

IB Subject: Biology

Title: Microclimatological patterns at an abrupt treeline and the effect on Engelmann Spruce (*Picea engelmannii*) seedling growth and survival.

Research Question: What microclimate patterns does an abrupt treeline produce, and what are its effects on the survivorship and growth of seedlings?

Word Count: 3988

Table of Contents

Introduction	3
Study 1	10
Study 2	14
Study 3	17
Conclusion	22
References	24
Appendix A: Statistics Tables	26
Appendix B: Dataset Samples	29

Microclimatological Patterns at an Abrupt Alpine Treeline and the Effect on Engelmann Spruce (*Picea engelmannii*) Seedling Growth and Survival

The microclimatological dynamics and feedbacks behind the structure and movement of treelines are not very well understood (Malanson et al., 2011). In a series of field studies, the current research aimed to study the microclimate and seedlings at the abrupt edge of an alpine treeline, specifically studying how treelines interact with wind patterns to form microclimates, the spatial distribution of Engelmann spruce seedlings around the treeline, and what the correlative pattern suggests could be the effect of the microclimate on seedling distribution and growth.

Introduction to Treeline Dynamics

A treeline is an ecotone—a transition zone with its own internal structure and microclimate between a habitat where trees can grow and a habitat where they cannot (Körner, 2012). Treeline elevation is primarily driven by constraints on tree growth from cold temperatures (Harsch et al., 2009). Temperature falls as elevation increases on a mountain due to the adiabatic lapse rate, so eventually trees encounter an elevation above which it is too cold to grow and survive. Global treeline position generally coincides with a growing season temperature of about 6-7°C (Körner & Paulsen, 2004).

Each plant species has certain temperature thresholds below which it is unable to carry out physiological mechanisms such as seed germination, photosynthesis, and growth. Above the temperature thresholds, the rate of each physiological process increases as temperature increases up to an optimal temperature, above which rates fall due to malfunctioning and denaturing of

critical enzymes. For example, spruce trees cannot carry out photosynthesis below about 0°C and cannot grow at temperatures below about 4°C (Grace et al., 2002).

Although temperature thresholds limit physiological mechanisms for all plant species, trees are especially susceptible to cold temperatures because they are less able to decouple their temperature from the ambient environmental temperature than low-lying vegetation. Low-lying plants are able to escape much of the wind and conserve heat, and warm up from daytime solar radiation (Körner & Paulsen, 2004). Sapling and adult trees are unable to escape wind in the same way, and so their temperature is far more dependent on atmospheric temperature (Grace et al, 2002).

Treelines, Climate Change, and Feedbacks

Treelines are bellwethers of the impact of climate change on ecosystems. With increasing temperatures, alpine treelines should advance into higher elevations. Indeed, the majority of treelines studied are advancing, and almost none are receding (Harsch et al, 2009). The treelines' response to climate change has major global impact because when treelines invade the alpine tundra, the encroaching trees threaten the biodiversity of the shrinking tundra ecosystems (Greenwood & Jump, 2014).

Interestingly, treelines' responses to climate change seem to be determined by their spatial structure. Treelines with diffuse edges have been highly responsive to warming. However, treelines where the forest has a hard, abrupt edge (abrupt treelines) and treelines composed of tree clusters beyond a hard forest edge (tree island treelines) are not very responsive: moving slowly, if at all (Harsh & Bader, 2011; Harsch et. al., 2009).

Modeling studies have found that abrupt treelines and tree island treelines form under conditions where trees strongly modify their microclimate. These sorts of feedbacks may play an important role in treeline response to climate change (Malanson et al., 2011).

Microclimate at Treeline

Microclimate is the climate in a small defined area, created in part by physical characteristics of the location (e.g., vegetation, physiography) (Oke, 1987). A location-specific microclimate modifies the base climate, making it either more or less hospitable for plant life (Jones, 2014). Trees and other vegetation then modify the base climate further, making their own microclimates. A microclimate that modifies the base climate by even a few degrees can be critical for trees at treeline where those few degrees could be the difference between survival and death (Greenwood et al, 2015).

Alpine treelines form microclimates when the trees modify the microclimate generated by the mountain's physical structure. Mountains create their own wind patterns: at night during the "night wind regime," cold air drains down the mountain, creating a downhill wind while in the "day wind regime," warmed air flows up along the mountain slopes (Ahrens, 2001; Oke, 1987). The treeline interacts with the mountain's wind patterns through sheltering to create its own location-specific microclimate (for details see hypotheses section; Pyatt et al., 2016; Smith et al., 2003).

The microclimate created by the treeline might help or hinder seedling growth and survival and therefore in turn affect the distribution of seedlings (Greenwood et al., 2015; Malanson et al., 2011). If this is the case, the treeline will have created a feedback loop in which the current treeline determines the structure of the microclimate, which in turn determines where

future trees will grow. As temperature warms under climate change, treelines that create favorable conditions for growth and survival above their edges may accelerate their own advancement.

The Current Research: An Abrupt Treeline at Pikes Peak, CO, USA

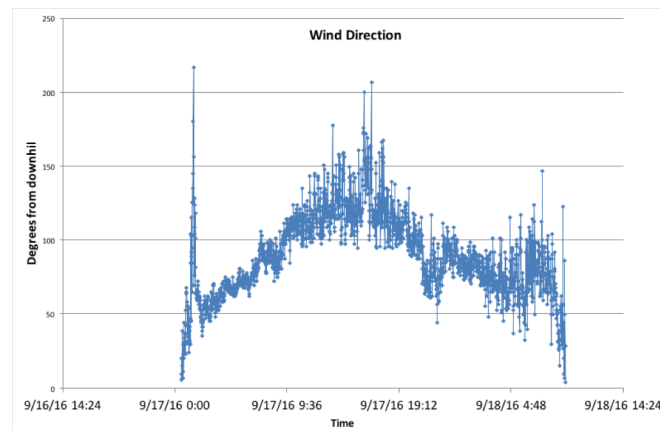
This research project aimed to study an abrupt treeline in Colorado, USA, to investigate how the treeline shaped its microclimate, and how the microclimate is spatially correlated to seedling distribution and growth. Several field studies were performed to investigate the treeline's microclimate (wind speed, air temperature, and ground temperature), seedling distribution, and seedling growth patterns.

The field site of the research was an abrupt *Picea engelmannii* treeline on the northwest side of Pikes Peak that established in the 1700s. It has migrated upward by 5-10 m in the last 30 years, ten times slower than diffuse treelines on the same mountain (Kummel, 2014).

Field site characteristics.

Wind patterns. Based on continuous wind monitoring over the course of the study, the wind direction was primarily askew uphill or uphill during the day and primarily askew uphill or downhill at night (Figure 1).

Figure 1. Wind angle on a representative day (downhill = 0-60 & 300-360 degrees, uphill = 135-225 degrees, uphill askew= 100-135 & 225-260 degrees, downhill askew=60-80 & 280-300 degrees, parallel = 80-100 & 260-280 degrees). See appendix B for full graph.



Description of the Sheltered Zone. The

treeline at the field site appeared to shelter from wind an area directly upslope of it, where seedlings and saplings showed no wind damage. The sheltered zone ended with a distinct line, upslope of which all surviving trees were stunted and showed signs of wind damage (Figure 2).

Research approach and hypotheses. To

study the microclimate created by this abrupt treeline, a series of field studies measured temperature (air and ground) and wind speed upslope of, at, and downslope of the treeline field site. To study the survivorship and growth of seedlings, locations of live and dead *P. engelmannii* seedlings were mapped using GPS and the most recent growing season's growth was measured.

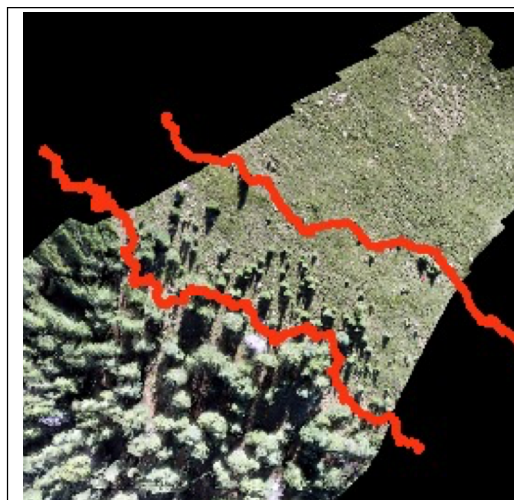


Figure 2. Aerial picture of the field site taken by a UAV. The lower line (left) is the old growth treeline. The space between the two lines is the sheltered zone. The trees above the upper line (right) show signs of wind damage.

There were 3 hypotheses:

Hypothesis 1: When the wind blew uphill (during the day or at night), if the treeline created a sheltered eddy upslope of its edge, then ground and air temperatures in the eddy should be warmer than the surroundings during the day and colder than the surroundings at night (Figure 3).

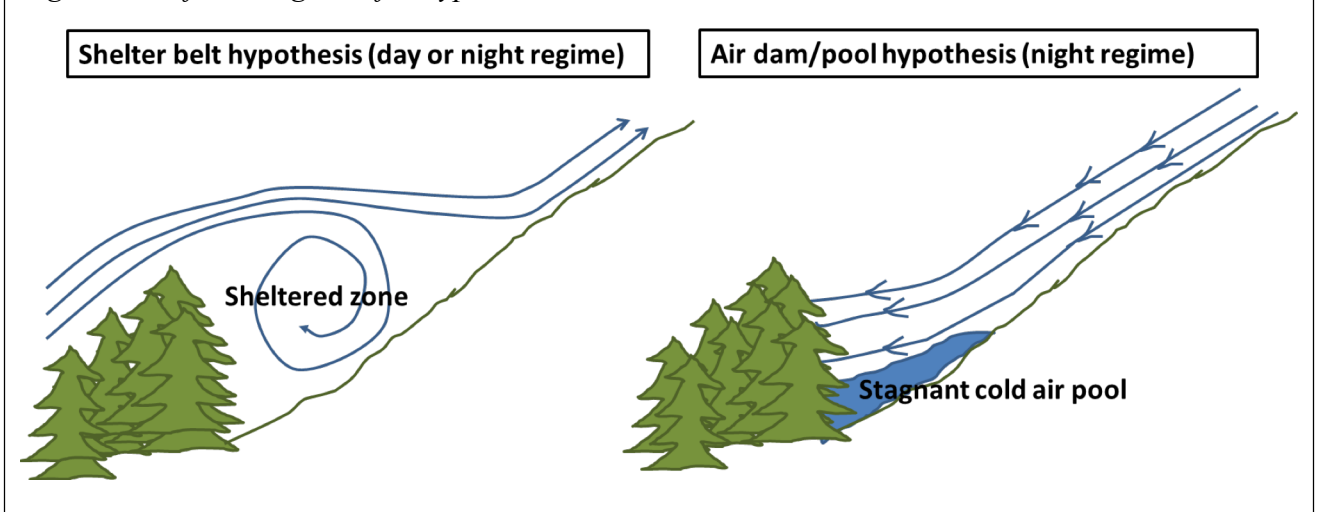
A sheltered eddy would prevent air within it from mixing with the surrounding air. During the day, the air close to the ground in the eddy would be warmed up by the

ground but would not mix with cooler air above, hence retaining heat so the ground and air would be warmed. During the night, the ground would lose heat into space through radiative cooling. The air immediately next to the ground would lose heat to the ground and would cool in turn. Still air in a sheltered eddy would not mix with the surrounding air, so the air in the eddy and the ground in the sheltered zone would become exceptionally cold (Oke, 1987).

Hypothesis 2: When the wind drained downhill at night, if the treeline acted as a cold air dam by obstructing the air drainage, it would create a stagnant pool of cold air (Figure 3).

This pool of air would put a barrier between the cold ground (which would be losing heat to space) and the warm air higher in the atmosphere. This should prevent the warm air from replenishing the heat loss, making the ground extremely cold (Oke, 1987).

Figure 3. Airflow diagrams for hypotheses 1 and 2.



Hypothesis 3: If the microclimate described in hypotheses 1 and 2 impacted seedlings, then seedling survival and growth should correlate with microclimatic patterns:

3a) If daytime temperatures mattered more than night temperatures, seedlings should survive and grow best in areas that were warm in the daytime and worst in areas that were cold in the daytime.

3b) If nighttime temperatures mattered more than daytime temperatures, the seedlings should survive and grow best in the areas that were warm at night and worst in the areas that were cold at night.

Materials List

Steel pipe towers

Cup anemometers

Logging thermometers

Data loggers

Trimble Geo explorer 6000 GPS

Flags

Aluminum tags for labeling seedlings

Thermal camera

Computer

Excel, FLIR, SPSS, Calculator

Study 1: The Sheltered Zone in the Air Column

Procedure

A transect stretching from just above the old growth treeline to the tundra above the sheltered zone included 8 equally spaced measuring stations at which data was taken. An 8m tall meteorological tower with instruments to measure and log air temperature and wind speed (at 0.5, 1, 2, 4, 6, 8m) was placed at each station for 2-4 days to record data. For the entire data collecting session, a stationary 2m tall tower was recording wind speed and temperature in the tundra. Data from the moving tower were normalized to the stationary tower to increase the reliability of wind pattern analysis. Data were first sorted into day and night measurements, then by wind direction, and then interpolated by ArcGIS. Interpolation models the trends in the unknown spaces between known points. It assumes that closer points are more similar and more closely related (Childs, 2004; Esri, 2016).

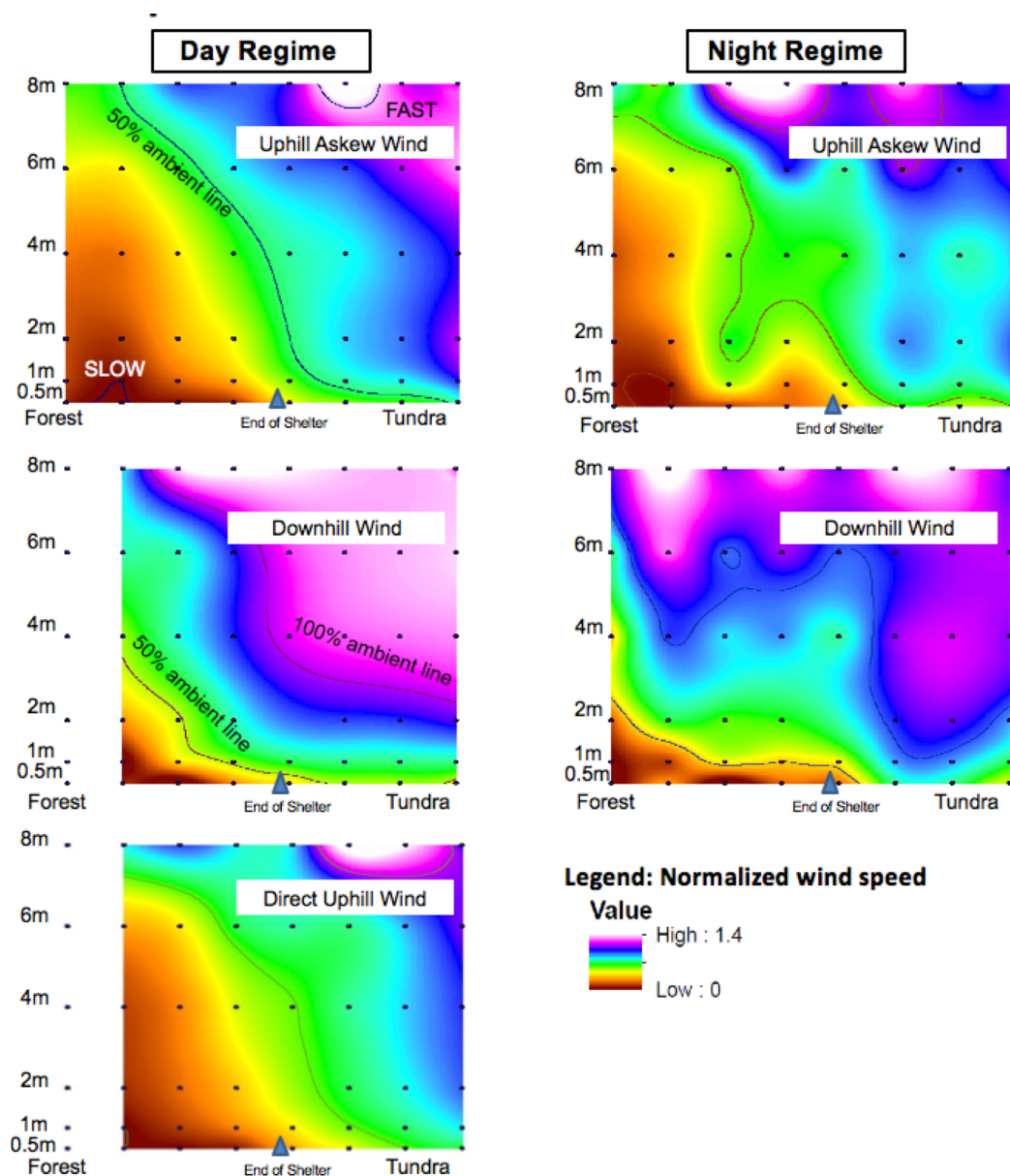
Wind Speed Results

A sheltered zone with reduced wind speed existed under all wind conditions, and extended at least to the wind damage boundary, the edge of the sheltered zone. During the day, uphill and uphill askew wind interacted with the treeline to form large sheltered zones. Wind speed less than 50% of the ambient wind speed in the tundra existed well past the wind damage boundary. Downhill wind in the day (very uncommon) heavily reduced the height and area of the sheltered zone, but an area with reduced wind speed still existed close to the ground (Figure 4).

At night, areas with wind speeds less than 50% of ambient wind again extended out to the end of the sheltered zone for all recorded wind conditions, but the area of low wind speed was

generally smaller than during the day. There was almost no direct uphill flow recorded by the tower, and thus not enough data to create an ArcGIS map.

Figure 4. Wind speed vertical cross-sectional map in the day and night, in different wind directions. Purple represents the fastest wind speed, and red the slowest wind speed. The x-axis shows the distance from the edge of the forest (left edge of each map). The tundra (on the right side of the x-axis) is further from the forest than the end of the shelter zone (marked with the triangle on the map). The y-axis represents the height (0.5m to 8m) in the air column at which the wind speed was measured.



The data showed that a sheltered zone existed in both night and day regimes, although the shape and extent varied depending on wind direction and whether the treeline was under a day or night wind regime. This supported the premises of hypotheses 1 and 2, showing that sheltered areas above the treeline did exist in both downslope and upslope wind patterns.

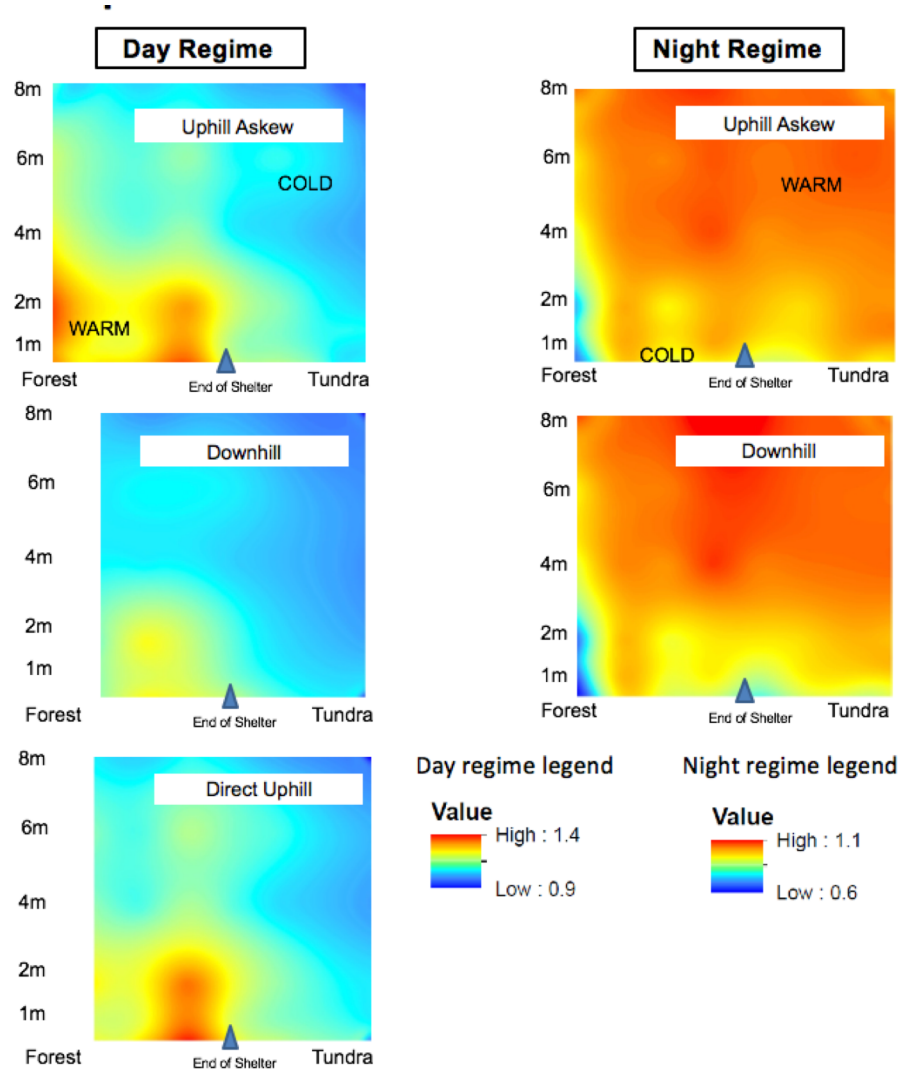
The ArcGIS maps represent a compilation of averages of hundreds of wind speed points per measuring point across time (data points were collected at 1 minute intervals across 2-4 days), so present a reliable representation of the wind dynamics at that specific cross-sectional area. However, wind speed dynamics were measured only across one transect, so there is some degree of uncertainty in the ability of the maps to describe the entire treeline. If enough equipment to measure wind speed at multiple cross-sections was available, that would have increased the reliability of the maps as a descriptor of the entire treeline. The measurement uncertainty of the anemometers was 0.25m/s, which makes the measurements less accurate at very low wind speeds. The ambient wind speed was typically over 2m/s, but wind speeds inside the sheltered zone ranged from 0-1m/s, so errors due to uncertainty could account for some of the observed variation within the sheltered zone.

Air Temperature Results

The presence of the sheltered zone seemed to affect temperature: it corresponded to warm pockets of air in the daytime and cold pockets of air near the ground in the night. During the day, temperatures in the sheltered zone warmed up to about 140% of ambient temperature, although downhill wind corresponded to a warm spot temperature about 120% of ambient temperature and a shift of the warm air back towards the base of the treeline. At night, air near the ground could be about 30-40% colder than air in the tundra, with downhill wind corresponding to slightly lower temperatures than uphill askew wind (Figure 5). While this correlation does not imply

causation, given how air temperature and wind speed interact it seems likely that the interaction between the treeline and airflow caused the temperature patterns.

Figure 5. *Temperature vertical cross-sectional map in the day and night, in different wind directions. Red represents the warmest temperature, and blue the coldest. During the day regime, red represents approximately 140% ambient temperature, light blue represents approximately ambient temperature, and dark blue 90%. At night, red represents approximately 110% ambient, dark orange represents ambient temperature, and blue approximately 60%. Ambient temperature was measured 2m above the ground in the tundra. For exact legends see Appendix 1. The x-axis shows the distance from the edge of the forest (left edge of each map). The tundra (on the right side of the x-axis) is further from the forest than the end of the shelter zone (marked with the triangle on the map). The y-axis represents the height (0.5m to 8m) in the air column at which the wind speed was measured.*



The results supported hypotheses 1 and 2, showing that the sheltered zone did correspond to warmer air temperatures during the day and colder air temperatures at night (i.e., created its own microclimate different from that of the adjacent tundra).

The temperature measurements were taken using the same methodology as the wind speed measurements, so the same general uncertainty concerns apply. The uncertainty of the measurements on the logging thermometers was 0.1°C , which was far smaller than the differences in temperature between the tundra and sheltered zone (typically at least 2°C).

Study 2: Ground Temperatures

Procedure

A 30m wide and 60m long area of interest (AOI) was established, stretching from the old growth forest to the treeless tundra, and encompassing the sheltered zone. Four zones were defined: the forest below the old-growth treeline, the tundra above the wind damage boundary, and the upper and lower halves of the sheltered zone. To map the spatial distribution of temperature, a grid of 110 sampling points was established and mapped with a high-precision Trimble GPS. An infrared camera was used to take a picture of a 1-meter-squared area around each sampling point, and FLIR tools software was then used to average the temperature within each photograph. The average ground temperature readings corresponding to points on the sampling grid were interpolated using ArcGIS. Additional thermal photographs of the area were taken for qualitative analysis.

Results

In the day regime, the temperature in the forest was the lowest, the tundra was slightly warmer, and upper sheltered zone was very warm (Figures 6 and 7). A One-way ANOVA with a Welch correction (for unequal variances) showed statistically significant differences between the sections, $F(3, 49.52) = 12.66, p < .005$. Bonferroni post-hoc tests showed that the upper sheltered zone temperature was significantly warmer than the lower sheltered zone, the lower sheltered zone was warmer than the forest, and the forest was colder than the tundra and the upper sheltered zone ($ps < .05$). The Bonferroni post-hoc test showed no other statistically significant differences (notably, the tundra temperatures were between those of the upper and lower sheltered zones, and did not differ significantly from either). The fact that warm temperatures extended past the wind damage boundary of the sheltered zone into the tundra could be explained by the fact that the wind damage line would occur at smallest extent of the sheltered zone, but the daytime sheltered zones extended past the wind damage boundary (Study 1 Figure 4). Cold temperatures in the lower sheltered zone likely came from the effect of cold shadows of saplings.

In the night regime, the ground in the forest was the warmest, the lower sheltered zone and the tundra were colder, and the upper sheltered zone was the coldest (Figures 6 and 7). A One-way ANOVA with a Welch correction showed statistically significant differences between the sections, $F(3, 52.78) = 36.59, p < .005$. Post hoc tests (Bonferroni) showed that the upper sheltered zone ground temperatures were colder than all others, which appeared to be an effect of the still, cold air in the sheltered zone. The lower sheltered zone temperatures differed from all but those in the tundra—temperatures in the lower sheltered zone may have been warmer than in the upper sheltered zone due to saplings in this section radiating heat to the ground. Forest

temperatures were warmer than those in all other sections (the trees in the forest radiated heat to the ground), tundra temperatures differed from all but the lower sheltered zone ($ps < .05$).

Figure 6. Interpolation of temperature points by ArcGIS for daytime and nighttime readings. The color on the map represents temperature in Celsius: Green is the coldest, and pink and light pink are the hottest.

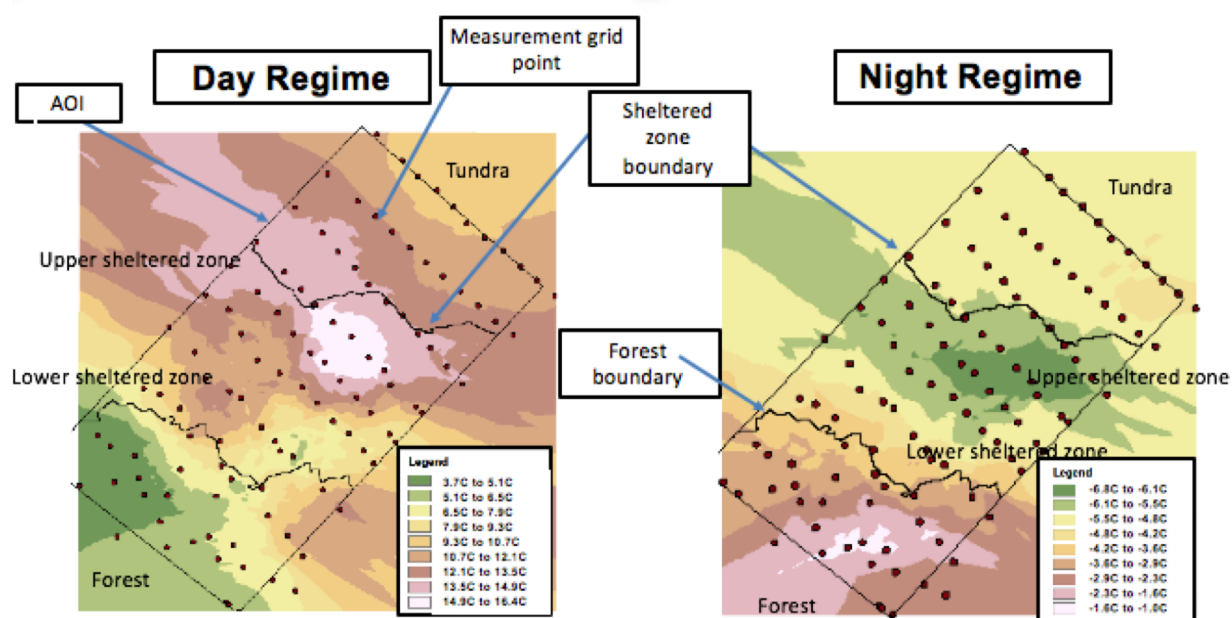
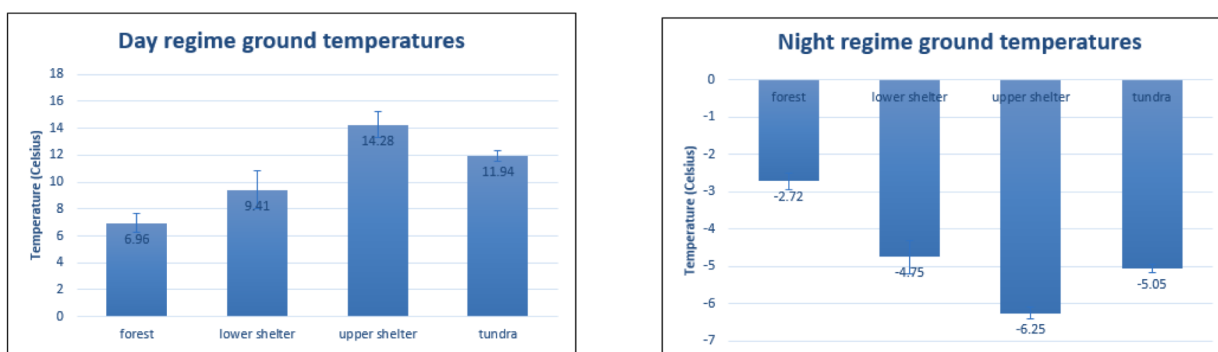


Figure 7. Average daytime and nighttime temperatures in the 4 zones: forest, lower shelter, upper shelter, tundra.



The results mostly supported hypotheses 1 and 2: the trees of the treeline created a microclimate where the ground in the upper sheltered zone was very warm during the day and very cold at night. However, the lower sheltered zone's ground temperatures were cooler during the day and warmer at night than expected—likely an effect of shadows and heat radiation by mid-sized saplings. Overall, the ground temperatures corresponded with the air temperatures described in study 1.

The measurement uncertainty on the FLIR E6 thermal camera was 0.06 °C for each pixel. The effects of these random errors were further reduced through averaging of the 19,200 pixels per thermal photograph. However, the measurement points were spaced on a 3m by 3m grid, so small-scale microclimatic patterns such as individual tree sheltering and shadows were not captured accurately. This was problematic within the lower sheltered zone, where open space interspersed with tall saplings meant that very high (open, sheltered space in the day, below trees at night) and very low (open space at night, tree shadows in the day) temperatures existed in close proximity. A tighter measurement spacing could have allowed for higher resolution. In addition, temperature patterns were taken at one instant in time, so may not capture variations in the temperature pattern across days and seasons.

Study 3: The Effect of the Sheltered Zone on Seedlings

Procedure

The same 30m wide and 60m long area of interest (AOI) was used as in Study 2. All 243 living and dead seedlings between 10 and 30 cm tall in the AOI were mapped using a high-precision Trimble GPS. Seedling height and growth (the length of apical growth of the most recent growing season) were measured using a meter stick and digital calipers.

The seedlings were plotted in ArcGIS and categorized into one of four zones based on location (tundra, upper sheltered zone, lower sheltered zone, forest). The frequency distributions of live seedlings and of dead seedlings into these four location categories were analyzed using chi-squared tests.

The growth of the seedlings was matched to each seedling's location. ArcGIS then used interpolation to generate a map of seedling growth. A multiple regression was used to regress seedling leader growth against daytime temperature (predictor variable) and seedling height (to control for the fact that larger seedlings grow more).

Results

The majority of live seedlings occurred in the sheltered zone (Table 1), in particular, in the upper sheltered zone (USZ) (Table 2). However, the majority of dead seedlings occurred in the lower sheltered zone (LSZ) (Table 3). This is interesting because the upper sheltered zone experienced both the highest and lowest temperatures. If seedling survivorship is linked to microclimate, then it appears that seedlings are not inhibited by the low nighttime temperatures but instead assisted by the warm daytime temperatures in the upper sheltered zone. The lower sheltered zone had the highest frequency of dead seedlings, which was unexpected, but it is possible that the seedlings were harmed by the presence of saplings through competition for resources. Very few seedlings survived in the tundra, and almost all of those were clustered close to the edge of the sheltered zone, and very few survived in the forest, so it appears that the tundra and forest are inhospitable for seedlings whereas the microclimate of the upper sheltered zone is the most hospitable.

If seedlings were unaffected by the microclimate of the treeline, both live and dead seedlings should be randomly distributed through the AOI and the chi-squared tests should show no difference between expected frequency (random distribution) and observed frequency. Given that the chi-squared tests show very clear variation in seedling frequency, it appears that the results support hypothesis 3, which is that the microclimate affects seedling survivorship.

In addition, the distribution of seedlings appears to have a very abrupt edge (Figure 8). This could indicate that the abrupt treeline's microclimate prevents seedling growth and survival above a certain boundary, leaving the abrupt-edged seedling cluster to grow into an abrupt treeline edge.

The measurement uncertainty on the Trimble GPS was less than 0.15m, so seedling placement within the AOI was very reliable. Only seedlings within 15cm of the borderlines could have been incorrectly categorized.

Table 1. Distribution of live seedlings in the three major zones. (see Figure 8 for map representation).

Zone	Number of Live Seedlings	Expected Number (based on area)	χ^2	<i>p</i>-value
Tundra	23	60.3	33.03	$p < 0.0001$
Sheltered Zone	150	88.8	75.60	$p < 0.0001$
Forest	27	50.83	14.95	$p = 0.0001$

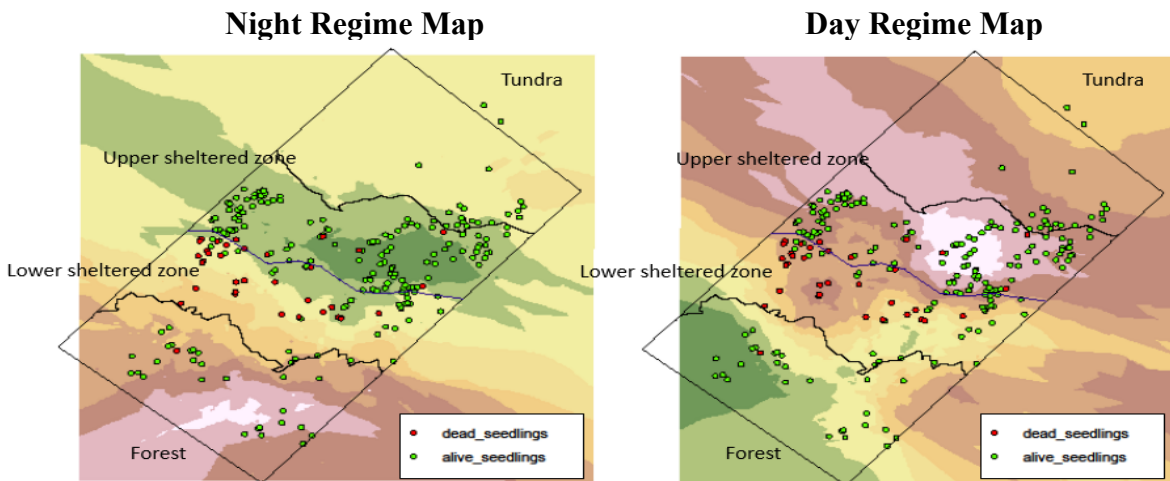
Table 2. Distribution of live seedlings within the sheltered zone.

Zone	Number of Live Seedlings	Expected Number (based on area)	χ^2	<i>p</i>-value
USZ	114	76.1	37.77	$p < 0.0001$
LSZ	38	75.9		

Table 3. Distribution of dead seedlings within the sheltered zone.

Zone	Number of Dead Seedlings	Expected Number	χ^2	p-value
USZ	7	16.5	10.10	$p < 0.0009$
LSZ	26	16.5		

Figure 8. Distribution of dead and alive seedlings plotted against day and night temperatures.



The lowest rate of growth occurred in the forest (warmest at night and coldest during the day), while the highest rate of growth occurred in the upper sheltered zone where it was coldest at night and warmest during the day (Figure 9). This suggests that seedlings respond to daytime microclimate.

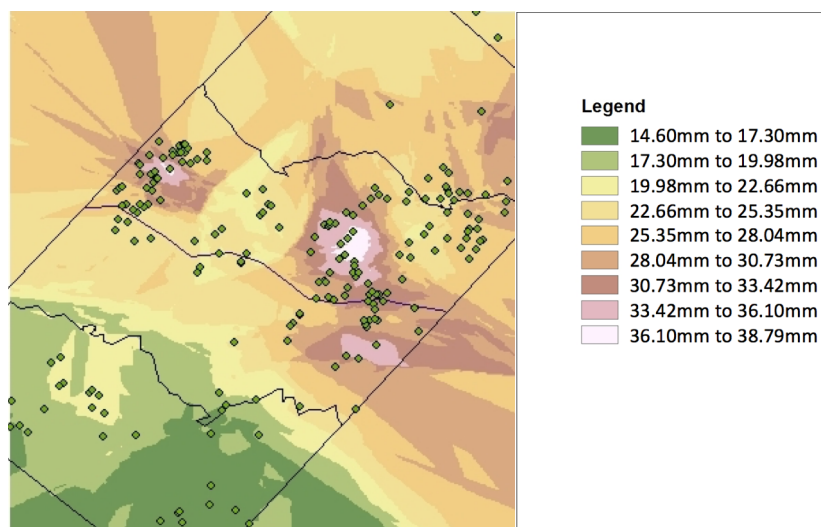
A multiple regression was performed using day temperature and seedling height as predictors for the outcome variable of seedling growth. The regression model was significant ($R^2 = 0.171$, $F(2,183) = 18.9$, $p < .001$). Seedling growth increased with increasing daytime temperature (beta = 0.375, $p < .001$) and increasing seedling height (beta = 0.258, $p < .001$). So, seedling growth is positively correlated with both day regime temperature and seedling height.

This result supports hypothesis 3a, seedlings grew better at sites with high daytime temperatures than at sites with low daytime temperatures.

A significant positive correlation indicates that there is a relationship of some sort between seedling growth and temperature. It is possible that some external factor caused both the growth and the temperature variation. However, given that temperature is known to impact plant growth and research has found that treelines are temperature-limited, it would make sense if higher daytime temperatures affected seedling growth. However, it is possible that seedling growth depends on competition (areas with more trees generally had lower daytime temperatures), but this is unlikely to be the sole factor given that seedlings grew poorly in the tundra despite lacking competition. To further investigate, a laboratory experiment under controlled conditions could be carried out.

Uncertainty on the calipers was 0.01mm and uncertainty on the meter stick was 1mm, so neither should have contributed much uncertainty through random measurement error (seedlings were 10-30cm tall, growth was usually at least 1mm).

Figure 9. Spatial pattern of growth rate. Green indicates slower-than-expected growth, light and dark pink indicate faster-than-expected growth.



Conclusion

The abrupt edge of the treeline appears to cause the formation of a sheltered zone with lower wind speeds. Uphill wind interacted with the treeline to form a sheltered eddy; downhill flow also interacted with the treeline to form a sheltered zone by creating a slow-draining pool of air at the base of the treeline. This sheltered zone is spatially correlated with warmer air and ground temperatures during the day, and colder during the night. Seedlings do not appear inhibited by the nighttime cold temperatures in either recruitment or growth—perhaps growth at treeline is not limited by cold temperatures at night but by the lack of sufficient warmth in the day, as the area seedlings survived and grew best in was the one with the warmest daytime temperatures. As the seedlings grow it appears that the edge they will establish in the future will be a new abrupt treeline slightly shifted up the slope in line with the edge of the current sheltered zone. This may shed some light on why abrupt treelines move so slowly (Harsch et al., 2009)—the area of hospitable climate available for seedling recruitment they create is limited to a very narrow stretch of upslope land.

The fact that this was a field study significantly reduces the confidence I can have in any causal relationships between variables: it was not possible to control for all the variables that could affect the data, and it is possible that some uncontrolled variable within the ecosystem would account for the patterns found in the research. My conclusions were drawn primarily from correlative evidence, so it is not certain if there are causal relationships between the variables, although the relationships I found are consistent with known causal mechanisms.

Further research could study other types of treelines to explore microclimatological patterns and feedbacks created by other treeline patterns (diffuse treeline, island treeline). This would allow microclimatic and seedling trends to be compared across treeline types, possibly

allowing broader conclusions to be drawn about the role of microclimates in treeline movement.

It would also be interesting to study whether the microclimatological patterns change from season to season as the overall seasonal weather changes, as well as which season has the greatest effect on the treeline structure.

References

- Ahrens, C. D. (2001). *Meteorology Today: An Introduction to Weather, Climate, and the Environment* (6th ed.). Pacific Grove, CA: Brooks/Cole.
- Childs, C. (2004, July-September). Interpolating Surfaces in ArcGIS Spatial Analyst. *ArcUser*, 34-35.
- Esri. (2016). *Understanding interpolation analysis*. Retrieved from <http://desktop.arcgis.com/en/arcmap/10.3/tools/spatial-analyst-toolbox/understanding-interpolation-analysis.htm>
- Grace, J., Berninger, F., & Nagy, L. (2002). Impacts of climate change on treeline. *Annals of Botany*, 90, 537-544.
- Greenwood, S., Chen, J., Chen, C., & Jump, A. (2015). Temperature and sheltering determine patterns of seedling establishment in an advancing subtropical treeline. *Journal of Vegetation Science*, 26(4), 711-721.
- Greenwood, S. & Jump, A. S. (2014). Consequences of Treeline Shifts for the Diversity and Function of High Altitude Ecosystems. *Arctic, Antarctic, and Alpine Research*, 46(4), 829-840.
- Harsch, M., Hulme, P., McGlone, M., & Duncan, R. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, 12, 1040-1049.
- Harsch, M. & Bader, M. (2011). Treeline form - a potential key to understanding treeline dynamics. *Global Ecology and Biogeography*, 20, 582-596.

- Jones, H. G. (2014). *Plants and Microclimate: A Quantitative Approach to Environmental Plant Physiology* (3rd ed.). Cambridge, UK: Cambridge University Press.
- Körner, C. (2012). *Alpine Treelines: Functional Ecology of the Global High Elevation Tree Limits*. Basel, Switzerland: Springer.
- Körner, C. & Paulsen, J. (2004). A world-wide study of high altitude treeline temperatures. *Journal of Biogeography*, 31, 713-732.
- Kummel, M. (2015). The spatial structure of the moving edge and treeline migration: detailed study on Pikes Peak, CO, USA. *Poster presentation at International Association of Vegetation Science Conference*.
- Malanson, G., Resler, L., Bader, M., Holtmeier, F., Butler, D., Weiss, D., Daniels, L., & Fagre, D. (2011). Mountain Treelines: a Roadmap for Research Orientation. *Arctic, Antarctic, and Alpine Research*, 43(2), 167-177.
- Oke, T. (1987). *Boundary Layer Climates* (2nd ed.) New York, NY: Routledge.
- Pyatt, J., Tomback, D., Blakeslee, S., Wunder, M., Resler, L., Boggs, L., & Beveney, H. (2016). The importance of conifers for facilitation at treeline: comparing biophysical characteristics of leeward microsites in Whitebark pine communities. *Arctic, Antarctic and Alpine Research*, 48(2), 427-444.
- Smith, W., Germino, M., Hancock, T., & Johnson, D. (2003). Another perspective on altitudinal limits of alpine timberlines. *Tree Physiology*, 23, 1101-1112.

Appendix A: Statistics Tables

Day Regime (afternoon)

Descriptives

PM_Temp

	N	Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Minimum
					Lower Bound	Upper Bound	
Tundra	31	11.9387	2.09725	.37668	11.1694	12.7080	6.80
Upper Sheltered Zone	24	14.2833	4.79399	.97857	12.2590	16.3077	.80
Lower Sheltered Zone	24	9.4083	6.89032	1.40648	6.4988	12.3179	.00
Forest	32	6.9563	4.90463	.86703	5.1879	8.7246	1.00
Total	111	10.4622	5.50720	.52272	9.4263	11.4981	.00

Test of Homogeneity of Variances

PM_Temp

Levene Statistic	df1	df2	Sig.
9.973	3	107	.000

ANOVA

PM_Temp

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	837.997	3	279.332	11.964	.000
Within Groups	2498.224	107	23.348		
Total	3336.221	110			

Robust Tests of Equality of Means

PM_Temp

	Statistic ^a	df1	df2	Sig.
Welch	12.659	3	49.518	.000

a. Asymptotically F distributed.

Post Hoc Tests

Multiple Comparisons

Dependent Variable: PM_Temp
Bonferroni

(I) Treeline_Zone	(J) Treeline_Zone	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
Tundra	Upper Sheltered Zone	-2.34462	1.31377	.463	-5.8763	1.1870
	Lower Sheltered Zone	2.53038	1.31377	.341	-1.0013	6.0620
	Forest	4.98246*	1.21769	.000	1.7091	8.2559
Upper Sheltered Zone	Tundra	2.34462	1.31377	.463	-1.1870	5.8763
	Lower Sheltered Zone	4.87500*	1.39487	.004	1.1253	8.6247
	Forest	7.32708*	1.30478	.000	3.8196	10.8346
Lower Sheltered Zone	Tundra	-2.53038	1.31377	.341	-6.0620	1.0013
	Upper Sheltered Zone	-4.87500*	1.39487	.004	-8.6247	-1.1253
	Forest	2.45208	1.30478	.378	-1.0554	5.9596
Forest	Tundra	-4.98246*	1.21769	.000	-8.2559	-1.7091
	Upper Sheltered Zone	-7.32708*	1.30478	.000	-10.8346	-3.8196
	Lower Sheltered Zone	-2.45208	1.30478	.378	-5.9596	1.0554

*. The mean difference is significant at the 0.05 level.

Night Regime (Pre-sunrise)

AM_Temp

	N	Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Minimum
					Lower Bound	Upper Bound	
Tundra	31	-5.0548	.61581	.11060	-5.2807	-4.8290	-6.60
Upper Sheltered Zone	24	-6.2458	.80918	.16517	-6.5875	-5.9041	-7.80
Lower Sheltered Zone	24	-4.7542	2.20237	.44956	-5.6841	-3.8242	-7.00
Forest	33	-2.7212	1.70363	.29656	-3.3253	-2.1171	-5.60
Total	112	-4.5580	1.94323	.18362	-4.9219	-4.1942	-7.80

Test of Homogeneity of Variances

AM_Temp

Levene Statistic	df1	df2	Sig.
20.202	3	108	.000

ANOVA

AM_Temp

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	188.282	3	62.761	29.359	.000
Within Groups	230.871	108	2.138		
Total	419.153	111			

Robust Tests of Equality of Means

AM_Temp

	Statistic ^a	df1	df2	Sig.
Welch	36.591	3	52.780	.000

a. Asymptotically F distributed.

Post Hoc Tests

Multiple Comparisons

Dependent Variable: AM_Temp
Bonferroni

(I) Treeline Zone	(J) Treeline Zone	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
Tundra	Upper Sheltered Zone	1.19099 [*]	.39753	.020	.1225	2.2594
	Lower Sheltered Zone	-.30067	.39753	1.000	-1.3691	.7678
	Forest	-2.33363 [*]	.36570	.000	-3.3165	-1.3507
Upper Sheltered Zone	Tundra	-1.19099 [*]	.39753	.020	-2.2594	-.1225
	Lower Sheltered Zone	-1.49167 [*]	.42207	.004	-2.6261	-.3573
	Forest	-3.52462 [*]	.39224	.000	-4.5788	-2.4704
Lower Sheltered Zone	Tundra	.30067	.39753	1.000	-.7678	1.3691
	Upper Sheltered Zone	1.49167 [*]	.42207	.004	.3573	2.6261
	Forest	-2.03295 [*]	.39224	.000	-3.0872	-.9787
Forest	Tundra	2.33363 [*]	.36570	.000	1.3507	3.3165
	Upper Sheltered Zone	3.52462 [*]	.39224	.000	2.4704	4.5788
	Lower Sheltered Zone	2.03295 [*]	.39224	.000	.9787	3.0872

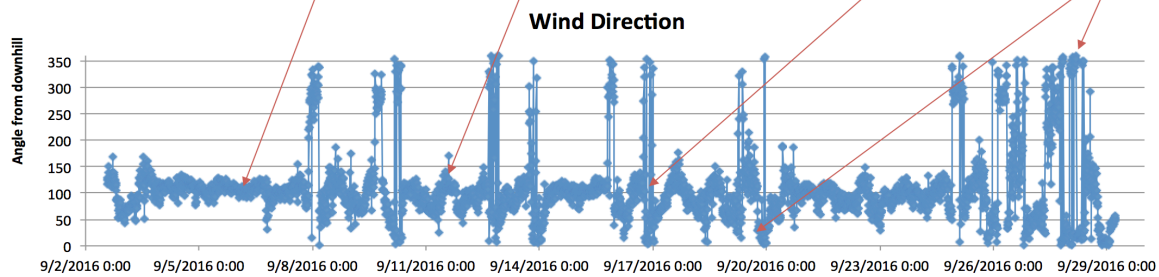
Appendix C: Samples of dataset

All raw data files available upon request.

Wind direction: 73,515 data points

Full wind direction graph.

- Day wind flow: askew uphill to uphill. Night wind flow: askew uphill or downhill



Stationary tower data (including wind direction)

#	Temp, °C	RH, %	Wind Speed,	Gust Speed,	Wind Directi	V
1	9.386	74.9	5.29	8.31	105.3	
2	9.485	74.1	4.78	6.8	101.1	
3	9.682	74.2	5.04	7.05	108.1	
4	9.756	73	5.79	8.56	102.5	
5	9.756	72.9	5.79	8.06	96.9	
6	9.682	73.1	5.54	7.3	98.3	
7	9.632	73.5	5.79	7.3	102.5	
8	9.509	73.4	5.54	7.05	96.9	
9	9.534	74.3	4.53	5.79	99.7	
10	9.509	74.3	5.29	7.05	96.9	
11	9.386	74.4	5.29	6.3	92.7	
12	9.41	74.8	4.03	5.54	103.9	
13	9.509	75	4.28	5.79	106.7	
14	9.509	74.4	5.29	6.8	105.3	
15	9.632	74.6	3.78	5.29	113.7	
16	9.805	74.4	4.03	5.04	109.5	
17	10.247	74.1	4.53	8.06	109.5	
18	10.443	72.6	4.28	5.29	106.7	
19	10.59	72.5	4.28	5.29	96.9	
20	10.638	72	4.53	5.79	105.3	
21	10.541	71.4	4.53	6.8	106.7	
22	10.492	71.5	5.29	6.8	119.3	
23	10.296	71.2	4.78	6.3	115.1	
24	10.222	71.6	4.28	5.54	113.7	

41891		5.821	44.6	7.81	10.83	87
41892		6.051	45	7.3	8.81	77.2
41893		6.026	44.4	8.31	10.32	81.4
41894		5.616	44.4	9.07	11.58	81.4
41895		5.437	45.2	6.55	9.82	99.7
41896		5.591	45.5	6.8	8.31	87
41897		5.821	45.3	6.3	9.07	77.2
41898		5.975	44.8	6.8	9.07	70.2
41899		6.128	44.5	7.05	9.82	78.6
41900		5.745	44.2	8.81	11.84	70.2
41901		5.745	44.6	8.56	11.84	73
41902		5.898	44.6	7.05	8.81	81.4
41903		6.153	44.5	7.81	10.07	68.8
41904		5.77	43.9	7.81	11.33	88.4
41905		5.924	44.5	6.3	11.33	94.1
41906		5.796	44.3	7.81	10.58	77.2
41907		6.102	44.4	7.55	9.57	70.2
41908		5.924	44	6.55	9.32	77.2
41909		6.077	44.1	8.06	12.84	68.8
41910		5.796	43.8	8.56	11.84	82.8
41911		5.693	44.3	8.56	11.08	75.8
41912		5.898	44.3	8.06	11.58	68.8
41913		5.847	44.2	8.06	11.84	73
41914		5.796	44.1	7.81	11.33	81.4
41915		5.591	44.2	8.56	13.6	82.8
41916		5.77	44.3	7.55	9.07	68.8
41917		6.128	44.2	6.55	9.57	77.2
41918		6.026	43.7	6.04	8.81	75.8
41919		6.509	43.8	5.79	7.55	74.4
41920		6.433	43	6.8	8.31	92.7
41921		6.306	43	7.3	8.56	78.6
41922		6.204	43.4	7.55	9.57	82.8

Wind speed and air temperature:

time of day	Date Time, G	Temp 0.5m	Temp 1m	Temp 2m	Temp 4m	Temp 6m	Temp 8m	WS 0.5m	WS 1m	WS 2m	WS 4m	WS 6m	WS 8m
14	1 42615.5715	11.224	11.151	11.029	10.858	10.883	10.247	2.27	2.77	3.27	3.78	4.78	4.53
15	1 42615.5722	11.102	10.858	10.663	10.369	10.418	9.928	2.27	3.27	4.03	5.04	5.54	5.04
16	1 42615.5729	10.834	10.516	10.369	10.001	10.124	9.706	2.52	4.28	5.04	5.04	5.54	5.29
17	1 42615.5736	10.638	10.32	10.198	9.854	9.952	9.632	3.02	3.53	4.28	4.53	5.04	4.78
18	1 42615.5743	10.418	10.149	10.051	9.682	9.78	9.46	2.27	3.78	4.78	4.03	5.54	5.29
19	1 42615.575	10.247	10.026	9.928	9.657	9.682	9.46	2.27	3.02	3.78	3.53	4.28	3.78
20	1 42615.5757	10.222	10.026	9.903	9.657	9.682	9.485	1.76	3.27	4.03	3.27	4.78	4.28
21	1 42615.5764	10.149	10.001	9.854	9.583	9.608	9.435	1.26	3.53	4.53	2.52	5.29	4.78
22	1 42615.5771	10.075	9.952	9.805	9.558	9.608	9.435	1.76	3.27	4.03	2.77	4.53	4.03
23	1 42615.5778	10.1	9.952	9.805	9.583	9.608	9.435	2.01	3.02	3.53	3.53	4.28	3.53
24	1 42615.5785	10.149	10.001	9.829	9.608	9.657	9.46	2.52	2.52	4.78	3.78	5.04	4.53
25	1 42615.5792	10.32	10.124	9.903	9.657	9.682	9.435	2.27	3.02	4.03	4.53	5.29	4.78
26	1 42615.5799	10.492	10.247	10.001	9.731	9.756	9.534	2.01	3.02	3.78	3.53	4.03	3.53
27	1 42615.5806	11.175	10.834	10.443	10.1	10.149	9.879	1.76	3.02	3.53	3.53	4.28	3.78
28	1 42615.5813	11.613	11.2	10.785	10.296	10.394	10.051	1.76	3.27	4.03	3.27	4.53	3.78
29	1 42615.5819	11.807	11.321	10.956	10.541	10.565	10.296	2.01	2.77	3.02	3.02	3.53	2.77
30	1 42615.5826	11.807	11.37	11.029	10.59	10.638	10.32	2.01	3.02	3.78	3.53	4.28	3.53
31	1 42615.5833	11.759	11.273	10.932	10.541	10.614	10.271	2.27	3.53	4.28	3.53	4.53	4.03
32	1 42615.584	11.783	11.346	11.005	10.614	10.663	10.345	2.52	3.53	4.28	4.28	4.78	4.03
33	1 42615.5847	11.321	10.907	10.736	10.247	10.394	9.952	3.27	4.28	5.04	5.54	6.04	5.54
34	1 42615.5854	11.151	10.785	10.614	10.198	10.247	9.952	2.52	3.27	3.78	3.53	4.53	3.53
35	1 42615.5861	11.029	10.687	10.541	10.222	10.271	10.001	3.27	3.78	4.28	4.53	4.78	4.53
36	1 42615.5868	10.956	10.638	10.516	10.271	10.296	10.075	2.52	3.02	3.78	3.78	4.28	3.78
37	1 42615.5875	10.98	10.687	10.541	10.222	10.296	10.001	2.27	3.53	4.03	4.28	4.78	4.28
38	1 42615.5882	10.785	10.492	10.369	10.051	10.149	9.879	2.52	3.27	3.78	4.03	4.28	3.53
39	1 42615.5889	10.712	10.443	10.32	10.001	10.1	9.829	2.01	2.77	3.53	3.02	4.03	3.27
40	1 42615.5896	10.492	10.271	10.173	9.854	9.977	9.682	2.01	3.78	4.28	3.53	4.78	4.28

Summary data (normalized means) for station 8 (tundra):

	day					night			
	downhill	parallel	askew	uphill		downhill	parallel	askew	uphill
Temp 0.5m	1.05910327	1.0782011	1.08818623	1.10396791		0.89975869	0.92822025	0.95593884	
Temp 1m	1.04280736	1.05122447	1.05511998	1.06119096		0.9541124	0.97212977	0.99825499	
Temp 2m	1.01190233	1.04344884	1.04296346	1.05527836		0.98182173	0.99335571	1.01503726	
Temp 4m	0.99337197	1.00357937	1.00543877	1.00492978		1.05019898	1.02988716	1.03696968	
Temp 6m	0.99494765	1.00827996	1.00743046	1.01970162		1.04215441	1.04766596	1.05195528	
Temp 8m	0.988431	0.98125577	0.9822934	0.97939201		1.07085046	1.05137867	1.04727436	
WS 0.5m	0.49783032	0.45328763	0.5077999	0.57679355		0.54796713	0.44687952	0.49582986	
WS 1m	0.6670937	0.67835724	0.73001231	0.7098844		0.74896474	0.68276172	0.7515097	
WS 2m	0.933059	0.81648145	0.84914341	0.81788877		0.94861983	0.81348517	0.86790787	
WS 4m	1.12910901	0.7392776	0.76453485	0.8571623		1.12069061	0.71949546	0.76660522	
WS 6m	1.1817752	0.97073733	0.96840037	0.94299789		1.15289345	1.00107467	1.0041334	
WS 8m	0.69090577	0.87494488	0.83831833	0.75780021		0.86098599	0.9571785	0.96082792	

Seedling growth:

102	OBJECTID	Comment	GrowthIncr
103	101	ag	
104	102	161	13
105	103	281	33
106	104	159	28
107	105	295	31
108	106	304	32.7
109	107	246	17.14
110	108	245	20.1
111	109	179	16.9
112	110	162	26
113	111	224	11.6
114	112	308	21
115	113	244	15.2
116	114	188	25
117	115	269	23.6
118	116	250	28
119	117	241	12.6
120	118	350	17
121	119	347	13.63
122	120	342	15