

Effects of Altitude on the Growth, Mortality, and Recruitment of Subalpine Tree Species in the West Elk Mountains of Colorado.

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Abstract

Subalpine ecosystems in Colorado occur between 9,000-11,000ft in elevation and are composed of several species of conifers. The elevation range of each species is slightly different, but they tend to form established communities, such as the Engelmann spruce-subalpine fir community. It has been shown that many plant species adjust their range differently as the climate changes, leading to potential concerns about plant community assemblages changing. In this study, we are looking at the ways that different tree species in the subalpine habitat interact with altitude, specifically: Quaking aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and Rocky mountain douglas fir (*Pseudotsuga menziesii* var. *glauca*). We established five plots in the West Elk Mountains of Colorado. Each plot was 40 x 40m, and each tree was marked with a tagged number in every plot. A variety of measurements were taken for trees in 2018, and again in 2023. We used some of these measurements to calculate changes in growth, mortality, and recruitment for each of these five species at different elevations. We also used additional data from the Forest Service's Forest Inventory and Analysis database to supplement the data sample. The aim of the study is to see how these five species interact with elevation gradients. Our results did not indicate that there was a relationship between either mortality or recruitment and elevation, and there is most likely other factors more important in determining these things. However, there did seem to be a negative relationship between elevation and growth, in the form of DBH growth rate per year and basal area growth rate per year. Our FIA data analysis also confirmed this negative relationship between growth and elevation. Finally analysis of some of the FIA data shows an increase in mortality from 2012-2019 when compared to 2002-2011.

Introduction

Subalpine ecosystems occur just below the treeline at elevations of 2,700m-3,300m (9,000-11,000 ft) in Colorado. They are dominated by the subalpine fir-Engelmann spruce forest type, which is the climax forest for the region, though they also have significant amounts of quaking aspen and lodgepole pine in areas that have suffered disturbance (U.S. Department of the Interior, n.d.). There may also be Rocky Mountain douglas fir (*Pseudotsuga menziesii* var. *glauca*), and other varieties of pine such as limber pine (*Pinus flexilis*) and Rocky Mountain bristlecone pine (*Pinus aristata*) in smaller quantities. Quaking aspen tend to be seral in more moist sites, while lodgepole pine tend to be seral in drier sites (Habeck, 1987). Higher elevation sites tend to have more subalpine fir and Engelmann spruce, while quaking aspens, lodgepole pines, and Rocky Mountain douglas firs tend to grow on the lower altitude zones of

subalpine forests. However, due to the complexity of the landscape, there can often be exceptions, which can create conditions similar to higher or lower elevations (Habeck, 1987).

Altitudinal gradients are one of the most important factors in determining what a forest will look like in the southern Rocky Mountains. These gradients affect many factors that impact the growth and composition of the forest, including moisture levels, heat load, and average frost dates. However, climate change has already been recorded to have an effect on the distributions of some species in regards to elevation in the Rocky Mountains. A paper by Renwick, Rocca, & Stohlgren (2016), details how the range of lodgepole pine (*Pinus contorta*) is shifting due to climate change in the forests of the Rocky Mountain National Park. Recruitment of lodgepole pine trees at the lower elevation edge of the range has decreased, while mortality due to mountain pine beetles has increased. This has led to an increase in recruitment of Douglas fir (*Pseudotsuga menziesii*), which generally grows at lower elevations. The upper edge of the elevation range does have some increase in lodgepole pine recruitment, but more shade and beetle tolerant species were favored, which might mean an overall decrease in the range of lodgepole pine trees. Lesica & Crone (2017), studied 28 species of arctic-alpine or boreal plants at the southernmost end of their ranges between 1988-2014. Their field sites were found in northern Montana. Their results show a strong overall declining trend for arctic-alpine and boreal species at the southern end of their ranges in the Rocky Mountains, which were concurrent with increases in temperature and decreases in precipitation.

These examples support the idea that the effects of climate change are changing the way that altitude and latitude gradients, among others, interact with vegetation across the Rocky Mountains. However, it is generally accepted that during periods of climatic change, each species migrates according to its own environmental needs, resulting in associations of plants changing rather than whole plant communities migrating together. There is evidence in the form of pollen records that this has happened before, both in western North America (Chapin et. al., 2004) and in eastern North America (Crumpacker et. al., 2001). This can lead to entirely new species assemblages as climatic conditions change, changing available resources for both wildlife and human use.

As the climate becomes less predictable due to anthropogenic activities, it is important to understand how changes in temperature and moisture availability affect the way the forests in this area grow. The forests in the Rocky Mountains support a variety of wildlife species, as well as being used by many for recreational activities such as hiking and mountain biking. These forests are also crucial when it comes to capturing water which flows down to important rivers, such as the Colorado river. Understanding the ways that climate change affects both the current plant assemblages as well as individual species is also very important, so that we can understand how these assemblages might be affected in the future. In this study, we will use a gradient in altitude and slope angle to see how these differences affect mortality and recruitment of trees over time. We will primarily focus on five species: Quaking aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and Rocky mountain douglas fir (*Pseudotsuga menziesii* var. *glauca*), measuring at plot level and also species level. We expect to see each of the different species react in their own way to these conditions, however the *P. tremuloides*, *P. contorta* and *P. menziesii* should be expected to do better overall in lower elevations, while *P. engelmannii* and *A. lasiocarpa* are

expected to do better at higher elevations.

Methods

Species Background

Quaking aspen (*Populus tremuloides*) is a small to medium sized deciduous tree. Typically, mature stands average 20-25m (66-82 ft) tall and 18-30 cm (7-12 in) d.b.h. (Burns & Honkala, 1990). Quaking aspen trees have a tendency to clone themselves through root suckers, resulting in large stands which in truth are all genetically one individual tree and remain connected. They can tolerate a wide variety of soils and growing conditions, and are quick to pioneer disturbed sites with bare soil. However, they prefer moist, well-draining soils. They grow at sea level in both the Atlantic and Pacific coasts, and as high as 3505m (11,500 ft) in Colorado (Burns & Honkala, 1990).

Lodgepole pine (*Pinus contorta*) is a two-needle pine, often attaining sizes of 18 to 33 cm (about 7 to 13 in) in d.b.h. and 18 to 25 m (about 60 to 80 ft) in height. There are four varieties of Lodgepole pine, but here we are concerned with the Rocky Mountain lodgepole pine (*Pinus contorta* var. *latifolia*) (Burns & Hokala, 1990a). Lodgepole pines are intolerant of shade and grow better in sunny conditions. They can tolerate a variety of soil types but usually prefer moist soils. Lodgepole pine can be an important seral species and plays different roles depending on the site conditions. On warmer and more habitable sites, *P. contorta* is often one of the first species to grow after a burn or other event, but is relatively quickly replaced by more shade tolerant species. On poorer sites it can compete with other species better and in some cases comes to dominate certain sites as it can be hardier than other species (Burns & Hokala, 1990a). The cones of lodgepole pine require temperatures of 45°-60° C (113°-140° F), and often stay on the tree for several years. This makes them optimal for opening after a fire has swept through and cleared other less species.

Subalpine fir (*Abies lasiocarpa*) is the smallest of the eight species of true fir that occur in the western U.S. There are two recognized varieties the typical Subalpine fir (*Abies lasiocarpa* var. *lasiocarpa*), and Corkbark fir (*Abies lasiocarpa* var. *arizonica*), which has whitish, corky bark and occurs in the Rocky Mountains of Colorado and the southwestern US. Subalpine fir can grow near sea level at the northern end of its range and at 12,000 ft near the southern end. It can tolerate a wide variety of soils, often establishing on drier, less hospitable sites before other trees (Burns & Hokala, 1990a). It also often grows into stands of *Populus tremuloides* and *Pinus contorta*, shading out these earlier seral species and eventually establishing itself as a dominant species along with Engelmann spruce (*Picea engelmannii*), forming the relatively stable Engelmann spruce-Subalpine fir forest cover, which is a climax state in areas of the Rocky Mountains (Burns & Hokala, 1990a).

Engelmann spruce (*Picea engelmannii*) prefer humid climates with long cold winters and short cool summers. Average annual temperatures are often near freezing, and precipitation exceeds 61cm (24in) annually (Burns & Hokala, 1990a). *Picea engelmannii* grow best on moderately deep, well draining sandy loam soils, though they tolerate a variety of soils. Engelmann spruce grows in the subalpine zone (9,000-11,000 ft) in Colorado, and can grow to

timberline at 11,500 ft. Engelmann spruce most commonly grows in association with subalpine fir (*Abies lasiocarpa*), in the Engelmann spruce-Subalpine fir forest type. It is the last species to establish itself during secondary succession after subalpine fir has begun shading out more seral species, as it is more shade tolerant than associates such as lodgepole pine (*P. contorta*) and quaking aspen (*P. tremuloides*). Engelmann spruce seedlings are more successful when growing in shade as they can be damaged by radiation and lack of water in open sites (Burns & Hokala, 1990a).

There are two varieties of douglas fir, though here we deal with the Rocky Mountain douglas fir (*Pseudotsuga menziesii* var. *glauca*). Rocky Mountain douglas firs in Colorado generally grow in places with long cold winters and short warm summers (Burns & Hokala, 1990a). The biggest limiting factors in the growth of these trees are temperature in the north of the range and moisture in the south, such that, generally, douglas firs are found in south-facing slopes on the northern part of their range and northerly slopes in the southern part. However, in high elevations in the southern Rocky Mountains they can grow on sunny, dry sites (Burns & Hokala, 1990a). *Pseudotsuga menziesii* var. *glauca* does not grow at such high elevations as some of the other trees we have discussed, generally growing between 2440 and 2900m (8,000 and 9,500 ft) in the southern Rocky Mountains (Burns & Hokala). Rocky mountain douglas firs do form pure stands in some places, but in our area of study they are a minor member of forest communities, including in the forest types: Engelmann spruce-subalpine fir, lodgepole pine, and quaking aspen. However, the proportion of douglas fir can be greater depending on many factors.

Plots

Twenty-five plots were established over a period of five years as part of a larger study, however, we focused on one set of four plots which was originally censused in 2018 and 2019. Plots were established in or near the West Elk Mountains of Colorado, especially around the Rocky Mountain Biological Laboratory. Each plot measured 40x40m and was located in a section of forest similar to the surrounding area, without canopy gaps bigger than 10x10m, and further than 100m from forest edges. The plots were intentionally established to capture a significant amount of variation over several gradients, including altitude, heat load, Topographic Wetness index (TWI)_100, TWI_1000, slope, aspect, cos_aspect, sin_aspect, southness_205, Topographic Positioning Index(TPI)_1000 (Measures a locations altitude against its neighbors to create a relief model), TPI_2000, and curvature. All trees with a diameter at breast height (DBH) ≥ 1 cm in each plot were tagged with a number, with the tags attached using either a wire collar or a nail. All tags were attached at 1.3m above the ground. Tree species for each individual were recorded with a four-letter code (Ex. "PIEN" for *Picea engelmannii*), or recorded as unknown ("UNKN"). The plots were primarily composed of Engelmann spruce - Subalpine fir forest type, with only one (SG-NES2) having a significant population of lodgepole pines (*P. contorta*).

Jacobo sites 2023

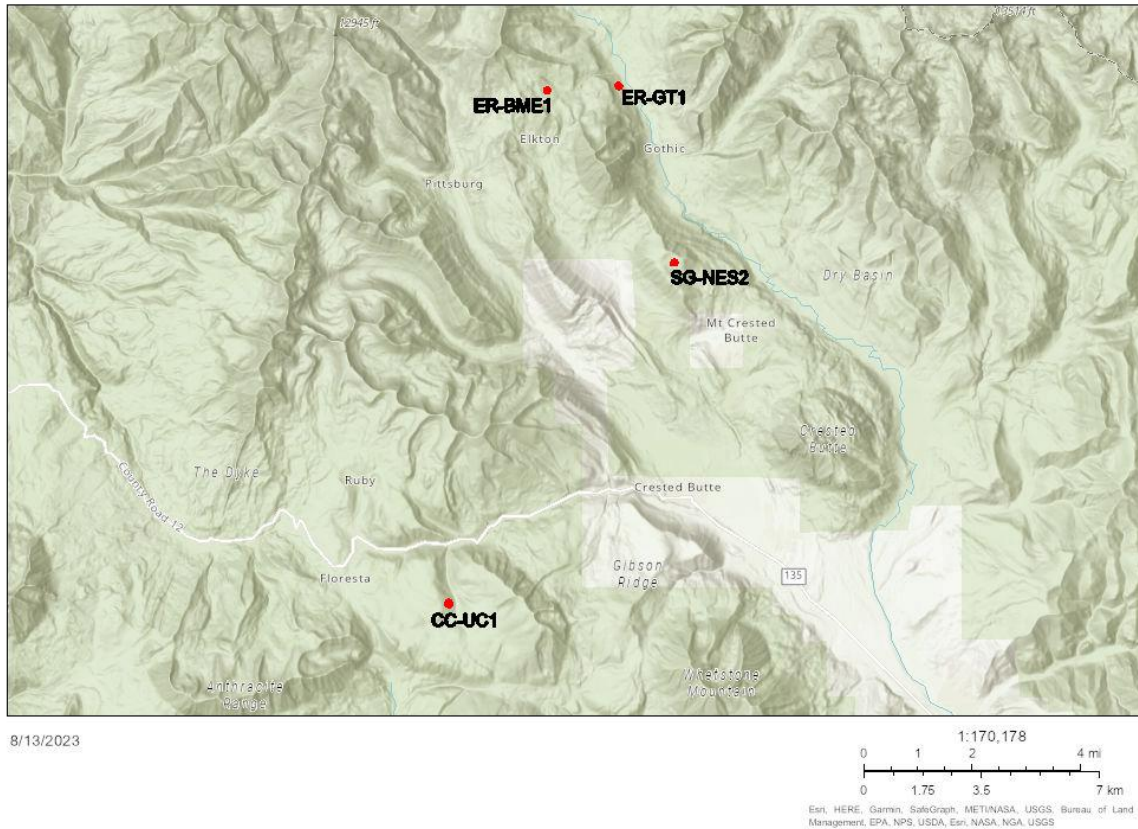


Figure 1. Locations of our plots

Forest Inventory Analysis Data

We also used data from the Forest Service's Forest Inventory and Analysis database. This data comes from a large number of plots the forest service maintains, where they sample many things about the trees every 5-10 years, including different metrics of growth, forest cover, invasive species surveys, soil surveys, etc. We looked for FIA data that matches the same factors that we measured in our plots, using this data to expand the total dataset. We restricted the FIA data to plots inside Gunnison, Pitkin, Lake, and Chaffee counties.

Measurements

Stem diameter at breast height (1.3m) was recorded for all tagged trees. Stem height was also measured, a rigid measuring tape was used to measure the height of those trees with a stem height ≤ 5 m, while a Nikon Forestry Pro II laser hypsometer was used to measure the height of trees < 5 m tall. Status of the trees was recorded, using the following classifiers: Living, Dead, Fallen (for previously tagged standing trees), Moved (for previously tagged standing trees whose location has shifted (e.g. due to an avalanche or landslide), and Missing (for previously tagged standing trees that cannot be located). Qualitative observations of standing living trees were made to record any significant health issues affecting the trees (ex. scars, burls, splits, infections/brooming, and bends), noting the presence and location of the damage. Trees whose crowns are visible from the air were geotagged (x,y coordinates, decimal degrees, WGS84 datum) using a GPS unit at 1.3m above the ground. Trees with crowns not visible from the air were associated with a tree that had been geotagged by measuring distance from the geotagged tree. In this study we focused on the measurements listed above, as they primarily gave us data for tree growth, mortality, and recruitment. However, other metrics were also recorded for each tree, including: crown illumination was measured using visual observation in accordance with Clark and Clark's (1992) indices (Table 1). Beetle infestation level was also recorded using an index value developed by Henry (2019): no sign of insects (0), sap with no visible holes (1), sap with visible holes (2), dead; red needles (3), and dead; needles off (4). The presence and proportion (ex. 15%) of red needles was also recorded. Other miscellaneous information that could be important was also recorded (ex. Multiple meristems). We resurveyed the four plots with the same methodologies.

5 Completely exposed to light from that part of the sky circumscribed by a 45° zenith angle.
4 Full overhead light. Lateral light blocked within part of the sky circumscribed by a 45° zenith angle.
3 Some overhead light (10-90% exposed to vertical light)
2.5 High lateral light (from one major or multiple medium-sized gaps)
2 Medium lateral light
1.5 Low lateral light (no large or medium sized gaps)
1 No direct light

Table 1. Crown Illumination Index

Data Analysis

Data analysis of our plots took place mostly in Microsoft Excel, and consisted of mainly of summary statistics to find rates of growth, mortality, and recruitment at the plot level.

Table 2 - we calculated New Recruits by subtracting the total number of tagged trees in the first survey from that in the second survey. This number was then divided by the total number of trees in the second survey to find a percent of these trees which were new recruits since the first survey.

Table 3 - DBH Average Difference was a measure of the total change in DBH per tree, and was calculated by subtracting the DBH in survey 1 from that in Survey 2 for each tree, then finding an average for the plot. Basal Areas were calculated from the DBH in both survey 1 and 2 using the formula $\pi(\text{DBH}/2)^2$, and the basal areas from survey 1 were subtracted from those from survey 2. The resulting values were then averaged to obtain a Basal Area difference at plot level.

The majority of the analysis for the FIA data took place in the program R. The data was divided into two periods: cohort 1 (2002-2011), and cohort 2 (2012-2019). We then compared these two cohorts to see if there were differences in the rate of mortality between the two periods. We also looked at differences in the annual diameter and annual height growth increments by species and elevation over the whole period of 2002-2019.

Results

Plots

Recruitment and Mortality

Recruitment rate was highest in our plot with the second lowest elevation (CC-UC1), and second highest in our plot with highest elevation (ER-BME1). There was not a significant trend linking recruitment to elevation in our plots. Mortality was highest in our lowest elevation plot (ER-GT1), however the other plots do not follow a clear pattern linked to altitude (Table 2).

DBH and Basal Area

Average change in DBH/tree (DBH Average Difference) seems to show a weak correlation with elevation (Table 3), and decreases as you move up in elevation, with our lowest elevation plot (ER-GT1) showing the highest DBH increase per tree, and our highest elevation plot (ER-BME1) showing the lowest DBH increase per tree.

Basal area difference per tree seems to follow a similar pattern (Table 3), falling as you increase in altitude. Basal area seems to show this pattern more strongly than DBH does, and once again our lowest elevation plot has the largest basal area increase, with our highest elevation plot having a significant decrease in basal area per tree, which could be due to

mortality of large trees.

Forest Inventory and Analysis

Growth (Figures 1 and 2)

Our results show a negative relationship between altitude and growth rate. Both annual diameter increment and annual height increment decreased in all species as elevation rose. However, *P. menziesii* seems to show an increase in annual diameter increment with elevation.

Mortality (Figures 3 and 4)

Our results suggest that there has been an increase in mortality in several of the study species between cohort 1 and cohort 2. *A. lasiocarpa*, *P. engelmannii*, and *P. menziesii* seem to be the most affected species, while both *P. contorta* and *P. tremuloides* seem to have had a decrease in mortality rate from cohort one to cohort 2.

Discussion

Plots

There were not any significant trends linking recruitment or mortality to elevation in our plots. In such a heterogeneous landscape, there are a variety of factors that could be affecting our results other than elevation, and it is very difficult to measure two places where we can control all the factors. It is possible that elevation is not one of the main factors that affect recruitment in a Engelmann spruce- subalpine fir forest, and there is another more important factor such as aspect or slope.

Average change in DBH/tree (DBH Average Difference) seems to show a weak correlation with elevation, and decreases as you move up in elevation, this seems to match our results from the FIA data, which also show the rate of DBH increase decreasing as altitude increases. One of our plots does not agree with the trend (SG-NES2), having a relatively high elevation and relatively high rate of DBH increase, however there a variety of other factors that could be affecting this, such as the fact that this plot was relatively level, and is in a location which tends to preserve snow cover for longer than many other places.

Basal area difference per tree seems to follow a similar pattern, falling as you increase in altitude. Basal area seems to show this pattern more strongly than DBH does. This could be due to an increase in mortality of large trees, which might bring down the average basal area in our highest plot.

Our results for mortality and recruitment do not support the idea that elevation is the main force driving these, and there are likely other more important factors. However, growth,

measured as both change in DBH and change in basal area does seem to show a negative relationship with elevation, suggesting that the tree species in these plots grow slower as you increase in elevation, which makes sense due to the shorter growing seasons. It is important to note that due to the nature of field ecology all of our plots had many factors acting on them, some measured and some not measured, which undoubtedly affected our results in some ways. Each of the variables we measured deserves more in depth research in the future to determine what other factors could be acting on them. We also were not able to do much of our work at species level as originally intended due to time constraints, so it would be a good idea to return to these plots and do a species level analysis in the future.

Forest Inventory and Analysis

Growth (Figures 1 and 2)

The negative relationship between elevation rate and growth shown by our results is not unexpected. As altitudes increase, there is generally more available moisture but shorter growing seasons. However, the deviation of *P. menziesii* from the general trend is very interesting. This could be due to errors in the data or could be a real phenomenon. Further research of this is required to determine if there is a real trend difference and if so what could be causing it.

Mortality (Figures 3 and 4)

Our results suggest that there has been an increase in mortality in several of the study species between cohort 1 and cohort 2. This could be due to a variety of factors. It could be possible that this decrease might be driven by climate related changes, which are already widely observable in different parts of the Rocky Mountains (Lesica & Crone, 2017) (Renwick et. al., 2016). This is especially likely due to the fact that the FIA dataset presents us with a large dataset over several counties, which is likely to reduce bias due to local mortality events not associated with climate changes.

Results Tables and Figures

Plot ID	Elevation (ft)	Measurement Interval	# Stems (2023)	Total Mortality (# trees)	Mortality rate (%/yr)	New Recruits (#trees)	Recruitment rate (%/yr)
ER-GT1	9834	2018-2023	317	43	5.2%	30	1.89%
CC-UC1	10422	2019-2023	200	5	2.62%	17	2.125%
SG-NES2	10928	2019-2023	518	7	1.275%	11	0.53%
ER-BME1	10947	2018-2023	212	14	2.94%	22	2.08%

Table 2. Mortality and Recruitment - Measurement interval refers to the year the plot was installed and then re-surveyed, # Stems is the total live and dead stems in the plot in the second survey, Total Mortality is the total number of trees that died between the two surveys, and New recruits is the total number of trees that grew to >1cm DBH after survey 1.

Plot ID	Elevation (ft)	Measurement Interval	DBH Average Difference per year (cm/yr)	Basal Area Difference per year ((cm ²)/yr)
ER-GT1	9834	2018-2023	0.376	20.66
CC-UC1	10422	2019-2023	0.0093	0.967
SG-NES2	10928	2019-2023	0.039	0.269
ER-BME1	10947	2018-2023	0.0163	-3.768

Table 3. DBH and Basal Area - Measurement interval refers to the year the plot was installed and then re-surveyed, DBH Average Difference is the average change in DBH/tree, Basal Area Difference is the average change in basal area/tree, and total DBH change is a measure of the average change in DBH when all trees were averaged, which represents an overall change in tree size over the plot.

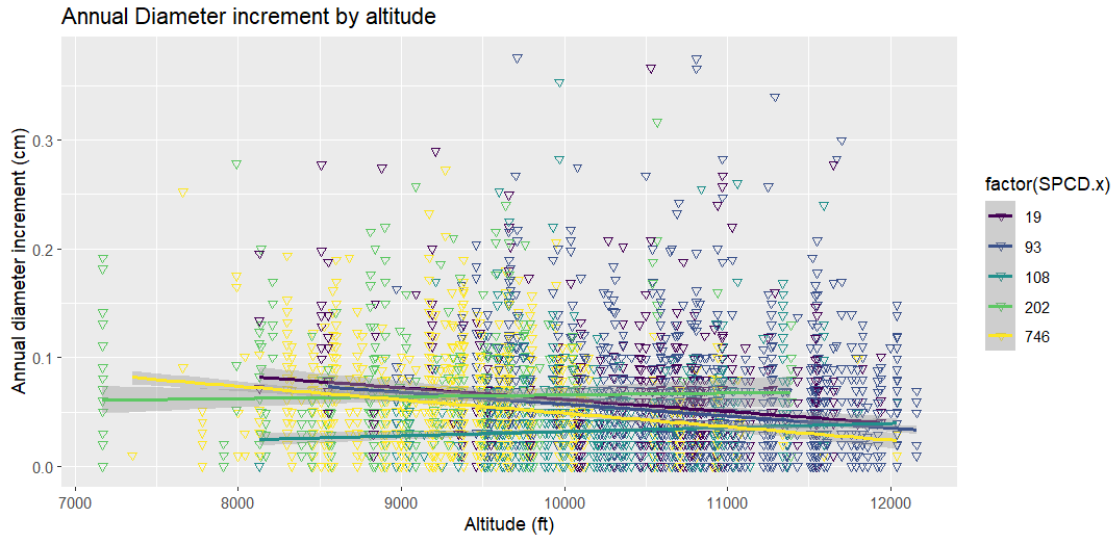


Figure 2. Annual Diameter Increment by altitude and species

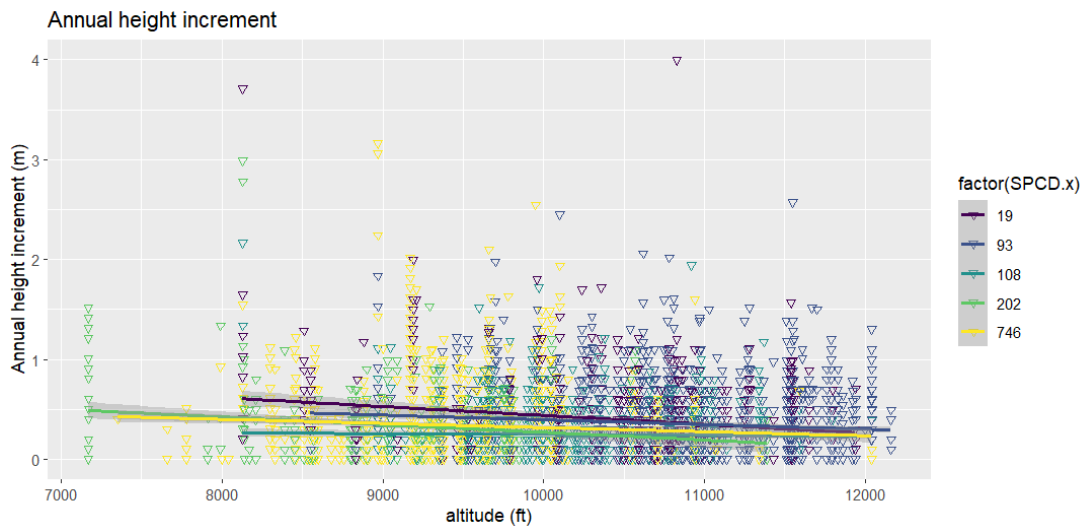


Figure 3. Annual Height Increment by altitude and species.

19	<i>Abies lasiocarpa</i>
93	<i>Picea engelmannii</i>
108	<i>Pinus contorta</i>
202	<i>Populus tremuloides</i>
746	<i>Pseudotsuga menziesii</i>

Tree species codes for Figures 1 and 2

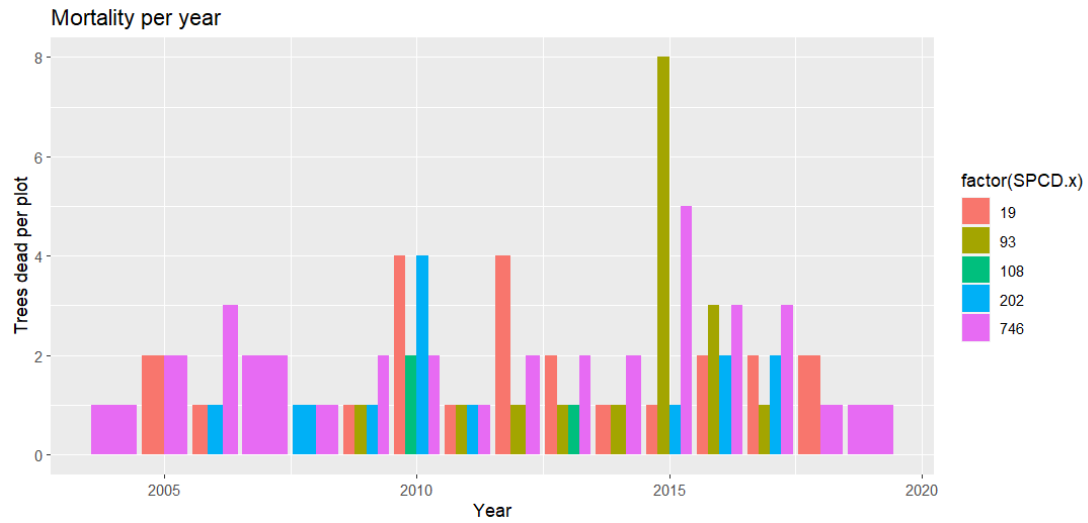


Figure 4. Mortality per species per plot for FIA data 2002-2019

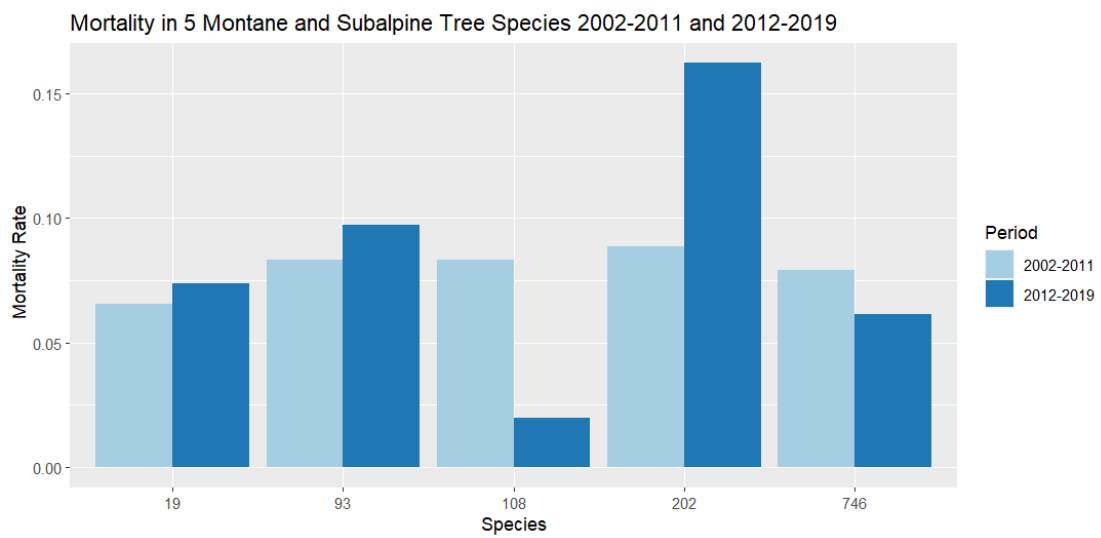


Figure 5. Mortality rate for each species in the periods 2002-2011 and 2012-2019

Citations:

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