NEIGHBOR INTERACTIONS AT AN ALPINE TREELINE SUPPORT

MULTIPLE MODELS OF THE STRESS GRADIENT HYPOTHESIS

A Thesis

Presented to

The Faculty of the Environmental Studies Program

The Colorado College

In Partial fulfillment of the Requirements for the Degree

Bachelor of Arts

By

Ella Hartshorn

May 2020

_____

Dr. Miroslav Kummel

Associate Professor

_____

Dr. Howard Drossman

Professor

TABLE OF CONTENTS

Abstract

The mechanisms that determine the spatial structure of ecotones are not entirely understood. The structure of an alpine treeline ecotone is likely determined by an interaction between plant physiology and the underlying harshness gradient, and these influences are modified by neighbor interactions among the trees. The stress gradient hypothesis (SGH) postulates that neighbor interactions are inhibitory at the benign end of the gradient and facilitatory at the harsh end of the gradient. Through neighbor interactions, the current spatial pattern of a treeline will influence the future pattern, thus it is essential to understand the extent these interactions influence treeline structure. This project hypothesized that seedling establishment and growth at this site could be modeled with a linear SGH. The study analyzed seedling establishment and growth with respect to canopies of adult trees (derived from a drone based orthomosaic) at a 380m by 90m treeline site on Pikes Peak, CO. The field site was divided into four equal sized zones along the elevation gradient.

The results indicated that neighbors influence seedling establishment and growth differently. The density of seedlings in each zone reflected patterns of seedling establishment across the entire site. Transition 1 had the highest seedling establishment, which indicated that seedlings preferentially established away from adults in the lower two zones but established randomly in in the upper two zones. Data regarding 10-year growth showed seedlings grew somewhat better outside the 1m tree buffer across the entire site (t=-1.804, df=224, p=0.073). In the Forest Zone and Transition 1 there was no significant difference between seedling

growth inside and outside the buffers. In Transition 2, seedlings grew significantly better within the buffers (t=2.552, df=33, p=0.016). Across the entire site, the growth in the Forest Zone and Tundra Zone was lower than the growth in the transition zones (one-way ANOVA: F (3,222) = 32.936, p<0.005). Additionally, a kriging interpolation of 1-year and 10-year growth for all seedlings, seedlings inside the 1-meter buffer, and seedlings outside the 1-meter buffer indicated that seedlings grew best at intermediate levels of stress. The results of this study indicate that the relationship between neighbor interactions on an underlying stress gradient at this site can be described with a linear model in regard to seedling establishment and a hump-shape curve in regard to seedling growth. Additionally, signals of neighbor influence are better detected over longer growth periods.

Introduction

Ecotones are the transitional zones between two distinct biomes or ecosystems. The interface of these ecosystems can be wide or narrow, and exhibit gradual or abrupt shifts. Underlying plant physiology and external abiotic conditions are known to influence ecotone structure (Körner, 1998; Körner & Paulsen, 2004), but ecotones are also formed through internal feedbacks, such as neighbor interactions between plants (Malanson *et al.,* 2011; Risser, 1993; Walther et al., 2005). The nature of neighbor interactions is contingent upon space. Short-range interactions, for example, occur directly between adjacent neighbors and therefore affect plants more rapidly than do long-range

interactions. Long-range interactions, on the other hand, impact entire communities of trees and the high tree density can impact overall site characteristics like snow depth, ground temperature, or wind shear. Neighbors impact each other differently through competition and facilitation, and the effects of these interactions impact the life stages and life history of plants. These can all occur simultaneously, such that within a single community short distance plant facilitation can create long distance inhibition, eliciting varied responses that will affect the establishment, survivorship, and growth of plants. These internal feedback loops operate on an underlying harshness gradient and are continuously impacted by external abiotic conditions. The balance of external mechanisms and internal feedbacks within an ecotone are delicate and easily influenced by environmental disturbances. As a result, ecotones are indicators of the effects of climate change and could provide insight into the ways transitional ecosystems will be affected by future climate change (IPCC, 2019; Malanson *et al.,* 2011; Risser, 1993; Walther et al., 2005).

Alpine treeline ecotones are marked by the transition from a closed canopy forest to the uppermost elevational gradient where tree species can survive, at which point the system transitions into a tundra landscape. The altitudinal extent of treelines is constrained and constructed by a variety of abiotic and biotic mechanisms, but the uppermost limit of growth is primarily constrained by temperature (Körner, 1998; Körner & Paulsen, 2004; Smith *et al.,* 2003; Grace *et. al.,* 2002). The growth-limitation hypothesis, originally argued by Körner (1998), proposed that trees at high elevation are unable to utilize carbon

sequestered during photosynthesis because of low soil temperatures. Trees at high elevations have a sufficient amount, or even a surplus of carbon, but are unable to convert the carbon into growth. Therefore, treelines should be especially affected by climate change because the effects of global warming are more pronounced at higher elevations and latitudes (IPCC, 2019; IPCC, 2019). In the context of global warming, the growth-limitation hypothesis supports the conjecture that treelines have been and will continue to be highly impacted by warming temperatures. Evidence of treeline advancement has been observed globally and is well documented in current literature (Feiden, 2010; Grace *et. al.,* 2002; Harsch & Bader, 2011).

Spatial Structures of Treelines

Treelines exhibit general similarities but are marked by distinct spatial structures at the stand-level, such as abrupt, diffuse, krummholtz, or island. Abrupt treelines exhibit sharp boundaries between the forest and tundra ecosystems. Diffuse treelines gradually decrease in height and density as elevation increases. Krummholtz treelines are comprised of stunted and deformed trees that appear in patches, bands, or as a gradual diffusion above the forest ecosystem. Krummholtz are sometimes excluded from treeline forms because the trees do not meet height requirements ($\geq 3m$) of the current literature's definition of a standard tree (Harsch & Bader, 2011; Körner, 1998; Körner & Paulsen, 2004). Island treelines are patches or bands of upright and krumholtz trees that establish above the forest but before the tundra ecosystem. (Harsch & Bader,

2011). Individual treeline forms are likely controlled differently by separate and overlapping external mechanisms and internal feedbacks (Harsch & Bader, 2011).

Treeline Dynamics

This study analyzed the dynamics at a diffuse treeline that is rapidly advancing due to climate change. Globally, diffuse treelines are advancing more frequently than other treeline forms (Harsch & Bader, 2011). This is partly due to growth-limitation which is the most dominant external mechanism at a diffuse treeline (Harsch & Bader, 2011; Körner, 1998; Malanson *et al.,* 2011). While advancements in understanding have been made in recent years, the ways in which external mechanisms specifically interact with internal feedbacks between neighbors to create treeline structure is not understood. In addition to the effect of external mechanisms on plant physiology (growth-limitation hypothesis), it is believed that the underlying harshness gradient (the changing severity of abiotic conditions on some gradient) greatly impacts internal feedbacks and may be responsible for the establishment and growth of seedlings at treeline.

The stress gradient hypothesis (SGH) has been referenced as a connection between the changes in internal feedbacks at varying degrees of harshness on a treeline gradient. The SGH postulates that neighboring plants will compete in benign conditions, but that facilitation will increase with abiotic environmental stress. In benign environmental conditions, the SGH posits that competition is the net result of neighbor interactions because effects of high-density neighbor competition for resources outweigh any benefits of environmental amelioration. In harsh conditions, positive effects of environmental amelioration by neighbors

compensates for negative impacts of resource competition (Butterfield *et. al.,* 2013; Callaway, 1998; Callaway, 2007; Callaway *et. al,* 2002; le Roux & McGeoch, 2010; Maestre *et. al.,* 2009; Klanderud *et. al.,* 2017).

Models of the Stress Gradient Hypothesis

The relationship between facilitation and competition along an environmental stress gradient is typically described with a linear model (Butterfield *et. al.,* 2013; Callaway, 1998; Callaway, 2007; Callaway *et. al,* 2002; Leong *et. al,* 2019). An increasing number of studies conducted in a variety of environments that have analyzed different parameters (multiple species, the removal of one species, the effects of multiple abiotic stressors, etc.) are now indicating that this relationship may be modeled differently. In addition to linear models, the curve has taken a symmetrical hump shape, an asymmetrical hump shape, and a plateau in recent literature (Figure 1) (Leong *et. al,* 2019; le Roux & McGeoch, 2010; Maestre *et. al.,* 2009; Michalet *et al.,* 2014; Klanderud *et al.,* 2017).
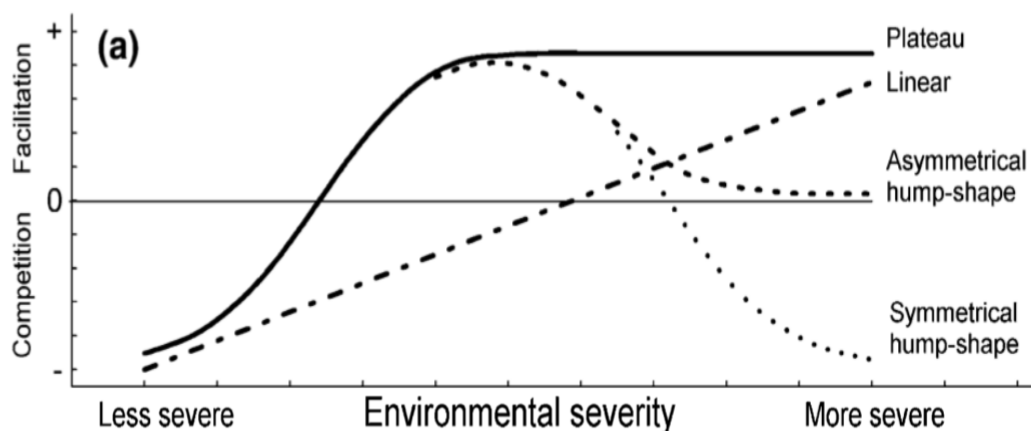

Figure 1: Hypothesized shapes of the relationship between facilitation and competition along environmental stress gradients. (Adapted from: le Roux & McGeoch, 2010, pg. 735, Figure 1a)

Symmetrical Hump Shape. The curve represented by a symmetrical hump shape is defined by facilitation at intermediate environmental stress and competition at both extremes of the gradient. The results of neighbor interactions at the benign ends of the harshness gradient are consistent with the linear curve of the SGH. The symmetrical hump shape operates under the assumption that competition does not decrease with increasing stress, such that neighbor facilitation cannot be sustained under extreme environmental severity, because benefits incurred by neighbors are negligible compared to their negative impacts.

Asymmetrical Hump Shape. Similar to the symmetrical hump shape, this curve exhibits the highest facilitation between neighbors at intermediate levels of environmental stress. Plant interactions become neutral under severe environmental conditions because both the amelioration of severe abiotic stressors and the competition for resources are equally insignificant. This model assumes the reduced competition is a result of the slow rate and minimal growth of plants in stressful environments.

Plateau. Similar to the linear shape, facilitation increases with the underlying harshness gradient, but the plateau model is constrained by a positive asymptote. This curve suggests that it is consistently beneficial to grow close to a neighbor across the harshness gradient, but that there is some limit to the strength of this net facilitation (le Roux & McGeoch, 2010).

Further speculation about how models of the SGH may describe the structure of treeline is needed. This study contributed to the field a better understanding of how internal feedbacks operating on an external gradient impact treeline structure. It was hypothesized that the diffuse treeline would exhibit a linear SGH response where trees would compete with neighbors at benign and low elevational gradients (in the forest ecosystem) and increasingly facilitate each other farther up the harshness and gradient (approaching the tundra ecosystem).

The research questions included: (1) What would the balance of competition and facilitation look like at treeline? (2) Would there be different responses to these interactions for establishment and growth? (3) Over what distances would signals be observable? These questions were addressed through a spatial analysis of neighbor interactions and the ensuing establishment and growth response of seedlings to help determine if the treeline structure exhibited a linear or alternative model of the SGH. An improved understanding of the structure and descriptive model of treeline ecotones will inform the ways ecotones in general are structured. This knowledge is critical in the context of climate change, as it will allow ecotones to be more accurate indicators of future disturbances in transitional ecosystems.

Methods

Site Description

The field site was a transitional ecotone between a closed canopy *Picea engelmannii* (Engelmann spruce) forest and alpine tundra. The ecotone boundary was a diffuse treeline that exhibited a gradual decrease in tree density with increasing elevation. The site was located in a bowl on the west slope of Pikes Peak within the Front Range of Colorado and was chosen because the diffuse treeline here is known to be significantly advancing (Earnst, 2011; Elwood, 2012; Feiden, 2010). The center of the site was located at 105º5'25" W and 38º51'35" N and the elevation across the middle of the transect was 3609m to 3719m a.sl. The field site was sectioned into an approximately 150 meters long and 60 meters wide transect that ran parallel to the elevation gradient with a northwest aspect. The transect spanned from the 1999 treeline (identified using a 1999 aerial photograph of the site and Jenks Natural Breaks Algorithm in ArcGIS Pro; Feiden, 2010) at the lowest boundary of the Forest Zone and extended to the uppermost tree in the Tundra Zone. The upper boundary of the transect aligned with the elevational limit at which trees can exist (approximately 3,700 m above sea level at this site). The transect was divided into four approximately equal zones (~35 meters by 60 meters). Starting in the forest and moving up the elevation gradient, the zones were labeled the Forest Zone, Transition Zone 1, Transition Zone 2, and the Tundra Zone. The space between the trees was occupied by tundra grass and forbs. No other tree or shrub species were present at the site. Granite boulders were present throughout the site with the most

significant outcropping located at a small rockslide near the bottom of the

Transition 1 zone. The vast majority of the *P. engelmannii* trees had a primarily

vertical stature. Very few krummholtz mats were present at the field site; instead,

some trees exhibited mild to moderate flagging, especially on the upper portion of

the ecotone. The site is generally covered with snow from early October until the

middle of June.

Field Methods

This field site transect was initially established by Elwood in 2012, and

the audit in this study was partially based on that prior research. Every Engelmann

spruce greater than 10 centimeters in height within the transect was given an

identification tree tag (n=1110), geolocated with a Trimble GeoExplorer GeoXT

GPS, and mapped within ArcMap 10 in the ArcGIS Pro geographical information

system. Engelmann spruce smaller than 10cm in height were not included in this

study because it was not possible to consistently find them among the tundra

grass. The Engelmann spruce were divided into three distinct size classes based

on height: seedlings (0.10m and 0.50m in height), saplings (0.50m to 3.0m in

height), and adults (greater than 3.0m in height). This study was primarily

interested in the seedlings, how they were distributed, and how they grew in

adjacency to saplings and adults. As such, the sapling and adult age classes were

grouped together in the analysis, and the combination is referred to as 'adults' for

the remainder of the paper. During data collection, age, height, 1-year growth

rate, 10-year growth rate, and percent damage were all recorded. Dead trees

greater than 10cm in height were tagged, geolocated with the GPS and mapped in

ArcGIS Pro, but no other data was collected. The age of seedlings was estimated by counting apical bud scars where the length from one bud scar to the next represents the growth of that year. One-year growth was estimated by measuring the distance from the top of the leader scar to the closest bud scar, and 10yr growth measured the distance from the top of the leader scar to the tenth bud scar. The tree height was recorded for all trees that could be accurately measured by hand. The height of trees that could not be measured manually were estimated in ArcMap 10 using a drone-based 3D orthomosaic of the transect site.

GIS Analysis

A map of trees and their canopies was created in ArcMap 10 in the ARGIS PRO geographical information system, to identify establishment and growth of seedlings in relation to adults over space. The Trimble geolocations and the ArcGIS mapped trees were cross-referenced to more accurately locate trees and project their spatial distribution. The trees and their canopies across the entire site were digitized using the drone-based orthomosaic and the tree geolocations. An individual layer was created for all seedlings (n=302), and groups of two or more adult trees were digitized as a single unit and are referred to as clusters (n=417). The impact of adult neighbors on seedling establishment was analyzed by creating a one-meter buffer around all clusters and individual adult trees. This buffer layer and the seedlings layers were joined to identify all seedlings established within the buffer area (n=131) and outside the buffer area (n=171). This was done across the entire site, and for each zone, in order to determine whether seedlings preferentially established close to or away from adult neighbors and clusters. The

drone-based orthomosaic map of the transect site in Figure 2 was created to allow a better visualization of the clusters of connected canopies and the diffusion of tree density with increasing elevation. The orthomosaic base-map in Figure 2 is overlaid with the layers depicting the boundaries for each zone, the adult trees and cluster areas, and the 1m buffer around clusters (values are displayed in Table 1).

An ordinal Kriging interpolation equation ($Z(s) = \mu + \varepsilon(s)$) utilized through the Raster Kriging tool in ArcMap 10 interpolated the 1yr and 10yr growth rates across the study transect for seedlings established in the buffers, seedlings established outside the buffers, and all seedlings to determine whether trees grew faster close to or away from clusters and adult neighbors. A spatial analysis of the Kriging interpolations highlighted how these relationships changed across the site as a whole and within each zone. The maps of the kriging interpolations were created to visualize seedling growth across the site and within each zone (Figures 3). The kriging interpolation of the 1-year growth rates are mapped for all seedlings (Figure 3A), seedlings inside the buffer (Figure 3B), and seedlings outside the 1m buffer (Figure 3C). The kriging interpolation of the 10-year growth rates are mapped for all seedlings (Figure 3D), seedlings inside the buffer (Figure 3E), and seedlings outside the 1m buffer (Figure 3F).

The area of the entire transect site (8581m²), the total cluster area (1008m²), and the total buffer area (4323m²) were calculated. The total area, cluster area, and buffer area were also calculated for each zone. Seedlings cannot establish directly into clusters, so cluster area was deemed unavailable for establishment. Thus, the area across the entire site and within each zone that was

available for seedling establishment was calculated as the difference between the total area and the cluster area. The density of seedlings was calculated to identify an overall pattern of establishment and survivorship in zones and across the entire site (Table 1). This was done by dividing the number of seedlings in each zone by the available space and multiplying the result by 100 to determine the number of seedlings per 100m².

Seedling Establishment and Spatial Distribution Analysis

A chi-square (χ^2) analysis was used to determine whether seedlings (0.10m ≤ seedlings ≤ 0.50 m) preferentially established inside or outside the 1meter buffers around adult trees (combined saplings and adults ≥ 3.0m) and tree clusters. It is possible that some adult krummholz trees may have been recorded as seedlings because their stunted not-upright stature resulted in a height measurement less than 0.50m. The chi-square analysis was run by determining the number of seedlings expected and actually observed in each zone, and across the entire site given the total area available for establishment (remember seedlings cannot establish directly into clusters).

Equation 1:

$$1\ meter\ Buffer\ Area \times \frac{Total\ Seedlings}{Available\ Area}\ Seedlings\ Expected\ in\ Buffer\ Area\ (S\varepsilon)$$

$$Seedlings\ Observed\ in\ Buffer\ Area\ (Table\ 1) = So$$

Equation 2:

$$\chi^2 = \sum_{i-1}^{r}\sum_{j-1}^{c}\frac{(So_{ij} - S\varepsilon_{ij})^2}{S\varepsilon_{ij}}$$

15

The number of seedlings that were expected inside the buffers was the product of the 1-meter buffer area and the ratio of seedlings to available area (Equation 1). The number of seedlings expected outside the buffers was the difference between the total number of observed seedlings and the number of seedlings expected in each zone (Table 2). This chi-square analysis (Equation 2) of the spatial distribution of seedling establishment determined whether seedlings were over- or under-represented inside and outside buffers.

Seedling Growth

Seedling growth was analyzed to determine how well seedlings faired at different gradients and in proximity to neighbors. Seedling growth is a function of the individual's size, so for each seedling, its growth was corrected for its size. To establish a function of seedling growth corrected for size, the height of each seedling in the entire site was compared to its respective 1yr and 10yr growth rate (1-year: $y = 0.0223x + 0.014$, $R^2 = 0.0525$; 10-year: $y = 0.4554x + 0.0568$, $R^2 = 0.5312$). The difference between the function of seedling growth corrected for size and the actual recorded growth for each seedling was used to find the 1yr and 10yr growth rate residuals. To estimate where seedlings grew best, the growth rate residuals were compared to seedling location within the transect site, within each zone, and within proximity to neighbors. An independent samples t-test was used to compare the corrected growth of seedlings established inside and established outside the buffers to determine where seedlings grow best in proximity to neighbors. A one-way ANOVA test with post-hoc Bonferroni tests was used to

test for significant differences in mean growth rates between the zones in order to better determine where seedlings grew best on the underlying harshness gradient.

Results

Spatial Distribution of Seedling Establishment

The density of seedlings in each zone was calculated in order to elucidate the overall pattern of seedlings establishment across the entire site (Table 1). Unsurprisingly, the lowest density of seedlings was found in the Tundra Zone (0.8±1.6 seedlings/m²), but the highest density of seedlings was found in Transition 1 (9.89±2 seedlings/m²), suggesting the conditions in this zone were the most hospitable for seedling establishment. The density of seedlings in the Forest Zone was 3.44±1.5 seedlings/m² and 2.15±0.9 seedlings/ m² in Transition 2. It appears that is it very challenging for seedlings to establish in the upper two zones of the transect and moderately challenging to establish in the Forest Zone.

The spatial distribution of seedling establishment determined whether seedlings were establishing preferentially next to adults, away from adults, or randomly in respect to adults. The chi-square analysis (Table 2) of the number of seedlings that were expected to have established within 1m buffer compared to the number of seedlings observed within the 1m buffer adult was less than expected based on a random distribution of seedlings for the total site area (χ^2=11.13, p<0.001)**.** This indicated that seedlings preferentially established outside the 1m buffers across the entire transect. Chi-square analyses were also conducted for the individual zones to better account for the impact of the

harshness gradient on seedling establishment. The number of seedlings established within a 1m buffer around adult trees was less than expected in the Forest Zone and in Transition 1, the two zones at the benign end of the harshness gradient. In the Forest Zone, seedlings preferentially established away from adult neighbors (χ^2=10.53, p=0.002) and in Transition 1 seedlings also preferentially established away from adult neighbors (χ^2=60.69, p<0.001). The number and distribution of seedlings established inside and outside the 1meter buffer in Transition 2 (χ^2=0.049, p=0.825) and the Tundra Zone (χ^2=0.82, p=0.365) were not significantly different from a random distribution. These results indicate that vicinity to neighbors does not significantly influence seedling establishment in zones at the stressful end of the harshness gradient.

Seedling Growth

Mean growth rates in each zone were compared to determine how well seedlings grew as the underlying harshness gradient changed between zones. The one-way ANOVA test comparing the mean seasonal growth between zones was significant (F (3,293) =5.904, p=0.001). The plot of mean growth for each zone is displayed in Figure 5A. The results of the post-hoc Bonferroni analysis indicate that the mean seasonal growth in the Forest Zone was statistically smaller than all other zones. In Transition 1, the mean seasonal growth was greater than in the Forest Zone but less than in Transition 2 and the Tundra Zone. The greatest mean seasonal growth was in Transition 2, and growth in this zone was statistically significantly larger than all other zones. The mean seasonal growth in the Tundra zone was also greater than the growth in the Forest Zone and Transition 1 but less

than in Transition 2. The one-way ANOVA test comparing the 10yr mean growth between zones was significant (F (3,222) =32.94, p<0.001) and the plot of mean growth for each zone is displayed in Figure 5B. After the post-hoc Bonferroni test the lowest mean 10yr growth was again in the Forest Zone and the highest mean 10yr growth was in Transition 2 where the growth was statistically significantly greater than all other zones. The mean 10yr growth in Transition 1 was greater than the mean growth in both the Forest and Tundra Zones. The mean 10yr growth in the Tundra Zone was greater than the Forest Zone but less than in both the Transition Zones. These results indicate that for both seasonal and 10yr growth, the seedlings grew the worst when the underlying harshness gradient was at its most benign (Forest Zone) but grew the best when the gradient was moderately harsh (Transition 2).

In addition, it was important to understand whether seedlings grew better when established inside or outside the 1m buffers. Seedling growth as a function of size was analyzed to determine how well seedling fared at different gradients and in proximity to neighbors. The function of seedling growth corrected for size is displayed in Figure 4A for a single season (1-year growth) and Figure 4B for 10 years of growth. The independent t-test comparing the seasonal growth of seedlings corrected for size that established inside the buffers and the growth of seedlings corrected for size that established outside the buffers across the entire site was not significant (t=-1.470, df=295, p=0.143). A t-test comparing the seasonal growth of seedling corrected for size established inside vs. outside the 1m buffers was run for each zone to understand how distribution on the elevation

gradient would effect establishment; Forest Zone (t=-0.219, df=50, p=0.828), Transition 1 (t=-0.0686, df=181, p=0.494), Transition 2 (t=0.549, df=43, p=0.586), and the Tundra Zone (t=-0.084, df=39, p=0.934) were also not significant. The independent samples t-test comparing the 10yr growth of seedlings corrected for size that established inside the buffers and the growth of seedlings corrected for size that established outside the buffers across the entire site was nearly statistically significant (t=-1.804, df=224, p=0.073), indicating that seedlings grew somewhat better outside than inside the 1m buffer across the entire site. As with the seasonal growth, the t-test of comparing the 10yr growth of seedling corrected for size established inside vs. outside the 1m buffers was run for each zone; Forest Zone (t=0.543, df=47, p=0.590), Transition 1 (t=-0.592, df=126, p=0.555), and the Tundra Zone (t=0.996, df=12, p=0.339) were also not significant. The results for Transition 2 were significant (t=2.2552, df=33, p=0.016), indicating that seedlings grew better inside the 1m buffer in this zone. It is important to note that the majority of seedlings were found in Transition 1 (n=185) and very few in the Tundra Zone (n=16). Although the t-test for both Transition 1 and the Tundra zone were insignificant, Transition 1 was the only zone with greater growth outside the buffer and may be affecting the results of the t-test for the entire site.

The maps of the kriging interpolation indicated that seedling grew better in Transition 1 and Transition 2 for both seasonal 1yr and 10yr growth inside the 1m buffers. The interpolations of seedling growth outside the 1m buffer indicated that seedlings grew better in the Forest Zone where impacts of competition with

neighbors were more severe. There were concentrated spots of extremely high and low growth within individual zones (especially Transition 1) on almost all the maps. Unlike the results of the t-tests, the maps of the kriging interpolation did have signals of neighbor interaction that impacted seedling growth, and that could be registered between zones. Additionally, these signals were bettered registered over the 10yr growth period than in the seasonal growth.

Table 1: Total area, cluster areas, areas available for establishment, and seedlings counts for each zone and across the entire transect.

	Total Area (m²)	Cluster Area (m²)	1-meter Buffer Area (m²)	Available Area (m²)	Total Seedlings	Seedlings Established Inside Buffers	Seedlings Established Outside Buffers	Seedling Density (seedlings/100m²)
Forest Zone	2153.65	529.12	1631.47	1624.52	56	44	12	3.44
Transition 1	2137.19	267.48	1458.15	1869.71	185	70	115	9.89
Transition 2	2192.06	107.27	720.91	2084.79	45	15	30	2.15
Tundra Zone	2098.97	104.71	513.46	1994.26	16	2	14	0.8
Entire Transect	8581.88	1008.59	4323.90	7573.29	302	131	171	3.9

Table 2: Chi squared (χ^2) of seedling establishment. Included are the number seedlings expected based given the area available for establishment and the number of seedlings observed inside and outside the 1m buffer for each zone and the entire site.

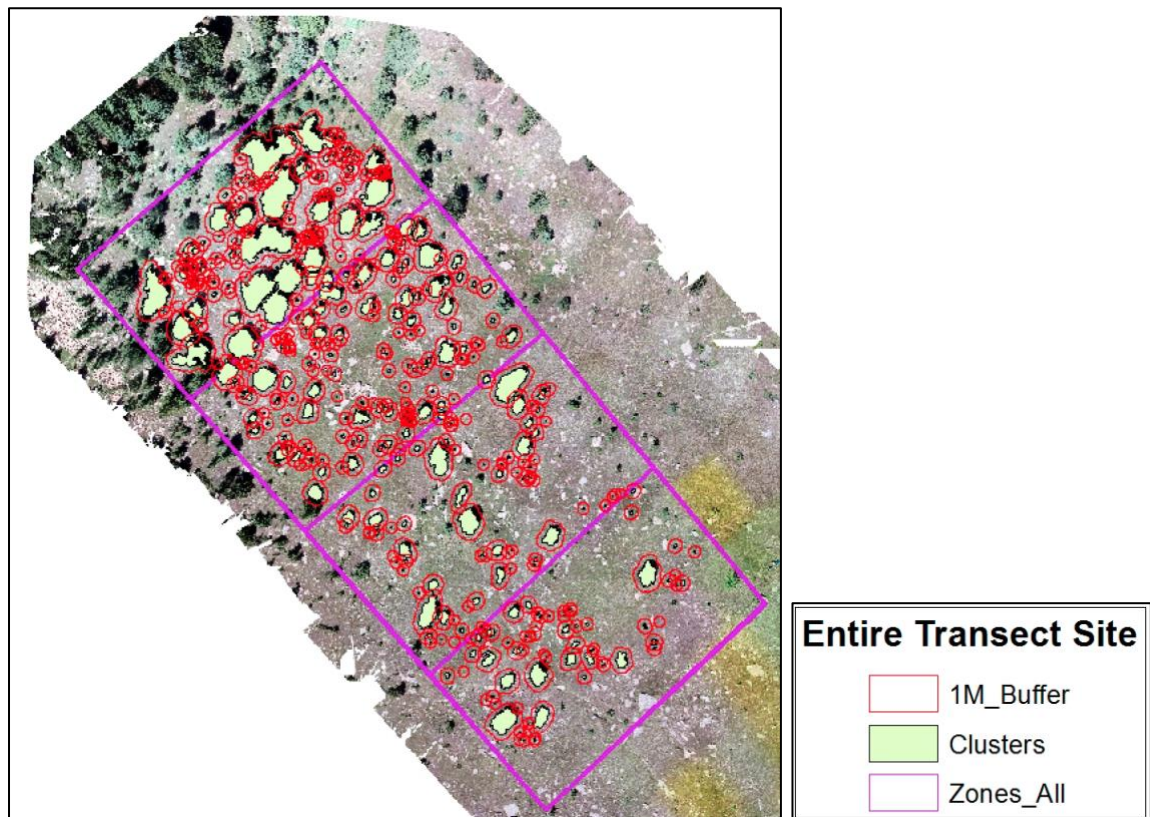|	Forest Zone			
	Seedlings inside Buffer	Seedlings Outside Buffer	χ^2	P-value
Expected	55	1	10.5299	0.00175
Observed	44	12		
	Transition 1			
	Seedlings inside Buffer	Seedlings Outside Buffer	χ^2	P-value
Expected	144	41	60.6913	0.00001
Observed	70	115		
	Transition 2			
	Seedlings inside Buffer	Seedlings Outside Buffer	χ^2	P-value
Expected	16	29	0.0492	0.824449
Observed	15	30		
	Tundra Zone			
	Seedlings inside Buffer	Seedlings Outside Buffer	χ^2	P-value
Expected	4	12	0.8205	0.36503
Observed	2	14		
	Entire Site			
	Seedlings inside Buffer	Seedlings Outside Buffer	χ^2	P-value
Expected	172	130	11.1326	0.000848
Observed	131	171		

Figure 2: The transect site drone based orthomosaic map. The transect boundary and zone division is in purple. The drone based orthomosaic is inverted. The upper left zone section is the forest that transitions to the tundra towards to bottom right of the image. Adult trees and clusters are digitized in the Clusters layer (green).
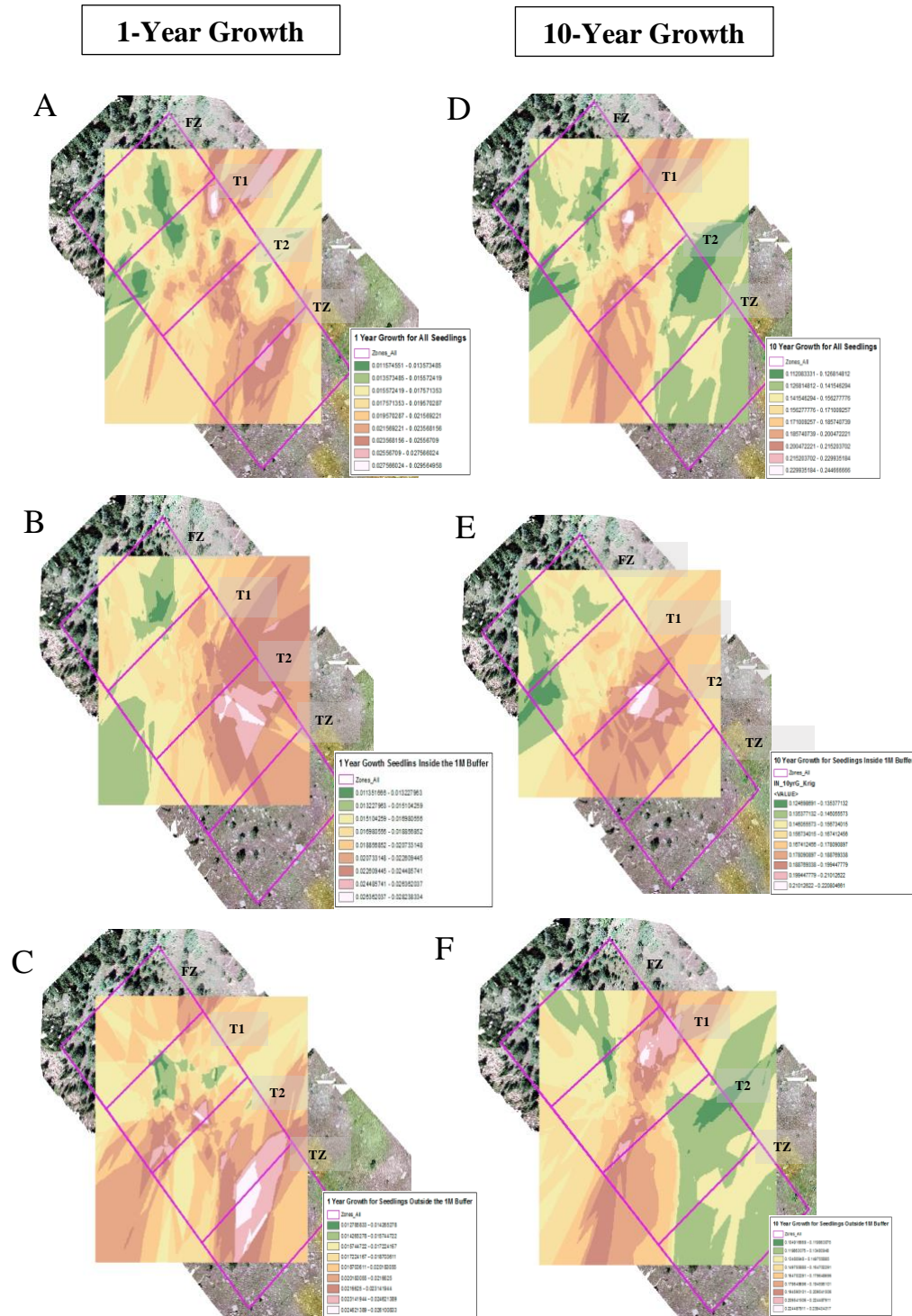
1-Year Growth

10-Year Growth

Figure 3: Kriging Interpolation across the entire site of A. 1-year growth for all seedlings, B. 1-year growth for seedlings inside the 1m buffer, C. 1-year growth for seedlings outside the 1m buffer, D. 10-year growth for all seedlings, E. 10-year growth for seedlings inside the 1m buffer, F. 10-year growth for seedlings outside the 1m buffer. The entire transect boundary is in purple and is also divided by zone. The drone based orthomosaic is inverted. The upper left zone section is the forest that transitions to the tundra towards to bottom right of the image. The legend displays the color ramp that is divided into nine colors associated with amount of growth (m).
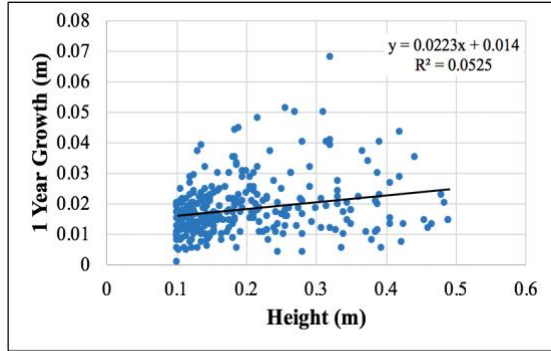
Figure 4A: Height (m) and 1-Year Growth (m) of all seedlings. Function of the Expected Growth is in dashed black.
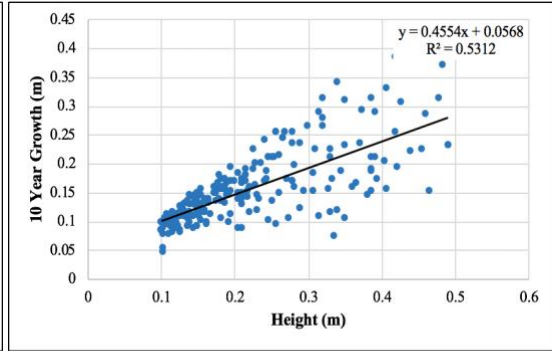

Figure 4B: Height (m) and 10-Year Growth (m) of all seedlings. Function of the Expected Growth is in dashed black.

Figure 5A: Curve of facilitation and competition along a stress gradient. Plot of Oneway ANOVA Analysis of 1-Year Mean Growth for each zone. Zone 1.00 = Forest Zone, Zone 2.00 = Transition 1, Zone 3.00 = Transition 2, Zone 4.00 = Tundra Zone.
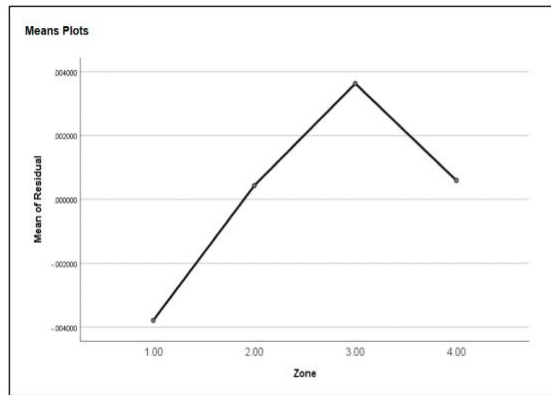

Figure 5B: Curve of facilitation and competition along a stress gradient. Plot of Oneway ANOVA Analysis of 10-Year Mean Growth for each zone. Zone 1.00 = Forest Zone, Zone 2.00 = Transition 1, Zone 3.00 = Transition 2, Zone 4.00 = Tundra Zone.
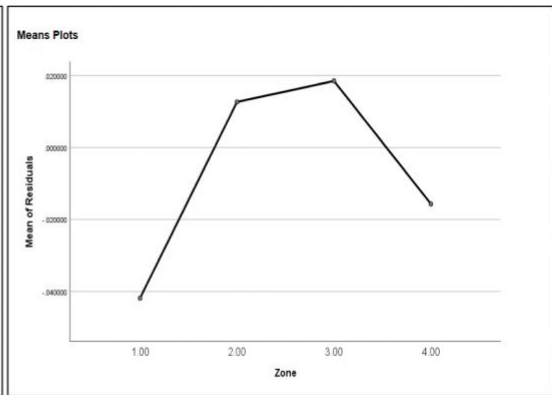
Discussion

Signals of neighbor interaction varied spatially and in intensity level which appear to affect seedling establishment and growth in different ways. The density of seedlings in each zone helped to establish an overall pattern of seedling establishment and survivorship across the entire transect site. The density of seedling establishment was moderately high in the Forest Zone and highest in the intermediate Transition 1 zone (Table 1). The density of seedlings decreased from Transition 1 to Transition 2 and was at its smallest in the Tundra Zone. The overall pattern of the density of seedlings established appears to fit a linear SGH, which is congruent with other studies of the SGH (Butterfield *et. al.,* 2013; Callaway, 1998; Callaway, 2007; Callaway *et. al,* 2002; Leong *et. al,* 2019).

The chi-square analyses indicated that seedlings preferentially established away from adult neighbors (outside the 1m buffer) in the Forest Zone and in Transition 1 and established randomly in Transition 2 and the Tundra Zone (Table 2). These findings indicate that growing close to adult neighbors is not advantageous at the benign end of the stress gradient. This may be a result of competition for resources in the high-density forest, where seedlings in close proximity to adult neighbors are outcompeted for light, water, and nutrients. Seedlings established randomly with respect to adult trees at the harsh end of the gradient, and it appears that proximity to neighbors does not significantly influence where seedlings establish when in stressful abiotic conditions (Table 2). It may be neither particularly advantageous nor disadvantageous to establish near adults under moderate to high environmental stress. This may be an indication of

25

a net neutral neighbor interaction where the benefits of neighbor facilitation barely compensate for the costs of competition and external abiotic stress. The linear model for establishment of seedlings near adult neighbors on the underlying harshness gradient is congruent to similar results that support the linear SGH (Butterfield *et. al.,* 2013; Callaway, 1998; Callaway, 2007; Callaway *et. al,* 2002; Leong *et. al,* 2019).

Across the entire site, seedlings grew significantly better away from neighbors. The majority of seedlings were found in the Transition 1 (n=185) where seedlings preferentially established outside the buffers. The chi-square finding for the entire transect site may be somewhat over-representative of establishment patterns exhibited in Transition 1. These findings are congruent with the linear model of the stress gradient hypothesis supported in current SGH literature (Butterfield *et. al.,* 2013; Callaway, 1998; Callaway, 2007; Callaway *et. al,* 2002; Leong *et. al,* 2019).

The independent samples t-test comparing the seasonal and 10-year growth of seedlings corrected for size that established inside the buffers and the growth of seedlings corrected for size that established outside the buffers indicated very little to no neighbor interactions across the entire site. However, if it was truly the case that neighbors were not influencing each other, the results of the t-tests should be congruent with the results of the chi-square analysis of seedling establishment or the Kriging Interpolations of seedling growth, which they are not. It appears that the inside vs. outside buffer analysis of the t-tests were unable to fully capture relationships of seedling establishment. This study

treated all clusters and adult trees equally, but it is likely that the density of clusters or size of individual adults impacts whether they inhibit or facilitate seedling establishment. Additionally, the 1-meter buffer around the adult trees and clusters was assumed to be the maximum spatial extent to which seedlings could benefit from adult trees, but this appears to be somewhat inaccurate. Signals of facilitation may better register or only register over a greater spatial area, and this may be an indication of facilitation on a communal but not an individual scale. This too may account for the random establishment of seedlings in the upper half of the transect site and how unaffected seedling growth rates were dependent on establishment inside or outside the buffers. Establishing within a 1-meter buffer may subject seedling to net competition with their adult neighbors; instead, establishing some intermediate distance may be most beneficial. A series of concentric buffers expanding out from adult trees and clusters could help to locate the distance from neighbors at which the benefits of facilitation outweigh the costs of competition and environmental stress. Alternatively, seedling establishment itself could be analyzed in continuous space so that instead of buffers around adults, bands of elevational gradients would be utilized to understand how distance from neighbors affects growth. Incorporating the different effects of multiple neighbors on a seedling within bands of elevational gradients could better capture community level facilitation in continuous space.

The overall relationship represented in the plots of the one-way ANOVA analysis was that of a hump-shaped stress gradient (Figure 5A & 5B). A general trend for both seasonal and 10-year growth emerged where seedlings grew best at

intermediate levels of stress (Transitions 1 & 2) and exhibited the lowest growth at the poles of the underlying stress gradient (Forest & Tundra Zone). The post-hoc Bonferroni test results showed that mean seedling growth increased from net negative interactions in the Forest Zone to positive net interactions in the transition zones for both seasonal 1-year and 10-year interactions. Neighbor interactions were weakly positive for seasonal 1-year growth and strongly positive for 10-year growth in Transition 1. All neighbor interactions were strongly positive in Transition 2. The curve of 1-year growth indicated a low but positive net neighbor interaction in the Tundra Zone, and a net negative neighbor interaction for 10-year growth in the Tundra Zone. After peaking in Transition 2, the 1-year growth model in Figures 5A returns to a neutral to slightly positive net interaction, which best fits an asymmetrical hump shape model of the stress gradient. The shape of the 10-year growth curve in Figure 5B increases from negative in the Forest Zone to positive in the transition zones and returns to a net negative interaction in the Tundra Zone, which best fits the symmetrical hump shape model of the stress gradient. The results of this study are in support of alternate forms of the SGH that indicate a linear or monotonic curve may not be the best description of neighbor interactions on an underlying stress gradient (le Roux & McGeoch, 2010; Maestre *et. al.,* 2009; Michalet *et al.,* 2014; Klanderud *et al.,* 2017).

While this relationship is described by a hump-shape here, these relationships are likely site-dependent, spatially dependent, and dependent upon the qualities of the underlying stress gradient. The field site had a marked lack of

krummholtz mats (formed in response to strong snow blasts), so its underlying stress gradient is likely unrelated to the strength of wind and snow crystal abrasion. In this case, stress may be a measure of the effect that increasing elevation has on temperature or resource availability. This study assumed stress increased with the elevation gradient, but it did not account for the source or sources of severity associated with different elevations. A potentially improved conceptualization of site-dependent stress gradients would isolate the mechanisms of severity effecting seedling growth or establishment.

The Kriging Interpolation was an attempt to better understand seedling growth across a space. The interpolation of 1-year and 10-year growth of seedlings established inside the buffers indicated that growth was the highest in the two transition zones (Figure 3B & 3D). The difference in amount of growth between the zones was more extreme for 10-year growth where the Transition Zones had high concentrated growth, but the Forest and Tundra Zones had considerably smaller growth. Seedlings established inside the buffers grew best at intermediate environmental stress for both 1-year and 10-year growth. Neighbor interactions are most beneficial at intermediate levels on an underlying stress gradient. Poor growth at the poles of the stress gradient indicate that neighbor facilitation cannot outweigh the negative effects of competition at benign gradients nor extreme environmental stress at harsh gradients. The observation of the most successful plant growth at intermediate levels of stress is consistent with the hump-shape (symmetrical or asymmetrical) stress gradient hypothesis, which

has also been observed in SGH literature (le Roux & McGeoch, 2010; Maestre *et. al.,* 2009; Michalet *et al.,* 2014; Klanderud *et al.,* 2017).

The interpolation of 1-year seasonal growth of seedlings established outside the buffer (Figure 3C) showed the greatest growth along the boundary of Transition 1 and the Tundra Zone. The high growth indicated in the Tundra Zone may be an overestimation of reality (i.e. a small shift in this otherwise arbitrary boundary would produce a large change in the mean growth and in the interpretation of the data). There were relatively high growth rates in the Forest Zone, which may be a result of the success of the seedlings that managed to establish away from the competitive influence of neighbors. Transition 1 had patches of extremely high and extremely low growth throughout the zone. It appears conditions within Transition 1 are varied, and as a result seedling growth is affected differently across the zone. The patches of poor growth in the lower region of Transition 1 may mirror conditions in the Forest Zone where competition with neighbors inhibits seedling growth. The patches of high growth in the upper regions of Transition 1, where tree density is decreasing, reflect a shift from competition to facilitation with neighbors benefitting seedlings at this moderately stressful gradient.

The interpolation of 10-year growth of seedlings established outside the buffer (Figure 3F) showed a concentrated patch of extremely high growth and a patch of extremely low growth in Transition 1. This was similar to the above interpolation of seasonal growth outside the 1m buffer where seedling growth varied across the zone. An area of moderately high growth extends from the patch

of extremely high growth in Transition 1 into Transition 2. There was moderate to low growth in the Forest Zone and very low growth in the Tundra Zone. These results are consistent with the hump-shape SGH again showing that seedlings grow the best at intermediate levels of stress but poorly at the most benign and harsh ends of the stress gradient (le Roux & McGeoch, 2010; Maestre *et. al.,* 2009; Michalet *et al.,* 2014; Klanderud *et al.,* 2017).

The overall growth of seedlings (joining of seedlings established inside and outside the 1m buffer) was interpolated in an attempt to identify general trends of seedling growth. The interpolation of the seasonal 1-year growth for all seedlings (Figure 3A), similar to the seasonal growth inside and outside the buffers (Figure 3B & 3C), exhibited a general increase in seedling growth along the stress gradient, with the exceptions of patches of extremely high and low growth in Transition 1. Seedling growth appeared to taper off in the Tundra Zone, but again the few seedlings found in this zone makes it difficult to draw conclusions The interpolation of the 10-year growth for all seedlings (Figure 3D) showed extremely poor growth in the Forest Zone and in the Tundra Zone and moderate to high growth in the transition zones. The results of the Kriging Interpolation Analysis strongly suggest that seedlings grow best under moderately stressful environmental conditions, congruent with the hump-shape SGH (le Roux & McGeoch, 2010; Maestre *et. al.,* 2009; Michalet *et al.,* 2014; Klanderud *et al.,* 2017). These environments were too harsh to support the high-density growth found in the Forest Zone where competition is the net outcome of neighbor interactions yet were not so harsh as to prevent facilitation being the net outcome

of beneficial neighbor interactions and abiotic stress. Additionally, the signals of facilitation and neighbor interactions in general were stronger in the 10-year growth than in the seasonal growth data, indicating that a longer growth period is necessary to register trends in neighbor interactions.

The combination of the Kriging Interpolation analysis and the one-way ANOVA analysis give shape to the model describing the relationship of neighbor interactions on a stress gradient. Seedlings consistently grew the best in Transition 1 and 2 at intermediate levels of stress but poorly in the Forest and Tundra Zones in highly competitive or stressful environments. This pattern of growth supports the stress gradient hypothesis described by a hump-shape.

The four zones were an approximately equal division of the transect site but otherwise were established somewhat arbitrarily. Specifically, the divisions of zones did not account for any underlying gradients and are potentially unable to accurately capture neighbor interactions over space. This may account for some of the lack of statistical insignificance of the seedling establishment in the t-tests or the variability in the kriging data where some of the highest growth areas were along a zone boundary. It appears that adult trees and clusters facilitate seedlings over a different conceptualization of space than captured by the zones. A follow up analysis should specifically account for spatial variability of seedling establishment and growth. A continuous conceptualization of space could potentially more accurately capture the desired relationships that the zonal conception of space. Comparing seedling growth along the elevation gradient would better identify how altitude and the stress mechanisms associated with

higher altitudes affects seedling fitness and growth rates. Such an analysis would flush out the hump-shape trends in the model of the SGH.

Conclusion

Generally, SGH literature suggests that the relationships between neighboring plants at an individual site are described with a single model of the SGH. However, the results of this study indicate that neighbors impact life history, stages, and characteristics (establishment, growth, survivorship, etc.) of seedlings differently. Multiple models of the SGH were present at this site, where seedling establishment was best described with a linear SGH where neighbors inhibit seedling establishment in benign environments but affect their establishment very minimally in harsh environments. In contrast, seedling growth was better modeled with a hump-shape SGH at this site. In this model, seedlings grew best at intermediate levels of stress where the benefits of facilitation compensated for intermediate environmental stress and competition with adult neighbors. At the benign end of the stress gradient, high tree density resulted in competition, and at the harsh end of the gradient, severe environmental conditions made benefits of neighbor facilitation negligible.

Generally, treelines worldwide and the diffuse treeline analyzed in this study are advancing. The rate of advancement observed in diffuse treelines is supported by the growth-limitation hypothesis (Feiden, 2010; Grace *et. al.,* 2002; Harsch & Bader, 2011; Körner, 1998). Treeline growth is also affected by ecological facilitation and competition within an ecotone (Harsch & Bader, 2011;

Smith, *et. al.,* 2003), and these relationships depend on the underlying stress gradient (Callaway, 1998). A combination of growth limits established by external mechanisms, tree physiology, and internal plant interactions and feedbacks is responsible for treeline form and seedling establishment. At this site in particular, treeline advancement appears to be a combination of neighbor interactions generated through the linear SGH describing seedling establishment and the hump-shape SGH describing seedling growth. The Forest Zone appears to be a relatively stable state where the net outcome of seedling establishment and growth leaves this area unchanged. The dynamics in Transition 1 are establishment driven where, unlike in the forest, seedlings are able to establish but the density driven competition prevents significant growth. These dynamics switch in Transition 2, where seedlings struggled to establish but grew very well once they did. In the Tundra zone, severe environmental stressors resulted in low seedling establishment and growth, but the system was changing unlike in the Forest Zone. It appears that the diffuse treeline at this site is advancing by seedlings establishing into safe sites in Transition 1. These seedlings reach a density level that allows them to alter the environment such that the conditions are similar to those hospitable to growth in Transition 2. Seedlings will continue to establish and grow in the patches between trees until the formerly diffusive edge of the treeline fills in and becomes a forest, thus advancing the treeline.

The zones within the site transect and 1-meter buffers around adult trees and clusters were created somewhat arbitrarily. These spatial conceptualizations failed to completely capture the impacts of facilitation on community dynamics in

this stressful environment. Stress does not affect all species of a community equally (López *et. al.,* 2013) and this study indicated that signals of facilitation were registered on a community scale. A continuous conceptualization of space would better capture community-wide interactions and would be a less arbitrary division of space. Building on the foundations of this study, a follow-up analysis of spatial variability could more accurately identify the spatial characteristics of the stress gradient at this site and the effects it has on neighbor interactions. Specifically identifying different mechanisms of severity would also be useful in determining forms of the stress gradient and the capacity of neighbor facilitation to compensate for these forms.

The purpose of this study was to understand the community dynamics of an advancing treeline ecotone. To understand ecotones, such as a treeline, neighbor interactions and how they change in abiotic environments is important (Callaway, 1998). This study predicted that changes in neighbor interactions would align with the SGH. This prediction was true, although the data took a hump-shape rather than a linear stress gradient form. Understanding these dynamics and the different curves of the stress gradient hypothesis is imperative in the face of climate change. Climate change will impact adult trees and seedlings differently, which can cause neighbor interactions to collapse, strengthen, or switch from competition to facilitation. Alpine species and ecotones are particularly vulnerable to these changes (Harsch & Bader, 2011; Malanson *et al.,* 2011), and the patterns described in this study will facilitate understanding of how climate change will help predict future treeline structures.

Acknowledgments

I would like to thank my thesis advisor Dr. Miroslav Kummel for helping me develop this project, his endless patience and encouragement, and for being a wonderful mentor. I would also like to thank Dr. Howard Drossman for his advice on this project and manuscript as my second reader. I would like to acknowledge The Colorado College Environmental Program for providing the tools, resources, and support needed for this research. Thank you to Matt Cooney for his GIS mastery and Sharron Johnson for her administrative support. Thank you to my field assistants Mira Peterson, Anya Steinberg, Caroline Peters, Lily Dog, and Willow without whom data collection would not have been possible.

References

Alftine, K. J., & Malanson, G. P. (2004). Directional positive feedback and pattern at an alpine tree line. *Journal of Vegetation Science*, *15*(1), 3-12.

Butterfield, B. J., Cavieres, L. A., Callaway, R. M., Cook, B. J., Kikvidze, Z., Lortie, C. J., ... & Zaitchek, B. (2013). Alpine cushion plants inhibit the loss of phylogenetic diversity in severe environments. *Ecology Letters*, *16*(4), 478-486.

Callaway, R. M. (1998). Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains, USA. *Oikos*, 561-573.

Callaway, R. M. (2007). Positive interactions and interdependence in plant communities. Springer Science & Business Media.

Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., ... & Armas, C. (2002). Positive interactions among alpine plants increase with stress. *Nature*, *417*(6891), 844-848.

Earnest, C. (2011). Treeline dynamics on Pikes Peak, Co: Is the treeline moving and what is controlling that rate of movement? Thesis, The Colorado College, Colorado Springs, CO.

Elwood, K. (2012). Spatial pattern and typology changes of an advancing treeline on Pikes Peak, CO. Thesis, The Colorado College, Colorado Springs, CO.

Feiden, M. (2010). Treeline dynamics on the west slope of Pikes Peak. Thesis, The Colorado College, Colorado Springs, CO.

Grace, J., Berninger, F., & Nagy, L. (2002). Impacts of climate change on the tree line. *Annals of Botany*, *90*(4), 537-544.

Gou, X., Zhang, F., Deng, Y., Ettl, G. J., Yang, M., Gao, L., & Fang, K. (2012). Patterns and dynamics of tree-line response to climate change in the eastern Qilian Mountains, northwestern China. *Dendrochronologia*, *30*(2), 121-126.

Harsch, M. A., & Bader, M. Y. (2011). Treeline form–a potential key to understanding treeline dynamics. *Global Ecology and Biogeography*, *20*(4), 582-596.

Harsch, M. A., Hulme, P. E., McGlone, M. S., & Duncan, R. P. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology letters*, *12*(10), 1040-1049.

Hättenschwiler, S., & Smith, W. K. (1999). Seedling occurrence in alpine treeline conifers: A case study from the central Rocky Mountains, USA. *Acta Oecologica*, *20*(3), 219-224.

IPCC (Intergovernmental Panel on Climate Change). (2019). Climate change and land. An IPCC Special Report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems. Summary for Policymakers.

IPCC, I. P. O. C. C. (2019). Special report on global warming of 1.5 C (SR15).

Leong, F. W. S., Lam, W. N., & Tan, H. T. W. (2019). Digestive mutualism in a pitcher plant supports the monotonic rather than hump-shaped stress-gradient hypothesis model. *Oecologia*, *190*(3), 523-534.

Le Roux, P. C., & McGeoch, M. A. (2010). Interaction intensity and importance along two stress gradients: Adding shape to the stress-gradient hypothesis. *Oecologia*, *162*(3), 733-745.

Lopez, R. P., Valdivia, S., Rivera, M. L., & Rios, R. S. (2013). Co-occurrence patterns along a regional aridity gradient of the subtropical Andes do not support stress gradient hypotheses. *PloS one*, *8*(3).

Maestre, F. T., Callaway, R. M., Valladares, F., & Lortie, C. J. (2009). Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, *97*(2), 199-205.

Maestre, F. T., Valladares, F., & Reynolds, J. F. (2005). Is the change of plant–plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *Journal of Ecology*, *93*(4), 748-757.

Malanson, G. P., Resler, L. M., Bader, M. Y., Holtmeier, F. K., Butler, D. R., Weiss, D. J., ... & Fagre, D. B. (2011). Mountain treelines: A roadmap for research orientation. *Arctic, Antarctic, and Alpine Research*, *43*(2), 167-177.

McGarigal, A. (2019). Spatial structure of treeline shows evidence of robust criticality. Thesis, The Colorado College, Colorado Springs, CO.

Michalet, R., Le Bagousse-Pinguet, Y., Maalouf, J. P., & Lortie, C. J. (2014). Two alternatives to the stress-gradient hypothesis at the edge of life: The collapse of facilitation and the switch from facilitation to competition. *Journal of Vegetation Science*, *25*(2), 609-613.

Kéfi, S., Rietkerk, M., Alados, C. L., Pueyo, Y., Papanastasis, V. P., ElAich, A., & De Ruiter, P. C. (2007). Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature*, *449*(7159), 213-217.

Kéfi, S., Rietkerk, M., van Baalen, M., & Loreau, M. (2007). Local facilitation, bistability and transitions in arid ecosystems. *Theoretical Population Biology*, *71*(3), 367-379.

Klanderud, K., Meineri, E., Töpper, J., Michel, P., & Vandvik, V. (2017). Biotic interaction effects on seedling recruitment along bioclimatic gradients: Testing the stress-gradient hypothesis. *Journal of Vegetation Science*, *28*(2), 347-356.

Körner, C. (1998). A re-assessment of high elevation treeline positions and their explanation. *Oecologia*, *115*(4), 445-459.

Körner, C., & Paulsen, J. (2004). A world-wide study of high altitude treeline temperatures. *Journal of Biogeography*, *31*(5), 713-732.

Rietkerk, M., & Van de Koppel, J. (2008). Regular pattern formation in real ecosystems. *Trends in Ecology & Evolution*, *23*(3), 169-175.

Risser, P. G. (1993). Ecotones at local to regional scales from around the world. *Ecological Applications*, *3*(3), 367-368.

Roberts, V.M.S (2010). Potential feedback mechanisms operating among Englemann spruce at alpine treeline on Pikes Peak, CO. Thesis, The Colorado College, Colorado Springs, CO.

Scheffer, M. (2009). *Critical transitions in nature and society* (Vol. 16). Princeton University Press.

Smith, W. K., Germino, M. J., Hancock, T. E., & Johnson, D. M. (2003). Another perspective on altitudinal limits of alpine timberlines. *Tree Physiology*, *23*(16), 1101-1112.

Vandermeer, J., & Perfecto, I. (2017). *Ecological complexity and agroecology*. Routledge.

von Hardenberg, J., Meron, E., Shachak, M., & Zarmi, Y. (2001). Diversity of vegetation patterns and desertification. *Physical Review Letters*, *87*(19), 198101.

Walther, G. R., Beißner, S., & Pott, R. (2005). Climate change and high mountain vegetation shifts. In *Mountain ecosystems* (pp. 77-96). Springer, Berlin, Heidelberg.