 2B). Temperatures increased in a linear pattern ($R^2=0.49$, n=5,000, $p<0.005$). The variability of temperatures remained relatively constant as reflected in a relatively constant approximate standard deviation.

Our results show that ground temperatures not only vary with elevation, but also with proximity to trees (Fig. 3). Below the windswept line, points within 1 meter of a canopy polygon had the greatest temperature variability, with temperatures ranging from approximately 3C to 8C ($\sigma=0.79$) and included significantly higher temperatures than areas removed from trees (Fig. 3A). Areas removed from the trees had significantly decreased temperature variability. Between 2-5 meters away from canopy polygons, temperatures hovered around 4 degrees and varied little over a half a degree in either direction ($\sigma=0.21$).

Above the windswept line and beyond 1 meter away from canopy polygons, temperatures maintained minimal variability (range=3.15-5.46C, $\sigma=0.24$), typically remaining between 4 and 5C, and steadily increased for points further away from trees (0.022C per meter) (Fig. 3B). However, within 1 meter of trees, similar to below the windswept line, temperature variability and temperature highs increased significantly (range=2.75-5.94, $\sigma=0.33$).

Day Regime

During the midday flight, the highest temperatures (26C) recorded were directly uphill and downwind of trees (upslope winds of <0.5 m/s). Zones of relatively higher temperatures also included canopy surfaces facing southeast (Fig. 1B). The lowest temperatures recorded (5C) were found in zones extending from the northwest faces of trees, in what appear to be the shadows of trees in all three zones. The low temperature areas in the ecotone and tundra (approx. 5-6.7C) are slightly colder than the low temperature areas within the forest (approx. 6.7-8.5C). As the hill slopes downward from the tundra to the sheltered area, the ground temperature remains relatively constant throughout the whole area of interest, at a temperature of approximately 11.9C.

Temperature and elevation analyses for daytime temperature regimes revealed greater variability in treed areas at lower elevations. Below the windswept line, temperatures appeared close to randomly distributed with respect to elevation with significant variability (range=5.08-18.05, σ=2.42) (Fig. 2C). However, warmer temperatures (approximately 10-15C) were more often found in higher elevations in the ecotone, while colder temperatures (approximately 7-9C) were more frequently found in lower elevations in the forest. The coldest temperatures of all (~5-6.5C) were located in the ecotone.

Above the windswept line, temperatures remained relatively constant through the tundra with a variability of approximately 4C (σ =1.05) (Fig. 2D). However, the highest and lowest temperatures (5.6C and 18.1C) were primarily present closest to the windswept line.

Daytime temperatures also varied significantly with proximity to trees. Below the windswept line, once again the lowest and highest ground temperatures (range=5.1-18.0C) were within 1 meter of canopy polygons (0-1 meters from trees, σ=2.6) (Fig. 3C). For temperature highs, this variability decreased steadily with increased distance from trees up to 5.5 meters (3-5.5 meters from trees, σ=1.06). The coldest temperatures seen below the windswept line (approximately 6-10C) were predominantly within 2 meters of trees.

Above the windswept line, once again the greatest temperature variability was closest to the trees (Fig. 3D). Within 2 meters of trees, temperatures ranged from approximately 6-18C. Beyond 2 meters, variability decreased to a range of approximately ~10-14C.

Microclimate Impact on Seedling Recruitment

Night Regime

Within the 12 classes of nighttime ground temperatures ranging from 1.70-6.40C, seedlings were found at significantly higher densities in classes 3-7 (2.48-4.44C) (Fig. 4A). No seedlings were found in locations with nighttime temperatures below 2.48 degrees, and only 27 seedlings (out of approximately 2,000) were found in locations with nighttime temperatures above 4.83C. The best line of fit for seedling density with regard to nighttime temperatures is a 3rd degree polynomial (adjusted R^2=0.58, F(3,8)=6.043, p=0.019). This pattern is corroborated by a relative distribution estimate function (Rhohat) analysis in R, in which the highest density of seedlings is present at sites with temperatures of approximately 3.7C (Fig 5A). Seedling density then decreases as temperature increases with a high degree of certainty up to 5C, above which there are relatively few datapoints and less confidence.

Day Regime

Within the 12 classes of daytime temperatures ranging from 5.0-25.92C, seedlings were found at a significantly higher density in low to moderate temperature locations (5.0-17.20C)

(Fig. 4B). This pattern was consistent except for one seedling in the 10th temperature class which was disregarded because it was considered at outlier (10th class seedling density (1.71) > (Q1-Q3)*1.5+Q1 where Q1=0.035, Q3=0). Seedling density dropped to 0 above 18.94C. The best line of fit for seedling density with regard to daytime temperatures is a 3^{rd} degree polynomial (adjusted R^2= 0.70, F(3,8)= 9.458, p=0.005). This pattern is once again corroborated by a relative distribution estimate function analysis, in which the highest density of seedlings is present at sites with daytime temperatures of approximately 14C (Fig 5B). Seedling density decreases with both lower and higher temperatures as 5C, with the association between lower temperatures and reduced seedling density in particular bearing a high degree of confidence.

Discussion

The goal of this study is to understand microclimate mediated feedbacks between the structure of the treeline and seedling establishment. To examine this, we examined diurnal treeline temperature regimes and seedling dynamics at a study site on the northwest side of Pikes Peak. Within an ecotone, sheltering from neighboring trees can kickstart a positive feedback cycle, through protection from wind abrasion or moderation of temperatures through reduced sky exposure (Germino & Smith, 1999; Resler, 2006). However, sheltering can also modify microsite temperatures by reducing turbulence, which creates "eddies" on the leeward side of trees in which temperature extremes can be found (Oke, 1987). Extreme temperatures can be damaging to seedling physiology. Based on these two seemingly contradictory understandings of the benefits or burdens a sheltering effect can provide, the key questions of this study are (1) How do trees modify their surrounding microclimate, and in turn (2) how do these microclimates impact seedling establishment?

Night Regime

Downslope winds (2 m/s) resulted in larger scale temperature trends across the study site. This is primarily visible as a steady decrease in temperature moving downslope towards the windswept line. Consistent with the analogy of moving water, it appears that once trees reach a critical density in the ecotone, cold, dense air moving downslope becomes “dammed-up.” This is likely due to air displacement from increasing pressure in front of the treeline (Oke, 1987). Because if its stagnant nature, this “dammed” cold air at treeline exchanges little heat with superior air, and is consequently much colder than sites with more air movement (M. Kummel, personal communication, April, 2021). Below the windswept line, temperatures increase approaching the forest edge, which may be attributed to the moderating role of canopy coverage in which trees radiate heat onto the forest floor, increasing nighttime temperatures (Davis & Gedalof, 2018). As expected, the warmest areas of the site were canopy tops, as they are coupled to the atmosphere (Grace et. al, 2002). This is a result of the poor coupling between the surface and the atmosphere and the ground-based radiation inversion of air temperatures that forms at night, where treetops extend towards the warmer air above the surface.

Thermal images of the nighttime temperature regime perhaps best exemplify the conflicting theories of sheltered areas as favorable or inhospitable microclimates. Longwave radiation from trees is visible as “halos” of warmer ground temperatures surrounding ecotone trees. This heating could be favorable to seedlings, as it appears to increase nighttime ground temperatures, which could reduce photoinhibition in seedlings (Germino & Smith, 1999; Germino et al., 2002). Also at play is the sheltering effect which reduces turbulence downwind of objects. This effect is visible in our thermal images as isolated pockets of low temperatures just downwind of trees. The lowest temperatures recorded at the study site were in these downwind eddies. This overall pattern matches with Oke's (1987) explanation of eddies as stationary pockets of air that do not exchange heat with the surrounding atmosphere, thus cooling to a lower temperature; pockets that have the potential to damage seedlings as cold nighttime temperatures can lead to photoinhibition (Germino & Smith, 1999).

Both in the forest and at the lower end of the ecotone, we can clearly see the competition of these two opposing effects of sheltering. Smaller canopy openings in the more densely populated part of the ecotone maintain relatively warm ground temperatures, likely attributed to the longwave radiation emitted by the surrounding trees. Here, the increased nighttime ground temperatures from trees seem to outweigh the low temperatures caused by stationary air pockets. Yet, there appears to be a limit on how far longwave radiation extends outward from trees. Because of this apparent limitation in larger canopy openings and in more open areas of the ecotone, we find low temperatures from leeward air eddies that result in relatively cold patches of ground. These competing effects are likely what cause ground temperatures closest to trees to have the highest variability. While these isolated air pockets certainly reduce wind, the combination of the ground-based radiation inversion with downslope winds results in the study area's coldest nighttime sites lying adjacent to trees, perhaps adding complexity to the underlying assumption that sheltering and neighbor interactions initiate positive feedback cycles.

Seedlings have thermal requirements for germination, establishment, and survivorship (Korner, 2012). Temperature extremes can have negative consequences for conifer seedling physiology, as previously discussed, and on a temporal scale, years with larger than average temperature ranges are inversely correlated with seedling emergence (Germino et al., 2002). However, some temperature oscillation is good, as germination often decreases under constant diurnal temperature conditions (Korner, 2012). In our study, seedling appeared to have high densities in areas with intermediate nighttime temperatures, and low densities in sites with temperature highs and lows. The low densities in cold sites were expected, as seedlings are well documented as having greater abundance in sites with low sky exposure to protect from extreme nighttime temperatures, which can lead to photoinhibition the following day (Germino & Smith, 1999). Areas with high nighttime temperatures were populated by few conifer seedlings. Generally, these locations were found closest to mature trees, likely warmed from longwave radiation from the conifers. Factors other than temperature may be at play in explaining the avoidance of these sites, including litter layer thickness and competition for resources such as water and nutrients that are associated with proximity to mature trees. Overall, nighttime data seems to primarily illustrate the ability of trees to create hostile microsites, sites that harbor the highest and lowest ground temperatures found in the study area, though a follow-up analysis should be conducted to directly link seedling distribution with proximity to trees.

Day Regime

Across the study site, increasing daytime surface temperatures disrupt the nighttime ground-based radiation atmospheric inversion in the roughness layer and create upslope winds (<0.5 m/s), likely resulting in the removal of the "damming" effect of cold air piling up against the treeline. Canopy tops are still among the warmest areas in the site, though from shortwave insolation rather than coupling with the warm nighttime atmosphere.

During the day, based on our orthomosaic images, the primary thermal factors at play are shade, and once again, the atmospheric eddy effect. The lowest daytime temperatures are present in the noon-time shadows. These low temperatures are concentrated in the lowest area of the ecotone, where trees are densest and there are the fewest opportunities for insolation to reach the ground. As expected, the leeward eddy effect is still persistent throughout the day, though the isolated air pockets are now uphill of trees as the wind direction had shifted (light upslope winds of <0.5 m/s). In the relatively stationary air pockets uphill of trees, opportunities for convective cooling are reduced, resulting in increased ground temperatures (Oke, 1987). This expected heating was visible in the thermal images.

Once again, these two microclimate modifiers come together to form a patchwork of temperature highs and lows. At the lower end of the ecotone, where trees are densest, shading appears to be the primary factor in determining microclimate. Minimal direct sunlight is reaching the ground, and subsequently ground temperatures are quite low (Korner & Paulsen, 2004). Moving up the ecotone, as trees become more sparsely dispersed, there are more opportunities for solar radiation to reach the ground, introducing a warming eddy effect downwind of trees. These warm pockets are visible as warm patches both on the leeward side of trees (which also happened to be facing the sun during the drone flight). These warm eddies are driven by insolation combined with reduced turbulence (Oke, 1987). As with nighttime temperatures, both of these opposing effects lead to the highest temperature variability closest to trees.

As expected, seedlings appear to be the in greatest abundance in intermediate microsite temperatures, with relatively low densities in microsites containing both high and low daytime temperatures. Reduced seedling density in zones of daytime temperature lows is likely a reflection of reduced seedling performance in areas that are consistently shaded. However, there appears to be particularly low densities in sites with high daytime temperatures as there are no seedlings in areas with noon temperatures exceeding 18.94C (Fig. 4B). The majority of pockets exceeding such temperatures were found in downwind tree eddies and were receiving direct insolation. While the absence of seedings in sites with extreme high temperatures is understandable, 19C is not considered "extreme" for seedlings on a summer day, so the low density of seedlings seen here is somewhat unexpected (Alexander, 1987; Davis & Gedalof, 2018). However, the thermal images used in this study are only single-day temperature readings, and the sites with the highest recorded temperatures likely have the potential to reach seedling damaging temperatures on hotter days. According to treeline literature, warmer than average conditions tend to be beneficial for seedlings (Danby & Hik, 2007; Holtmeier & Broll, 2007; Eliott, 2011; Greenwood et al. 2015). Warmer temperatures overall (both summer and winter) are associated with higher rates of seedling recruitment and establishment (Holtmeier & Broll, 2007; Elliot, 2011), as well as areas with warmer soil temperatures (Greenwood et al., 2015). Beyond the benefits of warm temperatures on seedling establishment, warmer temperatures are also positively associated with growth (Danby & Hik, 2007). Based on this understanding of warm temperatures being positively associated with seedling establishment and growth, the low seedling density in relatively warm microsites seen in this study could possibly be related to the interference from other factors such as drought, fungus, or changes in snowpack (Holtmeier & Broll, 2007).

Conclusion

We found that the microclimate temperature variations surrounding trees are defined by three factors: (1) the obstruction of boundary layer airflow, which leads to the "damming" of cold air at treeline as well as eddy-like isolated pockets of air that exhibit exaggerated diurnal temperatures, (2) longwave radiation from trees, primarily a nighttime phenomenon that warms a certain radius on the ground below a tree, and (3) shade, which accounts for most of the daytime temperature lows. These modifications of microclimate are important factors in seedling microsite preference, as seedlings appear to have a strong preference for moderate daytime and nighttime temperatures. In general, the limiting factors of successful seedling establishment and survivorship include temperature, wind, water, and light (Korner, 2012). While much literature shows that sheltering from neighboring trees can ease those burdens on seedlings (e.g., Germino & Smith, 1999; Germino et al., 2002; Resler et al., 2005; Resler, 2006) resulting in positive feedback loops, our study adds complexity to the subject, showing that trees also have the potential to create more hostile microclimates. The reduced sky exposure facilitated by a neighboring conifer *can* help by moderating temperature extremes during the night and day (Germino & Smith, 1999). However, the presence of a neighboring tree combined with other factors such as wind speed, wind direction, and degree of insolation has the potential to make temperatures even more extreme that the surrounding area, therefore making a microsite more hostile to seedlings.

Limitations

There are several limitations of this study, primarily in the number of thermal images that were analyzed. Only one daytime and one nighttime orthomosaic thermal image were recorded and analyzed. Analyzing thermal images from additional days and different times would allow for a clearer understanding of the variability of these results. Additionally, it would be beneficial to take thermal orthomosaic images over an area larger than the actual zone of interest, specifically are area that incorporates more of the completely forested area below the ecotone. The orthomosaic images used in this study were most distorted on the perimeter of the image. A wider area of thermal reading would allow for discrepancies in the georeferenced layers to be better resolved, so the impacts on microsites and seedlings could be discussed with more confidence. Looking ahead, there are several directions for this study to proceed. First, looking at the location of seedlings gives us only one moment in time. To gain a more complete understanding of temperature and seedling dynamics at treeline, it would be beneficial to examine not just seedling location but also seedling mortality with respect to temperature using thermal images.

Microclimate conditions are likely one of the most important limitations on seedling establishment above treeline (Davis & Gedalof, 2018). The data collected and analyzed in this study lends insight into how microclimate conditions may affect seedling establishment. This data is increasingly important as the thermal drivers of seedling establishment change. Increased global temperatures will fundamentally alter the climatic constraints that determine the location of treeline, along with other transitional ecosystems (Malanson et al., 2011; Grace et al., 2002). Beyond increased overall temperatures, researchers have found ranges of diurnal temperatures to be shrinking (Stafford et al., 2000). These large-scale, thermal changes will filter down to affect the small-scale processes that determine microsite conditions.

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Figures

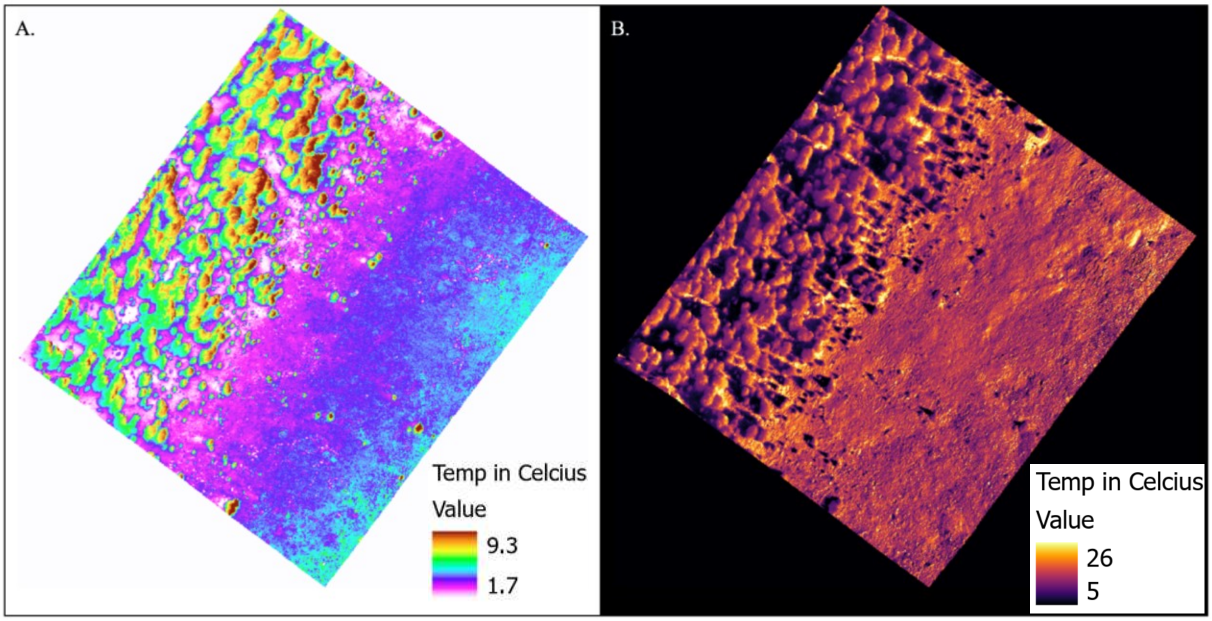


Figure 1. A) Thermal image of the study area taken just before sunrise on August 18th, 2017. The rust color corresponds to the warmest temperatures recorded (9.3C) and the white corresponds to the coldest temperatures (1.7C). B) Thermal image of the study area taken at noon on August 18th, 2017. The bright yellow corresponds to the warmest temperatures recorded (25.9C) and the black corresponds to the coldest temperatures (5C).

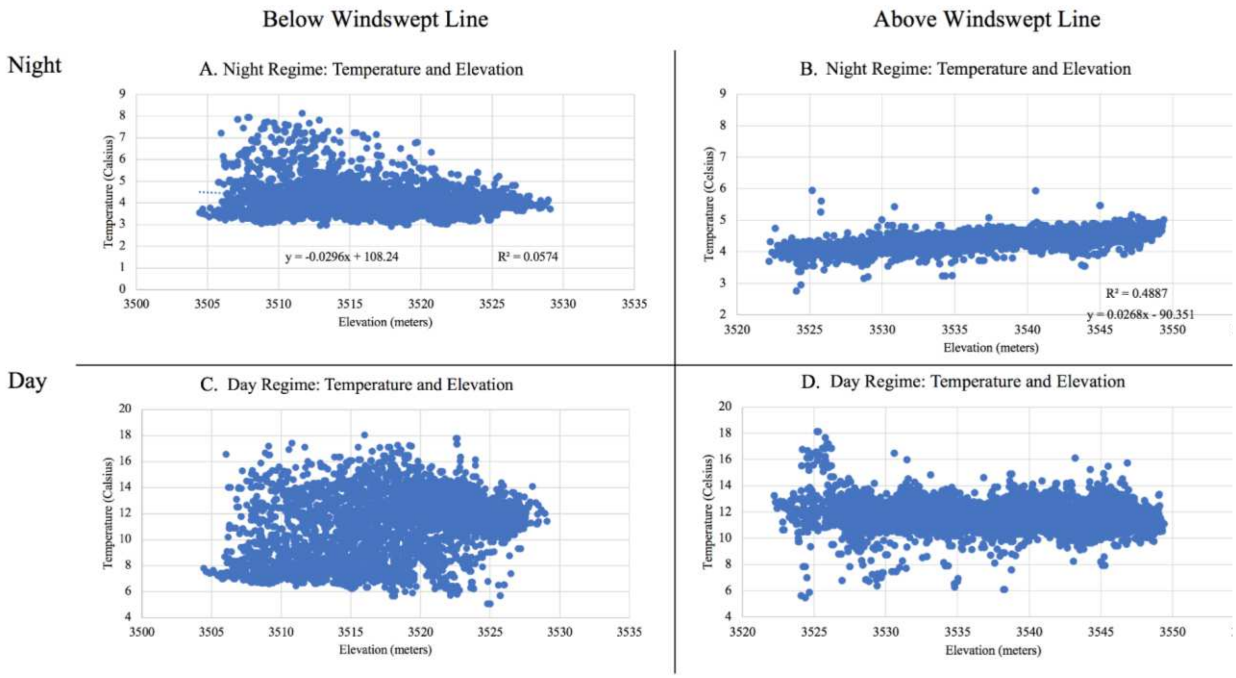


Figure 2. A) Nighttime ground temperatures in relation to elevation below the windswept line. B) Nighttime ground temperatures in relation to elevation above the windswept line. C) Daytime ground temperatures in relation to elevation below the windswept line. D) Daytime ground temperatures in relation to elevation above the windswept line.

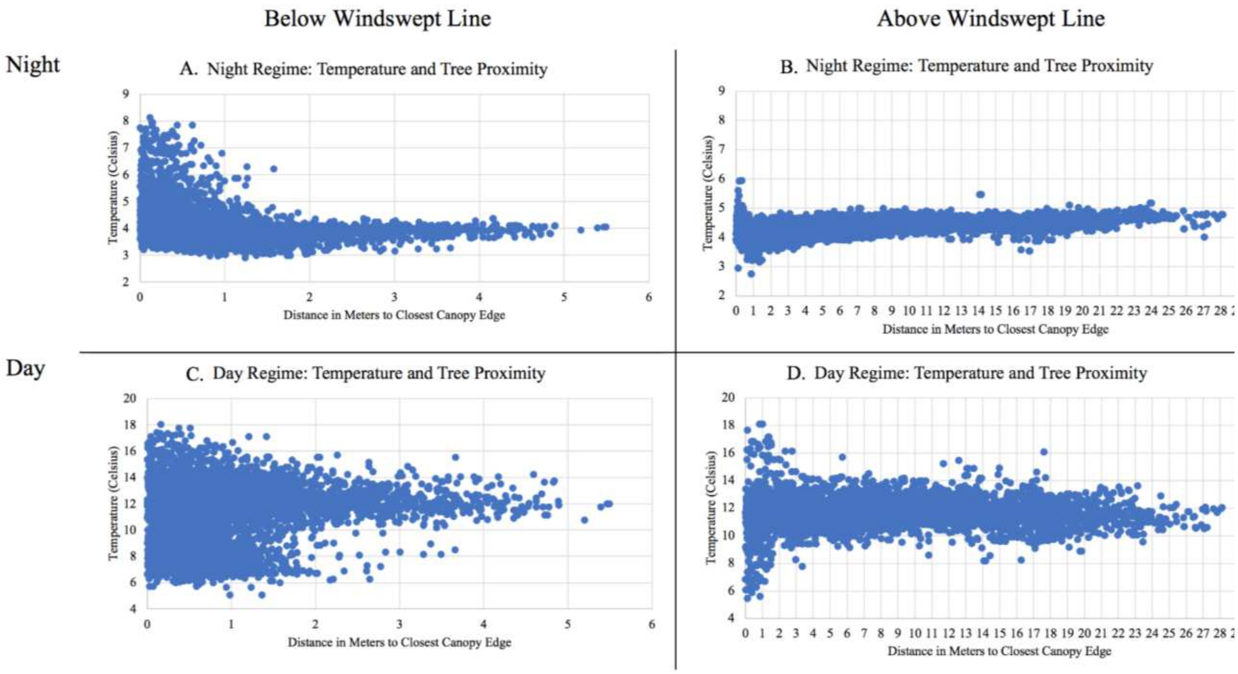
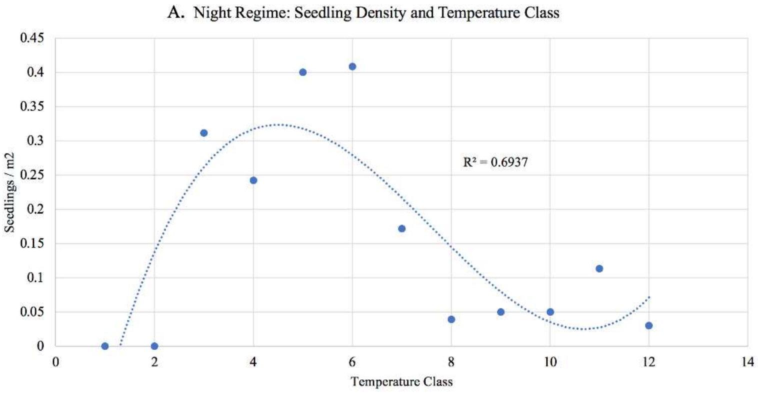


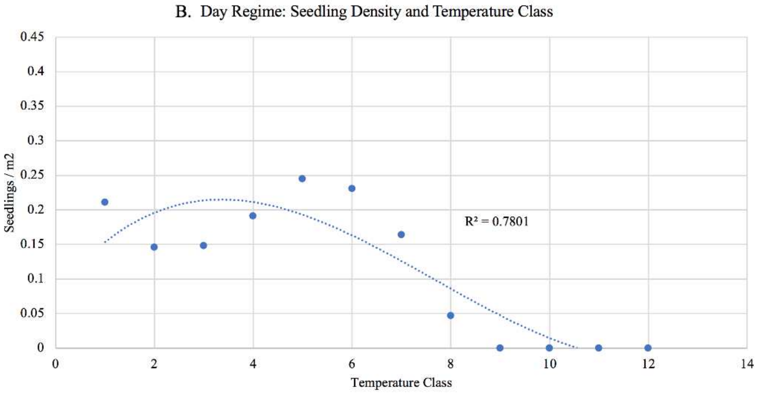
Figure 3. A) Nighttime ground temperatures in relation to tree proximity below the windswept line. B) Nighttime ground temperatures in relation to tree proximity above the windswept line. C) Daytime ground temperatures in relation to tree proximity below the windswept line. D) Daytime ground temperatures in relation to tree proximity above the windswept line.

Night


A. Night Regime: Seedling Density and Temperature Class

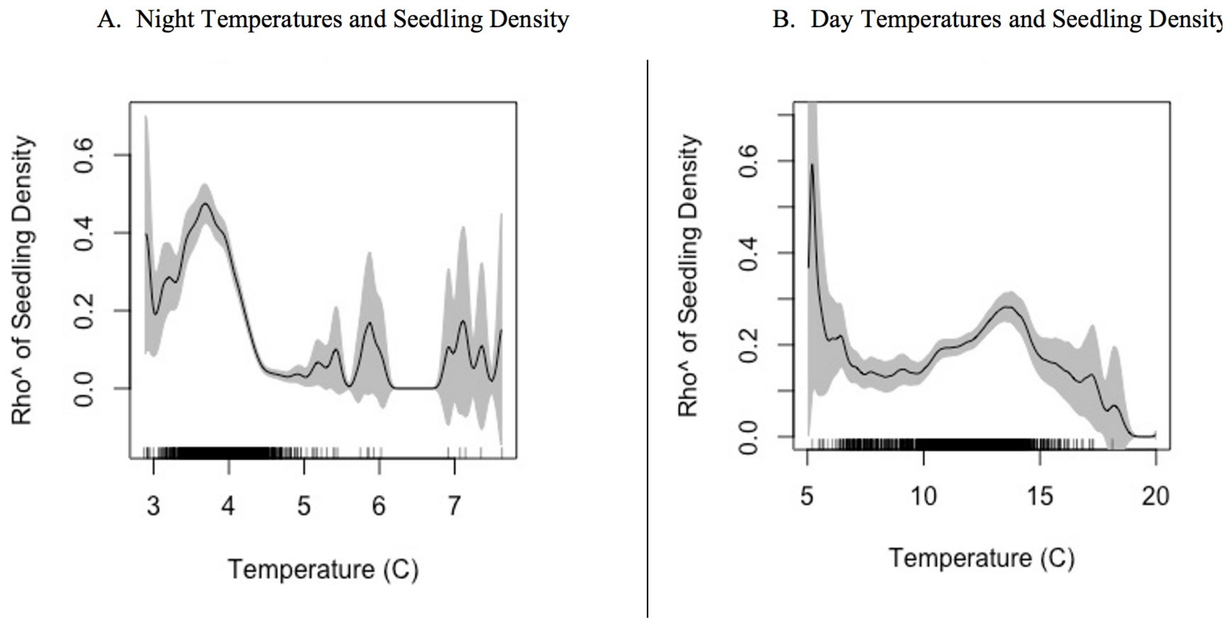
Class	Temperature (Celsius)
1	1.7-2.092
2	2.092-2.483
3	2.483-2.875
4	2.875-3.267
5	3.267-3.658
6	3.658-4.05
7	4.05-4.442
8	4.442-4.833
9	4.833-5.225
10	5.225-5.617
11	5.617-6.008
12	6.008-6.4

Day


B. Day Regime: Seedling Density and Temperature Class

Class	Temperature (Celsius)
1	5-6.743
2	6.743-8.486
3	8.486-10.229
4	10.229-11.972
5	11.972-13.715
6	13.715-15.458
7	15.458-17.201
8	17.201-18.944
9	18.944-20.687
10	20.687-22.430
11	22.430-24.173
12	24.173-25.916

Figure 4. A) Seedling density in relation to nighttime ground temperatures, in which each temperature class represents a range of 0.4C. B) Seedling density in relation to daytime ground temperatures, in which each temperature class represents a range of 1.7C.



A. Night Temperatures and Seedling Density

B. Day Temperatures and Seedling Densit

Figure 5. A) Nighttime temperatures in relation to the relative distribution estimate function (Rho^) of seedling density, in which the width of the grey band represents the degree of confidence. B) Daytime temperatures in relation to the relative distribution estimate function (Rho^) of seedling density, in which the width of the grey band represents the degree of confidence.