

BIOPHYSICAL GRADIENTS AND PERFORMANCE OF WHITEBARK PINE
PLANTINGS IN THE GREATER YELLOWSTONE ECOSYSTEM

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Biological Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

July 2019

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DEDICATION

To my parents, for encouraging curiosity and compassion.

To the writers, for providing good company and enriching my world view.

“aridity makes the various Wests one”

-Wallace Stegner, *Living Dry*, 1987

ACKNOWLEDGEMENTS

I thank my advisor, Dr. Andrew Hansen, and my committee, Dr. Jia Hu and Dr. David Thoma, for taking a chance on an educator-naturalist that hails from flatter landscapes. Colleagues in the Landscape Biodiversity Lab, Dr. Tony Chang, Dr. Kathryn Ireland, Dr. Arjun Adhikari, Kathleen Carroll, Kristen Emmett, and Kevin Barnett, were invaluable resources throughout my years on campus. I also thank the Rumely family, Montana State University, the USDA Forest Health Program, and the UW-NPS Research Station for financial support. Dr. Kristen Legg, Erin Shanahan (NPS), Dr. Robert Keane (USFS), and Dr. Jesse Logan (retired USFS) were valuable in discussions regarding GYE WBP and physiology. Additionally, Ellen Jungck, Clay Demastus, Avery Beyer, Becky Nedrow, and Kay Izlar (USFS) were helpful in providing and assisting with plantation data, Ann Rodman and Zach Wilson (NPS) for HOBO data loggers and expertise, and Michael Dillon, Bonnie Robinson (UW – NPS), Katie Roloson (Yellowstone Forever) and Julie Geyer (MSU) for facilitating field station and financial arrangements. Rob Daley (NPS) was instrumental in providing training to develop and utilize Esri's spatial software for use in the field. Graduate colleagues and comrades in the MSU Ecology Department that are too many to list here. Dr. Megan Higgs and Kenneth Flagg were helpful in study design and statistical consultation. Days in the field were a joy thanks to the hard work and good company of Jake Anton, Selecta Heinrich, and Florian "Flo" Heinrich.

TABLE OF CONTENTS

1. BIOPHYSICAL GRADIENTS AND PERFORMANCE OF WHITEBARK PINE PLANTINGS IN THE GREATER YELLOWSTONE ECOSYSTEM	1
Introduction.....	1
Methods.....	10
Study Areas	10
Physical Gradients	11
Sampling Design.....	12
Historic Data	15
Field Collected Data	15
Whitebark Pine Performance	15
Competition.....	16
Microsite	17
Aspect and Slope.....	17
Soil Field Capacity.....	17
Shading	18
Blister Rust.....	19
Remotely Sensed Data	19
Daymet.....	18
Water Balance Model	19
Predictor Variables.....	21
Mixed Effects Models.....	23
Individual Growth Rate.....	23
Site Density Change Ratio	24
Results.....	25
Variation in Biophysical Gradients.....	26
Individual Growth Rate.....	31
Site Density Change Ratio	35
Blister Rust Presence	38
Discussion	38
Actual Evapotranspiration, Competition, and Growth Rates.....	38
Temperature, Competition, and Density Change.....	39
Water Deficit.....	40
Scope and Limitations.....	43
Policy and Management.....	44
Conservation Status	44
Endangered Species Act	45
Custer Gallatin National Forest Plan Revision	46
Greater Yellowstone Coordinating Committee	47
Conservation Recommendations	48

TABLE OF CONTENTS - CONTINUED

Planting and Monitoring Recommendations	50
Conclusion	52
REFERENCES CITED.....	53
APPENDICES	60
APPENDIX A: Preliminary Study Methodology	61
APPENDIX B: Soil Field Capacity Estimates.....	63
APPENDIX C: Biophysical Data Plots	66
APPENDIX D: Site Field Data Tables	75

LIST OF TABLES

Table	Page
1. Potential evapotranspiration water balance model modifiers	20
2. Actual evapotranspiration water balance model modifiers.....	21
3. Description of predictor variables used in models.....	22
4. Statistics from the top models of individual growth rate.....	34
5. Statistics from the top models of site density ratio change.....	37

LIST OF FIGURES

Figure	Page
1. GYE WBP Mortality Map	2
2. Primary Productivity, AET, Precipitation, and Temperature	6
3. Hierarchical Sampling Design	11
4. Planting Unit Locations Map	13
5. Electronic Data Form	14
6. ESRI Survey123 Site Example Map	14
7. Shading Software Image	18
8. Mean Annual Temperature for all Units	24
9. Mean Annual Precipitation for all Units	25
10. Mean Annual Potential Evapotranspiration for all Units	25
11. Mean Annual Actual Evapotranspiration for all Units	26
12. Mean Annual Growing Season Water Deficit for all Units	27
13. Mean Annual Climograms for all Units	28
14. Mean Number of Competitors for all Units	29
15. Individual Growth Rates for all Units	30
16. Individual Growth Rates for all Sites	31
17. Individual Growth Rate Top Model Effects	32
18. Site Density Change Ratio for all Units	33
19. Site Density Change Ratio for all Sites	34
20. Site Density Change Ratio Top Model Effects	37

LIST OF FIGURE CONTINUED

Figure	Page
21. Blister Rust “Cankers”	38

ABSTRACT

The efficacy of planting efforts for species of conservation interest is important for ecosystem managers. Planting efforts represent an opportunity to conserve and manage species during a population crisis. Although federal agencies have been planting whitebark pine (WBP) in the Greater Yellowstone Ecosystem (GYE) for three decades, these efforts have been met with varying success. In this study, we use a combination of field sampling and remote sensing approaches in order to investigate local biophysical gradients as explanatory variables for WBP performance in GYE planting units. Present-day field sampling affords an opportunity to evaluate WBP performance relative to earlier planting and monitoring records. We used remotely-sensed temperature and precipitation alongside field measurements of elevation, aspect, slope, shading, and soils to utilize an adapted Thornthwaite-type water balance model to explain individual growth rates and site density change ratios (essentially survival and natural recruitment). We found that planting sites varied greatly in their biophysical characteristics and WBP performance. Five of twenty-nine sites had higher present-day density than at date of planting, therefore indicating some amount of natural regeneration occurring within those sites since time of planting. These sites were often higher in elevation, not south or southwest facing, and had soils that could hold moisture later in the season and for longer periods following precipitation events. Sites that experienced reductions in the density of WBP were often lower in elevation, with poorer soils, and facing south or southwest. They therefore experience greater potential evapotranspiration, and also greater water deficit when water demands are not being met. Notably, our two response variables, individual growth rate and site density change ratio represent short and long-term performance variables respectively. Although our results suggest that individual growth rates are likely more often limited by energy than water demands, the site density change ratio associated with this late to mature, long-lived species is likely a better benchmark for success. If they make it to maturity, trees planted this season will not begin to produce cones until the end of this century or the beginning of the next. Therefore, they must overcome forecasted periods of greater water stress in the coming decades and centuries. We strongly recommend planting efforts that seek to reduce the effects of increased drought stress by planting at sites with soils of greater water holding capacities (non-rhyolitic), planting on northerly and easterly aspects, and utilizing microsites particularly when planting at sites with potentially higher water stress. We also detected a negative relationship between the density of local competitors and WBP performance, but only at higher densities. Ecosystem managers will continue to plant WBP in the GYE for years to come, and this research helps to inform and identify high quality habitat during a period of changing climate and high GYE WBP mortality rates.

BIOPHYSICAL GRADIENTS AND PERFORMANCE OF WHITEBARK PINE PLANTINGS IN THE GREATER YELLOWSTONE ECOSYSTEM

Introduction

The Greater Yellowstone Ecosystem (GYE) is often considered the largest remaining, nearly-intact ecosystem in the contiguous United States (Wenk 2016). Whitebark pine (*Pinus albicaulis*; WBP) is widely recognized as a keystone and foundation species in the high country of the GYE, and over half of the aerial extent of WBP in the United States is found there (Hansen et al. 2016). Notably, nearly half of the GYE WBP distribution has exhibited severe mortality in recent years (Macfarlane et al. 2013; Figure 1) due to climate warming and the associated implications for pest outbreaks and an introduced pathogen (Logan et al. 2010, Bockino and Tinker 2012). A recent analysis indicates that 51% of all standing WBP (>22.8cm diameter breast height) in the US are dead (Goeking and Izlar 2017). Grizzly bears (*Ursus arctos horribilis*) are federally listed as threatened under the Endangered Species Act (ESA) in large part due to impact from the loss of WBP seeds which represent an important food source (Costello et al. 2014). Threats to WBP are imminent, of high magnitude, and thus the species warrants protection under the ESA (USFWS 2011). Indeed, the species has been a candidate for listing since 2011. Additionally, the Committee on the Status of Endangered Wildlife in Canada and the International Union for Conservation of Nature lists the status of WBP as “Endangered.”

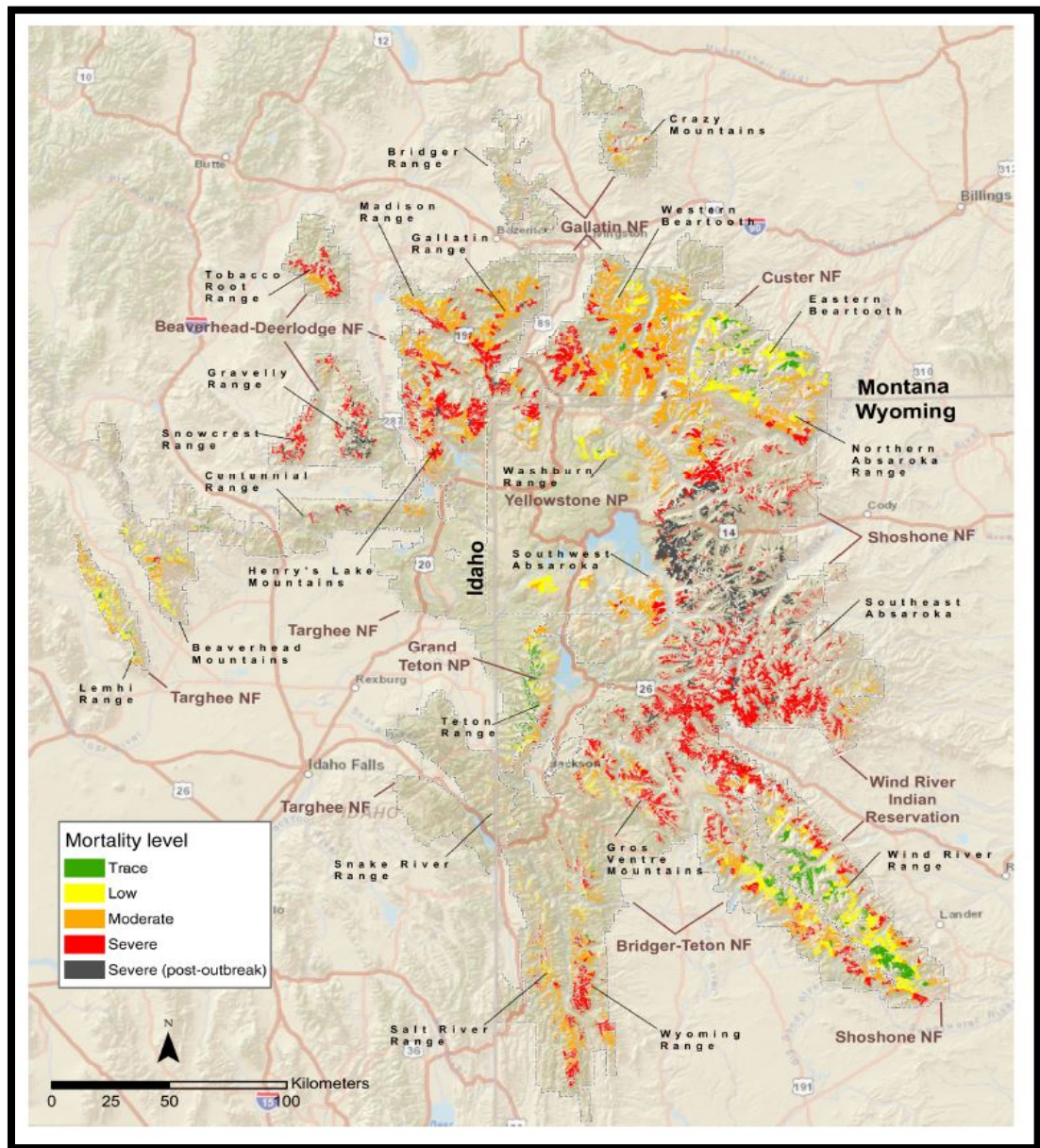


Figure 1. Whitebark pine mortality levels throughout the GYE (Macfarlane et al. 2013).

Climate warming has been associated with loss of taxa that formerly were restricted to high elevations, and research shows that in high altitude and latitude regions the climate is changing more rapidly than elsewhere (IPCC 2014). Since the early 21st century, mountain pine beetle (*Dendroctonus ponderosae*) outbreaks have been the

primary cause of mortality of WBP in the GYE (Buotte et al. 2016). Higher temperatures and drier conditions associated with climate change likely drive the major threats to WBP (Tomback et al. 2016, Logan et al. 2010, Jewett et al. 2011), and refugia represent an ecological mechanism by which WBP may remain viable under climate change (Hansen et al. 2016). Climate change refugia are areas relatively buffered from regional contemporary climate change that enable the persistence of species and functions through maintenance of biophysical processes, such as snow retention, soil moisture retention and evapotranspiration (Dobrowski 2011, Morelli et al. 2016). Identification of past and future refugia is important in the management of anthropogenic climate change impacts, and developing methodologies for their identification and description is a high research priority (Hansen et al. 2016, Keppel et al. 2012). Notably, other terrestrial populations have shown that for some species refugia can support enough individuals to eventually re-colonize earlier areas of loss (Frouz and Kindlmann 2001). Researchers believe that colder microclimates correspond to locations of potential GYE WBP refugia (Macfarlane et al. 2013). Environmental models that acknowledge local topographic effects on climate (Dobrowski 2011) are of interest because of their biological effects. Modern conservation planting efforts represent a synergistic intersection between refugia and the long-term viability of artificially planted seedlings.

As part of a strategy to conserve species, the United States Department of Agriculture's Forest Service – Northern Region incorporates climate change adaptation strategies into management actions based on the vulnerability of resources to climate change (Scott et al. 2011). WBP has been identified as the most vulnerable tree species in

its range to climate change (Hansen and Phillips 2014), and future climate change is projected to reduce habitat suitability dramatically (Chang et al. 2014). Additionally, WBP is slow to reach maturity and can live for more than 750 years (Luckman et al. 1984). Effects of climate influence life-history processes such as growth and seedling establishment well before noticeable biogeographic range shifts occur (Littell et al. 2008). Well-structured and studied planting efforts provide opportunities to learn about the climate drivers that influence species' tolerable biophysical range and realized niche. Therefore, it is important to consider future climate when evaluating management treatments, such as where to plant seedlings (Buermeyer et al. 2016, Hansen et al. 2016).

Seasonal snowpack in forested lands is the primary source of fresh water in western North America (Biederman et al. 2012), but snowpack is declining in the GYE and across the West (Hall et al. 2012, Pederson et al. 2011; Tercek et al. 2015). Although healthy coniferous forests tend to reduce under-canopy snow depth, they also greatly reduce melt rates, which leads to more water being available later in the growing season (Musselman et al. 2008). Historically, the GYE has supported a late-season snowpack that supplies water for agriculturalists and recreationalists, but this trend has been changing in recent decades (Tercek et al. 2015). Stakeholders in the GYE are concerned with water, or lack thereof, during this time of the year. For instance, low flows and high water temperatures are contributing factors to major fish kills and subsequent closures on the Yellowstone River (MTFWP 2016). It is important to note that in addition to Yellowstone River headwaters, there are also significant portions of the Snake and Green

River headwaters in the GYE. Declining snowpack and earlier snowmelt is likely affecting water availability for our agricultural systems (Backlund et al. 2008).

A number of ecosystem services are provided by pine forests such as delaying snowmelt and spring runoff (Tomback et al. 2016, Tomback et al. 2014, Farnes 1990). Although some GYE WBP are likely water stressed by late summer and fall similar to WBP in other areas of the West (Millar et al. 2012), this has not been well-studied (Shanahan et al. 2016). Water stressed individuals are likely to be more vulnerable to attacks from mountain pine beetle (Raffa et al. 2008). Notably, the likelihood of WBP mortality due to mountain pine beetle is directly related to water deficit (Shanahan et al. 2016). Water deficit can be estimated using water balance models that account for input and output of water from soil, thus estimating the water available to plants during the growing season. Significantly, depending upon the species, conifers exhibit different responses to water-stress.

Indeed, WBP has been shown to be less resistant to water-stress induced cavitation than its shade-tolerant competitor, subalpine fir (*Abies lasiocarpa*), although it is often found in drier sites at similar elevations (Pinol and Sala 2000). In this regard, there appears to be a trade-off between xylem conductance and cavitation, and WBP likely has greater stomatal control of water and lower leaf to sapwood ratios (Sala et al. 2001) in order to compensate for this vulnerability. Indeed, this appears to fit within WBP's generally long-lived and slow-growing life history strategy, but also indicates that it can be susceptible to periods of water stress. Water stress in plants can be predicted by periods of local water deficit (Stephenson 1998). Conversely, growth occurs when water

is available and energy is sufficient to move water from soil through a plant to the atmosphere. When stomata are open, carbon dioxide is captured and incorporated into structural components via photosynthesis, and water is lost to the atmosphere.

Actual evapotranspiration (AET) occurs when potential evapotranspiration (PET) is being met with adequate liquid water supply. That is, plants have access to biologically-relevant water during the growing season, and soils have not dried out. Water deficit (WD) occurs when water supply does not meet the demands of PET ($WD = PET - AET$). For a plant to utilize external energy or available water, both must be in local supply at the same time (Stephenson 1998). Younger plants, with shallower root systems, experience water deficit more readily given their inability to access water reserves deeper in the soil. Fortunately, spatio-temporal estimates of water balance are possible by integrating soil properties, slope, aspect, and precipitation alongside potential evapotranspiration. Importantly, although plant growth response to temperature and precipitation is elevation dependent (high elevations are generally temperature-limited whereas low-elevations are water-limited), the relationship between plant growth response and AET is always positive (Figure 2; Herrmann et al. 2016).

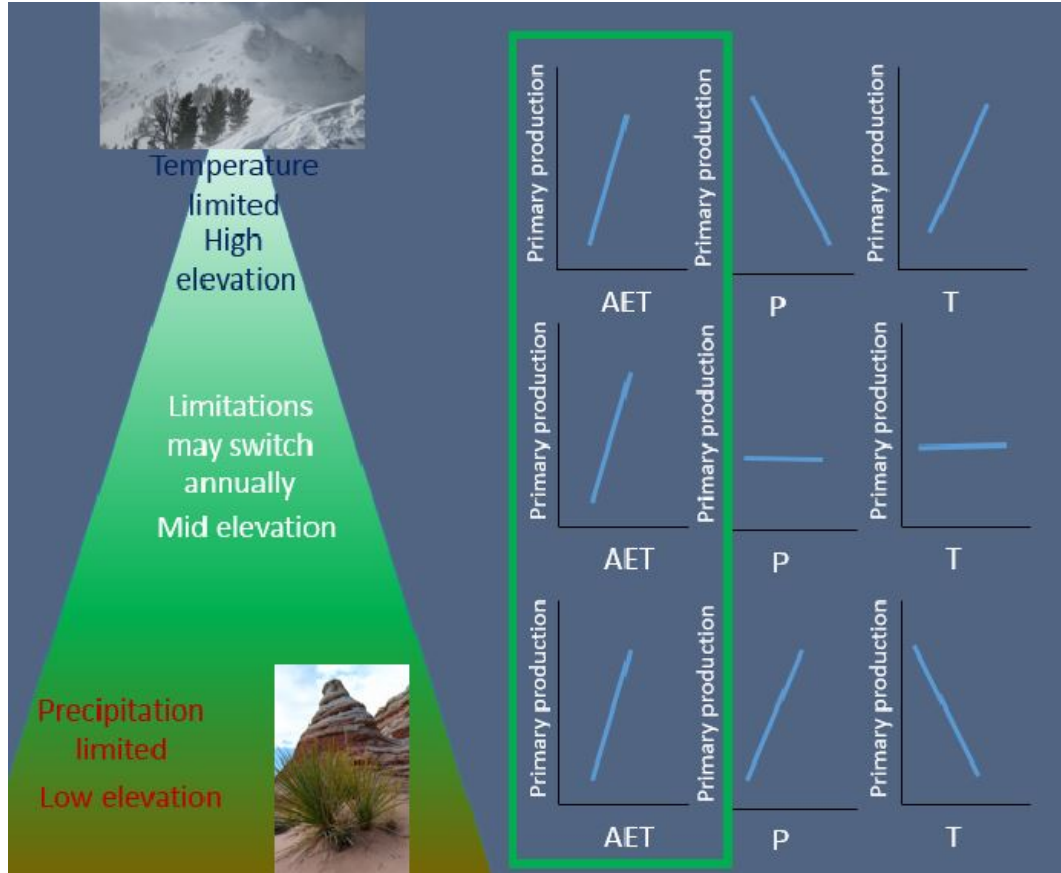


Figure 2. Relationships between Primary Productivity and AET, Precipitation, and Temperature across elevations (created by Dr. David Thoma; adapted from Herrmann et al. 2016).

Currently, as indicated by stake row surveys conducted within WBP planting sites in the Northern Region, there is a large disparity in survival rates. From 1998 to 2015, average first year survival ranged from about 79% to 98%, but average third year survival ranged from 41% to 92% (Milburn 2016). This large difference in survival rates suggests that it would be prudent to closely monitor planting sites into the future in order to get a better understanding of the variables related to the success or failure of the Forest Service's investment into each planting effort. As Scott et al. (2011) note, "the practice of growing and planting whitebark pine is relatively new compared to traditional conifers,

and with the high cost of cone collection and seedling production, survival is particularly important.”

Additionally, there are conflicting reports related to WBP tolerances. For example, federal managers recently stated that “observations of whitebark pine within other habitats demonstrate the adaptive capacity of whitebark pine to disperse and compete beyond what has been depicted in existing whitebark pine distribution maps. Localized site conditions, stand structures relatively free of competition, and potential genetic tree characteristics on low-elevation and mid-elevation sites that are currently mapped as “unsuitable” for whitebark pine in species distribution models could provide valuable information on where and how to manage and restore whitebark pine as suitable habitat changes in light of potential climate scenarios (Buermeyer et al. 2016). Thus, it is critical to quantify the range of conditions associated with survival of WBP in the GYE. In this long-lived species, the seedling life stage is likely the most sensitive to environmental factors (Jackson et al. 2009). The locations of GYE planting sites are generally consistent with the WBP planting guidelines Scott et al. (2011), and it is not currently known how the range of climate and soil conditions in these planting sites relates to water availability and species tolerance. Notably, asymmetric shifts in species distribution is anticipated with changing climate (Ettinger and HilleRisLander 2017). The drop in survival rates between years one and three suggest that some microsites within these planting sites exceed the tolerances of WBP seedlings. Thus, microsite-scale analysis of the correlates of WBP seedling survival is an opportunity to leverage spatial

variability within planting sites as a means to understand conditions conducive to survival and establishment.

In addition to abiotic controls, biotic factors such as competition affect WBP survivorship. Competition has an inverse relationship with WBP performance (Keane and Parsons 2010), particularly so in the GYE given that the ecosystem represents the species' southern range of its distribution (Loehle 1998). Planting efforts take advantage of post-burn habitat by establishing viable WBP saplings prior to site occupation by potential competitors. However, as vegetation begins to naturally re-establish at these sites, competition will likely develop between slower growing WBP and faster growing conifer species. With this in mind, although early stage monitoring efforts (1 – 5 years post-planting) may not indicate that competition affects young WBP, our monitoring efforts (>5 years post-planting) may begin to detect the early effects of competition. Potential coniferous competitors are lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and Engelmann's spruce (*Picea engelmannii*). We will also investigate the presence of an exotic pathogen, white pine blister rust (*Cronartium ribicola*), which to our knowledge, has not been documented in GYE WBP planting sites. The rust was introduced to North America in 1910, and has likely surpassed mountain pine beetle as a more probable cause for mortality and damage to GYE WBP, particularly those of smaller size classes (Shanahan et al. 2016).

This study builds upon understanding the fundamental niche (Chang et al. 2014) of GYE WBP by investigating biophysical conditions that affect seedling and sapling survival that in part determine the realized niche (where trees actually grow due to

competition, climate, and site factors). Our investigation will address this need and lay the basis for additional research and planting experiments that span the broader range of biophysical conditions necessary to more clearly identify WBP's niche in the GYE.

Our driving question is *to what extent do local biophysical gradients affect GYE WBP performance as represented at established planting locations?* In order to explore the answer to this question and inform future management efforts we used:

- 1) fine resolution (individual tree scale) field data alongside coarse resolution (1km) remotely sensed data to inform a recently developed water balance model as a predictor of pine performance since time of planting
- 2) field research in order to quantify the effects of potential competition

Methods

Study Area

The GYE is approximately 25 million acres of land that includes 2 national parks, 7 national forests, 2 national wildlife refuges, 2 tribal reservations and a number of state and privately managed lands. Over the past four decades, the United States Forest Service and the National Park Service have established approximately 1,500 acres of planted WBP in the GYE. In 2017, a collection of regional federal managers (Greater Yellowstone Coordinating Committee - Whitebark Pine Subcommittee) facilitated the transfer of planting and monitoring records from sites that were established prior to 2012 to Montana State University. There are five planting units identified for use in this study with each containing between two and eight planting sites. There are 29 planting sites in

total, and hundreds or thousands of WBP saplings planted at each site (Figure 3). The planting sites are grouped in areas that were disturbed by fire in the year or two prior to planting.

Physical Gradients. Results from a preliminary study by the author (unpublished) indicated that planting units are physically heterogeneous, and are within the tolerable range of WBP as indicated by earlier research (Weaver and Dale 1974), and the presence of living trees nearby. The study followed a replicable formula for analysis in ArcGIS (see Appendix A).

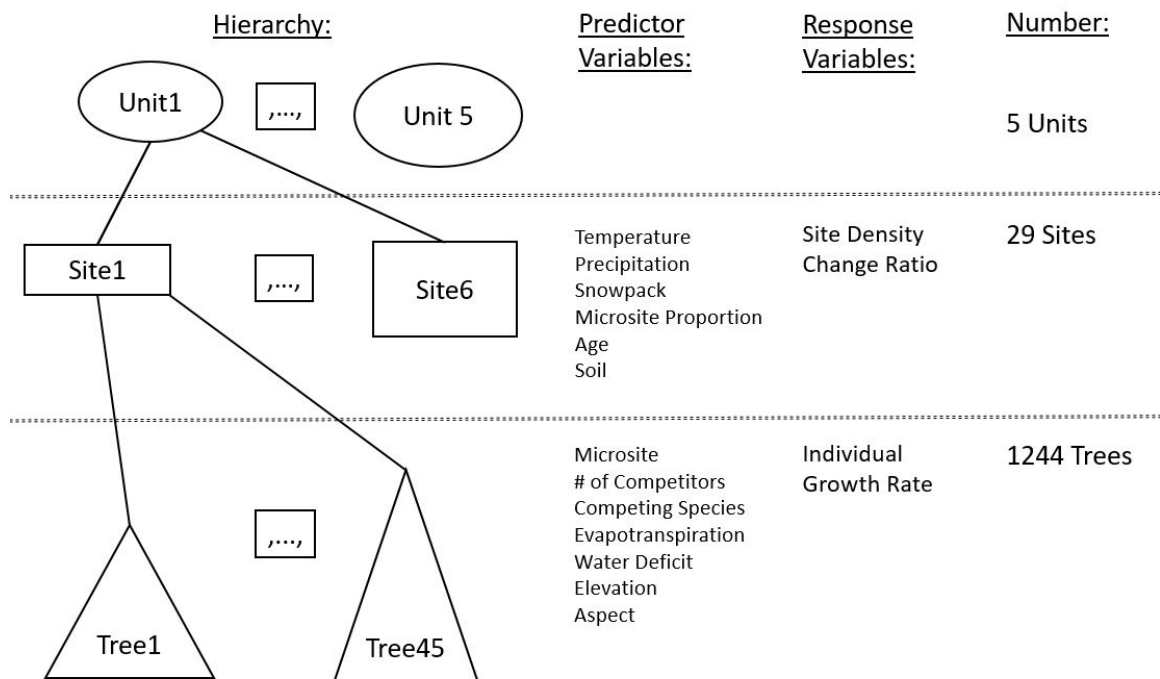


Figure 3. Hierarchical study design, modelled variables, and sample sizes.

The planting units are located near Union Pass in the Wind River Range (USFS Wind River Ranger District), Taylor's Peak in the Centennial Range (USFS Ashton/Island Park Ranger District), Tabletop Mountain in the Centennial Range (USFS

Ashton/Island Park Ranger District), Big Springs south of West Yellowstone (USFS Ashton/Island Park Ranger District), and Daisy Pass in the Beartooth Range (USFS Gardiner Ranger District; Figure 4).

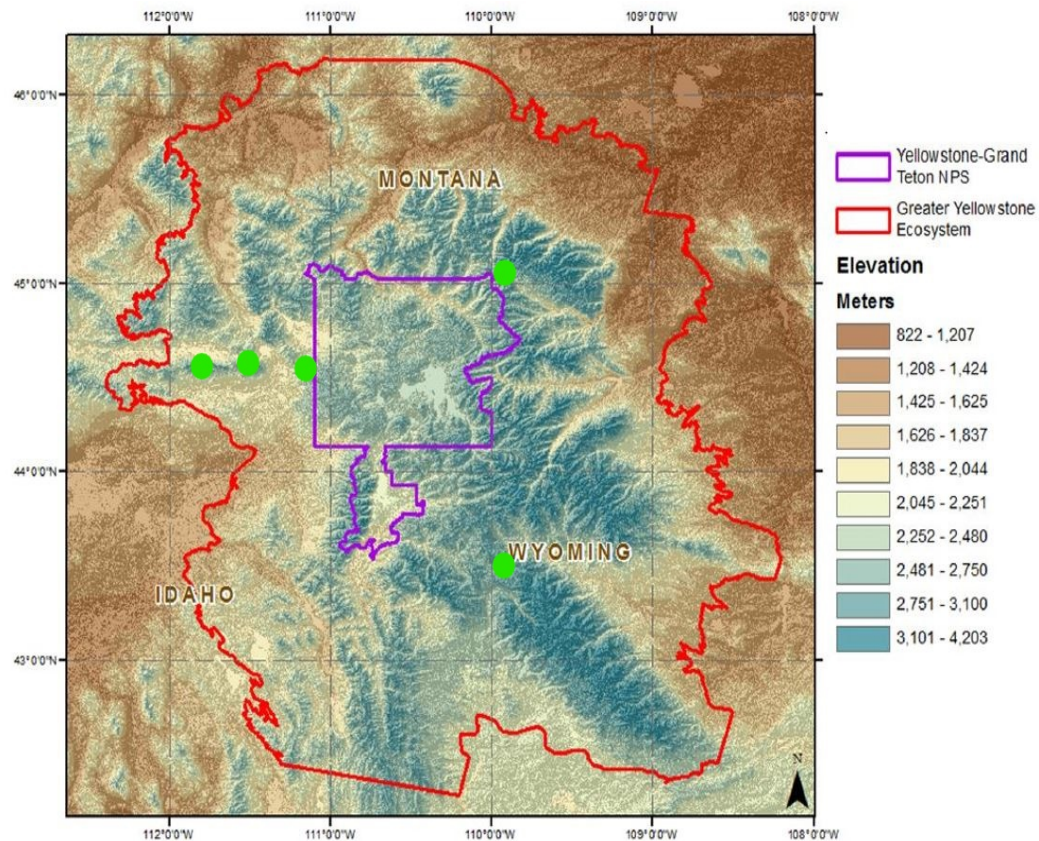


Figure 4. Greater Yellowstone Ecosystem with whitebark pine planting units (green dots) and Yellowstone and Grand Tetons national park boundaries (adapted from Chang et al. 2014).

Sampling Design

Sites were sampled from May 2018 to October 2018 using a random, systematic matrix of 10m X 10m grids. Planting sites ranged from 1.01 to 57.27 acres. Depending upon size and biophysical heterogeneity, 2% to 15% of each site was sampled.

Heterogeneity was assessed in the field, and sampling intensity depended upon the

variability of aspect, slope, microsites, and the number and species of competitors at the site. In general, larger sites had proportionately less sampled than smaller sites. Each WBP within every grid was digitally, spatially tagged (Bad Elf Pro GPS ensuring +/- 3.5m resolution). A digital survey form was designed by D. Laufenberg (Figure 5), and Esri's Survey123 software was used to collect field data of interest at each WBP, and the gridded sampling matrix was visually inspected in the field to ensure that each site was evenly sampled (Figure 6).

Date:
Sunday, March 24, 2019

Unit: *
☐ Beartooths (1)
☐ Washburn (2)
☐ West Yellowstone (3)
☐ East Centennials (4)
☐ West Centennials (5)
☐ Winds (6)

Site: *

Grid: *

Tree: *

Lat/Lon: *

No location
Position source closed error

Press to capture location using a map

▼ WBP Performance *

WBP Height: *

DBH: *

Condition: *
☐ Satisfactory
☐ Unsatisfactory
☐ Dead

Sample Collected? *
☐ Yes
☐ No

Blister Rust? *
☐ Yes
☐ No

▼ WBP Environs *

Slope: *
☐ 0 ☐ 5 ☐ 10 ☐ 15 ☐ 20 ☐ 25 ☐ 30 ☐ 35

Aspect: *
☐ N ☐ NE ☐ E ☐ SE ☐ S ☐ SW ☐ W ☐ NW ☐ Flat

Shading %: *

Microsite:
☐ Yes
☐ No

Ground Cover %:
☐ 0 ☐ 10 ☐ 20 ☐ 30 ☐ 40 ☐ 50 ☐ 60 ☐ 70 ☐ 80 ☐ 90 ☐ 100

Competition:
☐ Yes
☐ No

Soil Type:
☐ Sand ☐ Loamy sand ☐ Sandy loam ☐ Loam ☐ Silt loam ☐ Sandy Clay Loam ☐ Sandy Clay ☐ Clay loam ☐ Silty clay loam ☐ Silty Clay

Rock Content %:
☐ 0 ☐ 10 ☐ 20 ☐ 30 ☐ 40 ☐ 50 ☐ 60 ☐ 70 ☐ 80 ☐ 90 ☐ 100

Notes:

Image:

Figure 5. Digital data form developed for this study using Esri's Survey123 software.

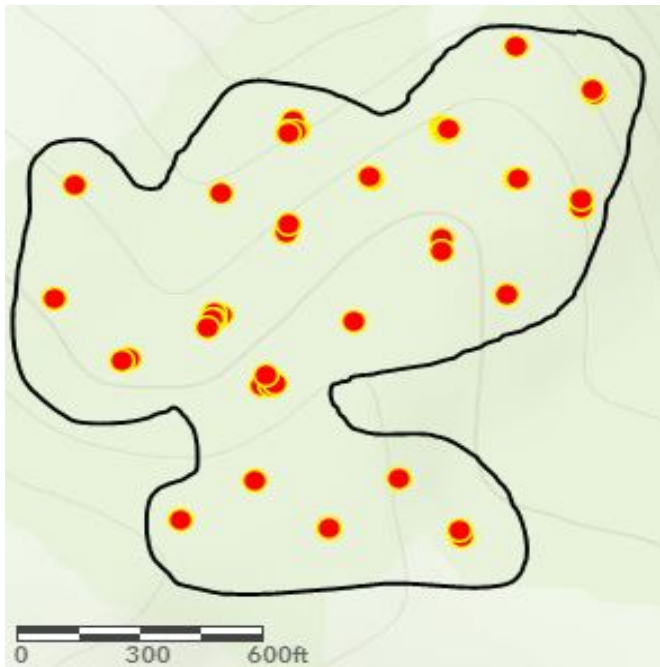


Figure 6. Example of random, systematic sampling at West Centennials Planting Unit, Site 6. Each red dot is either a sampled WBP within a 10m X 10m grid, or the center of a grid without a WBP.

Historic Data

Initial planting records were obtained from the forest districts with known WBP planting efforts and records prior to 2012. Sites that were planted in the 1990s and early 2000s were digitized from paper records, and recent sites were shape files with associated planting data. Estimated number of seedlings planted was divided by the estimated planting site area in order to calculate the initial WBP density at each site. Personal communication with managers indicated that seedlings were 15.24cm (6 inches) on average at time of planting.

Field Data

Whitebark Pine Performance. We collected WBP performance data at each site using methodology adapted from the USDA Forest Service. We documented the location and number of each living WBP, and its height (cm) within all sampled grids. Height was measured from the base of the tree to its highest point using a Biltmore Stick. Individual annual growth rates were estimated by the change in present-day height relative to planted height divided by the years since planting. This height was subtracted from heights collected in the field at time of study. Additionally, 2.5 years were subtracted from the years since planting to account for the establishment period whereby young seedlings are investing sequestered carbon and reserves into root instead of shoot growth.

$$\text{Growth Rate} = (\text{Present Height} - \text{Planting Height}) / \text{Adjusted Age}$$

Given that we measured the height of above-ground biomass, we did not want to penalize younger age planting sites where the establishment period represents a larger proportion of their years since planting.

Additionally, the WBP density change ratio at each site was determined by dividing the estimated present-day WBP density by the initial WBP planting density. We estimated current WBP site density by using the mean density of our sampled grids at each site. Many of the planting records needed to be digitally mapped in order to ensure an accurate measure of planting site area and therefore initial planting density.

Finally, a binomial of each individual's condition, either satisfactory or unsatisfactory, was recorded per USDA Forest Service protocol. A satisfactory individual had an intact apical meristem (or broken, but with significant regrowth characteristic of "candelabra" WBP growth forms impacted by snow), a full crown of leaves, and at least 2/3 of its leaves were green.

Competition. Per USDA Forest Service protocol, a 1/100th acre (circular plot with 3.59m radius) survey of the species, number, and mean height of conifers greater than 50cm height near each sapling was conducted in order to characterize potential competition within and among species.

It is possible that another pine, limber pine (*Pinus flexilis*), is present within the planting sites given the overlap in geographic range between the two species. Unfortunately, without seed or pollen cones it is impossible to distinguish one species from the other in the field, and our individuals were too young to have cones. However, it is likely that the vast majority of 5-needled individuals at our sites are WBP given that

they are at the upper-end of the elevational range of limber pine, and mature limber pine was not detected in the vicinity of any of the planting units.

Microsite. The presence or absence of a microsite was documented for each individual. A microsite was considered present when there was an object (rock or stump) of at least 5cm width and 10cm height within 20cm of the WBP.

Aspect and Slope. We could not find access to LiDAR for our study area, and although 30m spatial resolution Digital Elevation Maps (DEMs) exist, we wanted to characterize the habitat of each tree at a finer spatial resolution. For this reason, we also collected aspect (0°, 45°, 90°, 135°, 180°, 225°, 270°, 315°, or flat) and slope (0°, 5°, 10°, 15°, 20°, or 25°) at each WBP using a compass (11.5° E declination) and an inclinometer.

Soil Field Capacity. Soil field capacity, or water holding capacity, is the amount of water soil can hold after it drains freely from a saturated state by gravity alone. Estimates of planting site soil texture and rock content informed a categorical estimate of soil field capacity. Mean rooting depth (8inches or 203.2mm; discussions with US Forest Service managers) at the time of planting was used to estimate field capacity. We estimated coarse volume of soil occupied by rock (boulders, cobbles, stones >2mm diameter) that reduce water holding capacity of soil. Surface expression of rocks is generally a good indicator of subsurface rock fragment content in well-mixed colluvial soils. In depositional environments like toe slopes, large rock fragments are less common and would have minimal effect on soil field capacity. We looked for tree throws, burrows, and other natural disturbance like gullies that may indicate presence of below

surface rock fragments in and near stands to confirm estimates of rock fragment content from surface visual estimates. Estimating soil field capacity this way allowed us to estimate conditions deeper than we could dig in rocky environments (common in whitebark pine habitat). Combining estimates of surface and subsurface rock fragments we made a visual estimate of coarse fragment content in the soil. Soil texture was estimated using a texture-by-feel method field test of soil ribbon length and grittiness to determine textural class from a textural triangle of sand, silt, and clay fractions (Appendix B).

Shading. Shading at the individual-level was estimated by using photography software (CanopyApp), a smartphone (Apple iPhone 5s) and wide-angle lens attachment (AMIR for iPhone 0.4X Wide Angle Lens). Results from this method have been shown as an improvement to traditional methods such as a spherical densiometer (Davis et al. 2018). A photo was taken from a position 1.37m south and 1.37m (same as Diameter Breast Height forestry standard) above ground height of each WBP to quantify the percent of shading, and therefore reduction in energy received (Figure 7).



Figure 7. Example of CanopyApp software used for shading estimates at the individual pine level. Photo on the right includes the software’s generated mask (pink). This particular tree experienced 14.2% shading.

Blister Rust. Each tree was inspected for the presence of blister rust. Although “weeping” and squirrel gnawing can be indicative of blister rust in older trees, we also looked for fruiting bodies or “cankers” of the fungus on the bole and branches of sampled trees.

Remotely Sensed Data

Daymet. We utilized 1km gridded, daily temperature and precipitation data from the 1980 – 2017 Daymet dataset. Although an artificial warming trend has been detected in this dataset post-2000 (Oyler et al. 2015), it is amplified greatest at elevations higher than those at our study sites. Additionally, we required a dataset that included data for the year 2017. An alternative, TopoWx, does not yet provide 2017 data.

Water Balance Model

We used a Thornthwaite-type water balance model developed and coded by Dr. David Thoma that is based on pre-existing concepts and methods by Allen et al. (2006),

Zotarelli et al. (2013), Lutz et al. (2010), and Dilts et al. (2015). The model estimates daily, monthly, and annual cumulative growing degree days, potential and actual evapotranspiration, soil moisture, and water deficit as described by Stephenson (1990), and was used to analyze the relationships between water availability, use, and need with WBP performance. Our Thornthwaite-type water balance model computes water balance metrics at hundreds of locations using remotely sensed temperature and precipitation. Importantly, the base model was modified to mediate the effect of temperature and precipitation by accounting for heat load at the individual tree scale (Table 1). It uses the Penman-Monteith equations for potential evapotranspiration (PET) which is largely influenced by temperature, solar radiation, humidity and wind.

<u>Water Balance Driver</u>	<u>Relationship (+ / -) with PET</u>
Temperature (°C)	+
Elevation (m)	-
Aspect (°)	+ / - (45° is the lowest, 225° is the highest)
Shading (%)	-
Slope (°)	+ / - (minor impact, and dependent upon aspect)

Table 1. Potential evapotranspiration water balance model modifiers.

In order to calculate and distinguish between periods of accumulating WD and AET (recall that $PET = AET + WD$), the model is then further modified by varying water storage capacity due to soil texture and coarse fragment content (Table 2).

<u>Water Balance Driver</u>	<u>Relationship (+ / -) with AET</u>
Soil Texture (% of sand, silt, and clay)	+ / - (dependent upon textural triangle)
Coarse Fragment (%)	-
Temperature (°C)	+ / - (dependent upon elevation)
Precipitation (mm)	+ / - (dependent upon elevation)

Table 2. Actual evapotranspiration water balance model modifiers.

Relationships that focused on growing season were explored given that saplings are completely covered by snowpack during the winter months. Daily temperature and precipitation from Daymet are used in the model. Aspect (0°, 45°, 90°, 135°, 180°, 225°, 270°, 315°, or flat) and slope (0°, 5°, 10°, 15°, 20°, or 25°) was collected at each WBP using a compass and an inclinometer. Notably, digital elevation maps of the sites could not be obtained at greater than 30m spatial resolution, and we were interested at water balance effects at the individual-level. Growing degree days were modelled per McMaster (1997) and Lind (2017) with a temperature base of 5°C to represent biologically relevant temperatures.

Predictor Variables

We used the water balance model to generate estimates of PET, AET, WD, growing degree days, snowpack, and rain associated with each tree that was sampled in the field (Table 3). Instead of annual estimates that would include data during months of the year when WBP saplings are covered by snow, we focused on effects during the growing season across all sites and years (April – October.) Annual and monthly mean and maximum WD were also calculated for years post-planting. By calculating the

maximum monthly WD experienced by a tree in any month since planting, we are capturing intense, short-term drought conditions that could lead to mortality. We were also interested in WD during the seedlings' establishment period as this is considered to be a period of greater susceptibility to water stress. For this reason, we extracted WD for the year pre-planting, year of planting, and the two years post-planting. Alongside fixed effects of PET, AET, and WD, we also investigated models that included WBP performance (individual growth rate and site density change ratio) as a function of the number of local competitors, competing coniferous species, age of the planting site, and microsite presence/absence. Models were assessed through use of the corrected Akaike Information Criterion for finite sample sizes (AICc; Zuur 2009). We tested for collinearity between variables with a cutoff of 0.6. Statistical software "R" was used for all statistical analyses, and mixed-effects modelling efforts used the "lme4" package.

Predictor Variable	Definition
Age	Years since planting
T	Mean annual temperature
T _{max}	Maximum monthly temperature
PPT	Mean annual precipitation
Snowpack	Maximum spring (March – May) snowpack
Rain	Mean spring (March – May) rain
WD _{establishment_max}	Maximum monthly water deficit during planting establishment period (4 years; 1 year prior through 2 years post-planting)
WD _{annual_mean}	Mean cumulative annual water deficit (April – October)
WD _{annual_max}	Maximum annual water deficit (April – October)
WD _{month_mean}	Mean monthly water deficit
WD _{month_max}	Maximum monthly water deficit
PET	Mean potential evapotranspiration (April – October)
AET	Mean actual evapotranspiration (April – October)
GDD	Annual cumulative growing degree days (April – October)
Comp_number	Number of conifers within 3.59m radius of WBP individual

PIEN	<i>Pinus engalmanii</i> within 3.59m radius of WBP individual
ABLA	<i>Abies lasiocarpa</i> within 3.59m radius of WBP individual
PICO	<i>Pinus contorta</i> within 3.59m radius of WBP individual
Micro	Microsite presence or absence at the individual-level
Micro _{prop}	Proportion of WBP with a microsite at the site-level

Table 3. Predictor variables and their definitions for use in mixed effects models.

Mixed Effects Models

In order to identify the best models for explaining WBP performance, we compared multiple mixed effects models using various fixed effects, interactions, linear and polynomial functions, and variance structures (Zuur et al. 2009). I will address our two suites of models separately.

Individual Growth Rate. After plotting residuals of our first response variable, individual growth rate, results indicated that a transformation would likely help normalize the distribution. Indeed, a natural log transformation produced a residuals plot that did not violate normality, and still provides for interpretation. Quantile – quantile (QQ) plots indicate a slight-left skew of our data. We attempted to incorporate random slope models as well, but the data did not have the richness necessary to fit random slope models. By including random effects for site and unit, we also accounted for the spatial autocorrelation of our data.

We had a predictor variable correlation cutoff of 0.6. We had to decide whether to include “Age” or “Number of Competitors” (0.64). We chose to include the number of competitors for two reasons. One, our objectives include investigating the effect of competition on WBP performance. Two, age is a single number for each planting site. Therefore, it is already largely accounted for in our random effect for site. We could not

include PET and WD in the same model (0.92). For our growth response, we decided to use PET in our full model because it provided a slightly better fit than WD. Precipitation, rain, and snow were correlated above 0.87, so we chose precipitation to capture solid and liquid water input events. Annual GDD and temperature were highly correlated (0.99). We used temperature because it does not have various methods of calculation, as opposed to GDD which does, but is often not reported in publications. An interaction between temperature and precipitation was explored, but the Variance Inflation Factor indicated that this was not prudent ($VIF = 19.3$). This is not surprising given that the 1km grids are often unchanged within and sometimes between small sites that are close to one another.

Site Density Change Ratio. Similar to growth rate, density change ratio also needed a natural log transformation. Given that our response is at the site-level, we removed the mixed effect for site. In order to characterize our sites we aggregated the water balance output of interest to use as explanatory variables. To do this, we took the mean of each variable grouped by site. Again, we had to choose between PET and WD in our full model, but this time we used WD given that it represents times of water stress and potential death of an individual and therefore impact on the site density change ratio. Temperature and precipitation could not be used for this site-level analysis because they each led to a “singular fit” error. I believe this is because the 1km dataset yielded the same temperature and precipitation in three cases. Essentially, this reduces the site-level dataset’s sample size, which is already small ($n = 29$). The site-level proportion of species of competitors, number of competitors, and microsite presence or absence were generated as continuous variables for analysis.

Results

Variation in Biophysical Gradients

Biophysical gradients varied across sites and units (Appendix C). Mean annual temperature was one of the predictor variables of interest, and the mean across units ranged from 1.41°C to 3.22°C (Figure 8) since year of planting (1991 is the oldest site and 2012 is the youngest site).

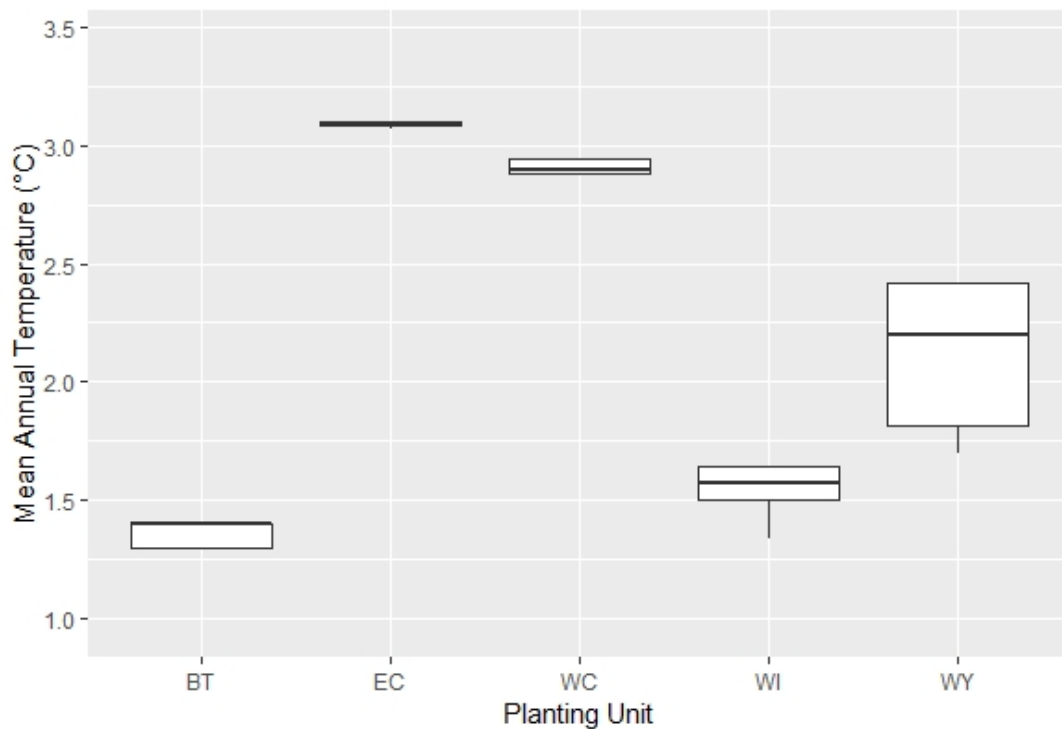


Figure 8. Mean annual temperatures for all units (BT = Beartooth, EC = East Centennial, WC = West Centennial, WI = Wind River, WY = West Yellowstone).

Annual precipitation across units ranged from 595mm at the Wind River Planting Unit to 1082mm at the West Yellowstone Planting Unit (Figure 9).

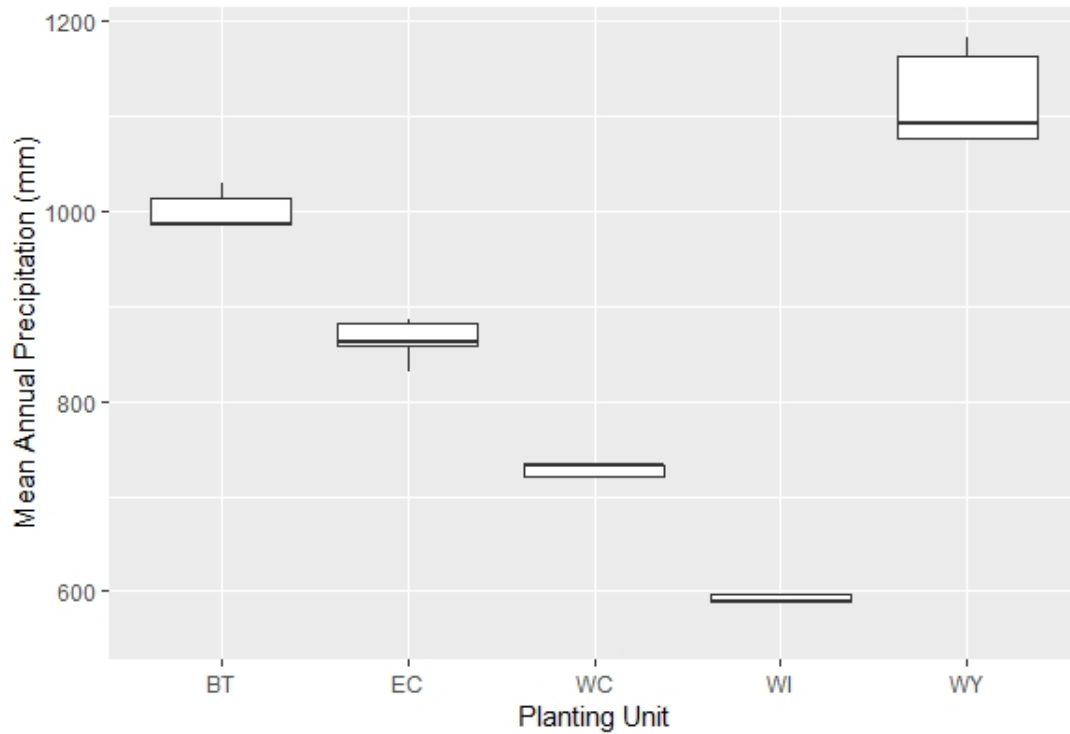


Figure 9. Mean annual precipitation for all units.

Mean growing season potential evapotranspiration (PET) did not exhibit the amount of variation as temperature and precipitation, but there were differences between units. The West Centennial Planting Unit had the lowest mean PET (630mm) and the West Yellowstone Planting Unit had the highest (885mm; Figure 10). Recall that in addition to temperature, our estimates consider the effects of shading, aspect, slope, latitude, elevation, and wind (held constant at 1m/second per Allen et al. 1998).

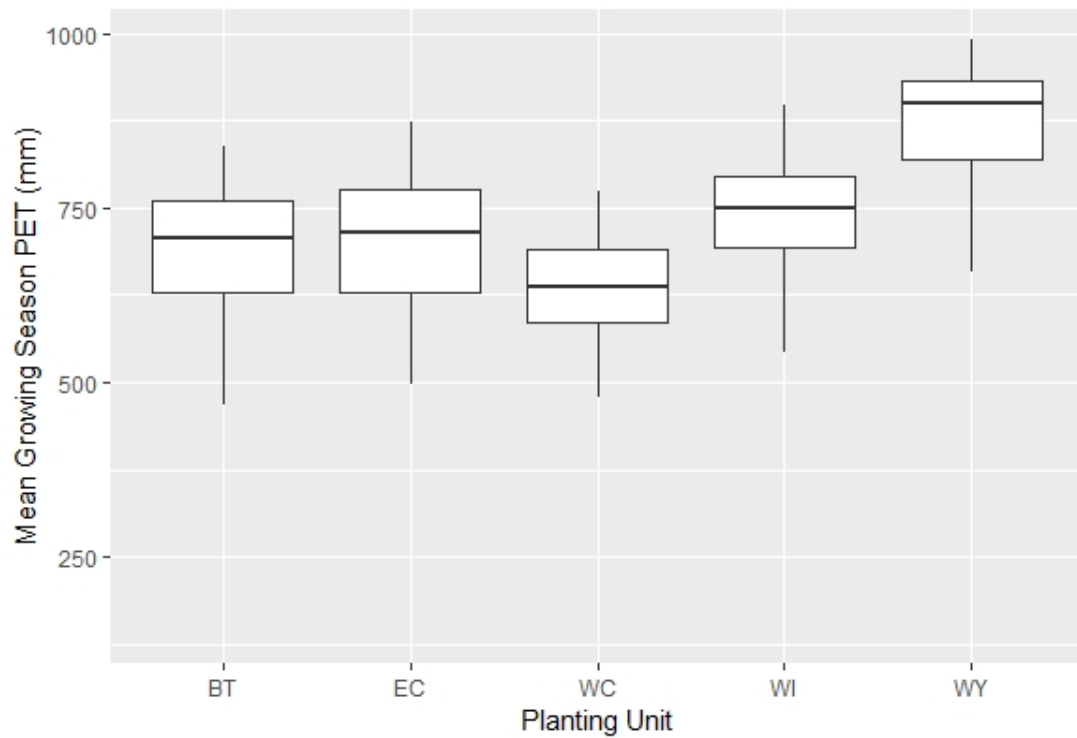


Figure 10. Mean growing season PET across all units.

Mean annual growing season actual evapotranspiration (AET) was highest at the Beartooth Planting Unit (335mm) and lowest at the West Centennials Planting Unit (230mm; Figure 11).

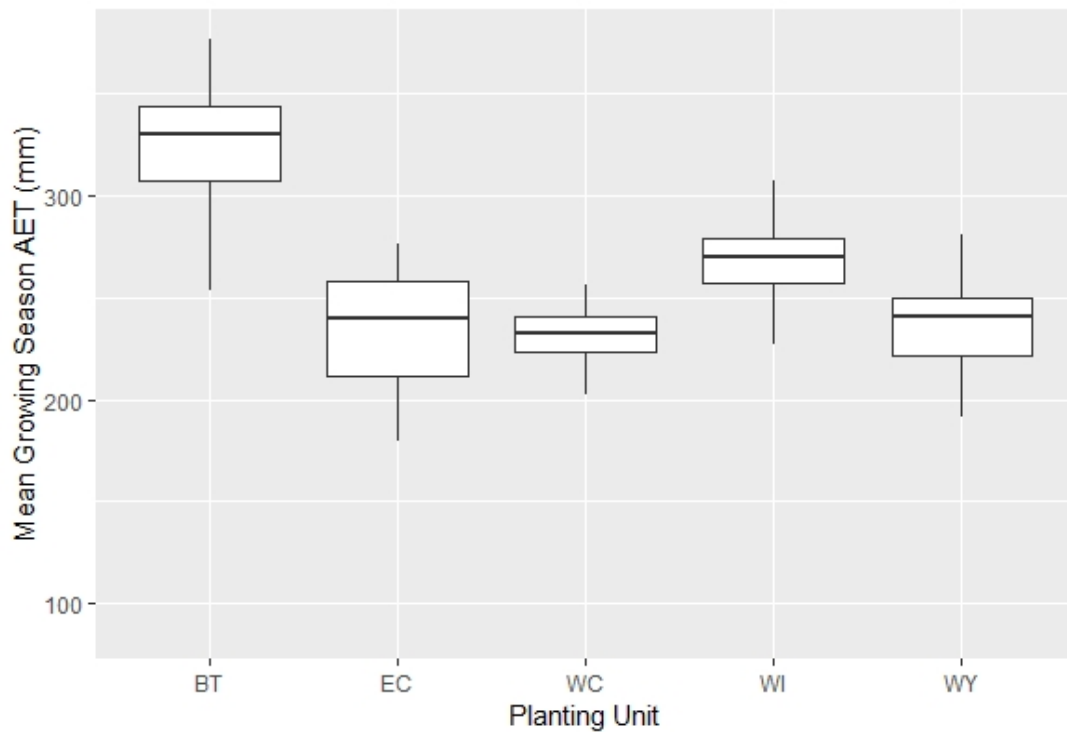


Figure 11. Mean growing season AET across all units.

Mean growing season water deficit (WD) had a large amount of variation. It was lowest in the Beartooth Planting Unit (390mm) and highest in the West Yellowstone Planting Unit (655mm; Figure 12). Recall that measurements of soil field capacity are included in estimates of WD, and that the West Yellowstone Planting Unit had the least (18.74mm) relative to the Beartooth Unit (27.01mm; Appendix C).

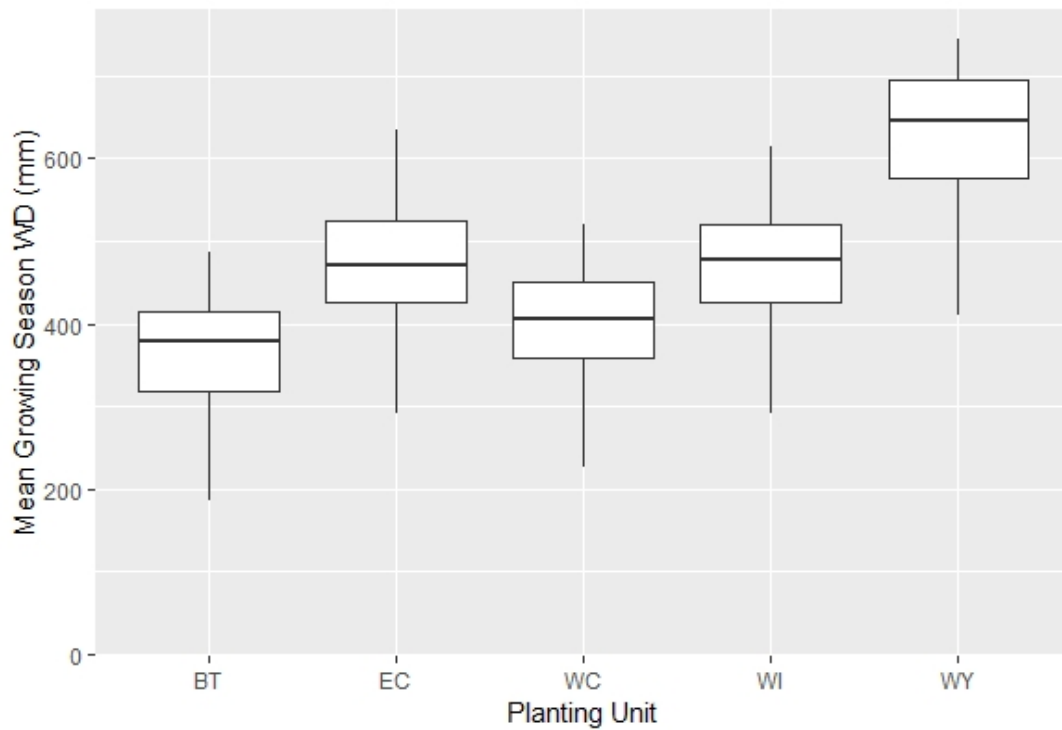


Figure 12. Mean growing season WD across all units.

Climographs were developed to help visualize the temporal aspects of mean PET, AET, and WD for each unit since the year 2000 (Figure 13). Although the curves across units are similar, the West Yellowstone Planting Unit has the highest PET (solid line) and lowest AET (dotted line) during the growing season (months 4 - 10), and therefore the highest WD (the difference between the solid and dotted lines) during the growing season

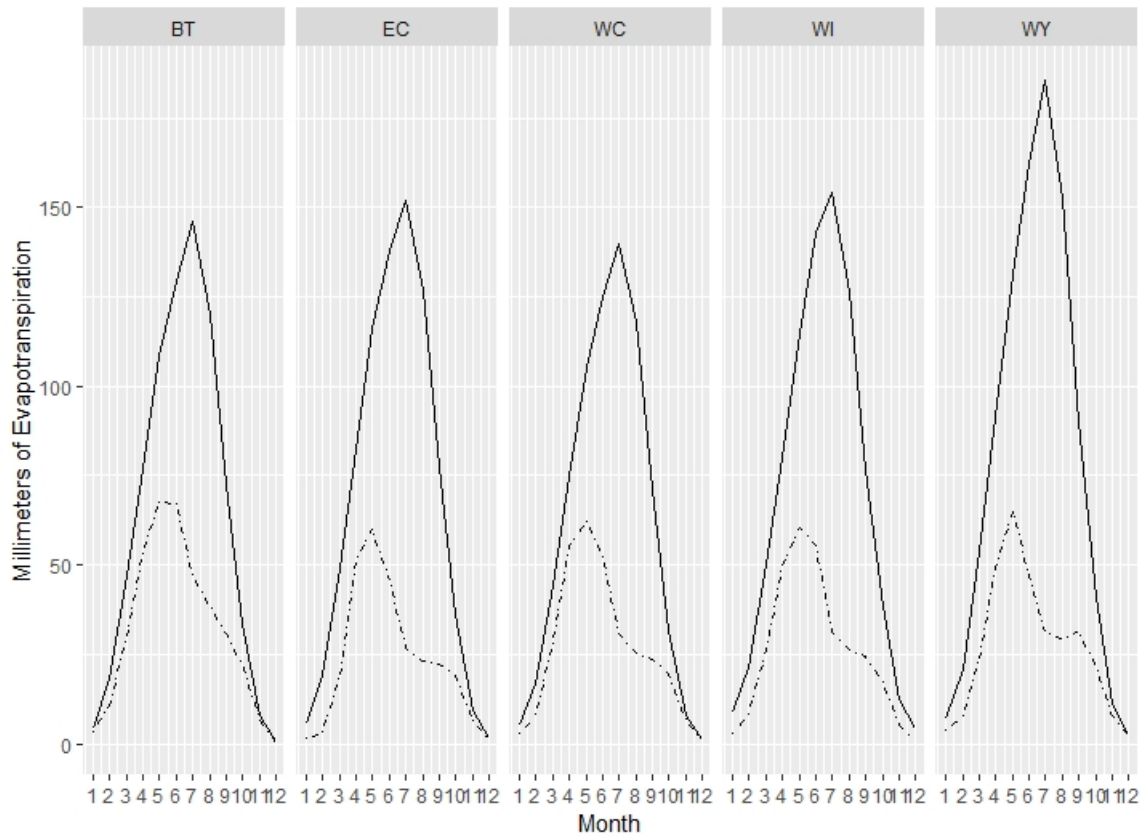


Figure 13. Unit climographs of mean water balance since the year 2000; PET = solid line, AET = dashed line, WD = PET – AET. Only months 4 – 10 (April – October) were used for analysis.

The number of competitors within 1/100th acre of each WBP varied from 0 to 25, and the unit mean's ranged from 0.4 to 8.5 (Figure 14). In general, younger sites had fewer competitors, but this was not always true (correlation of 0.64). Some of the older sites in the Beartooth and Wind River Planting Units did not have a great number of competitors.

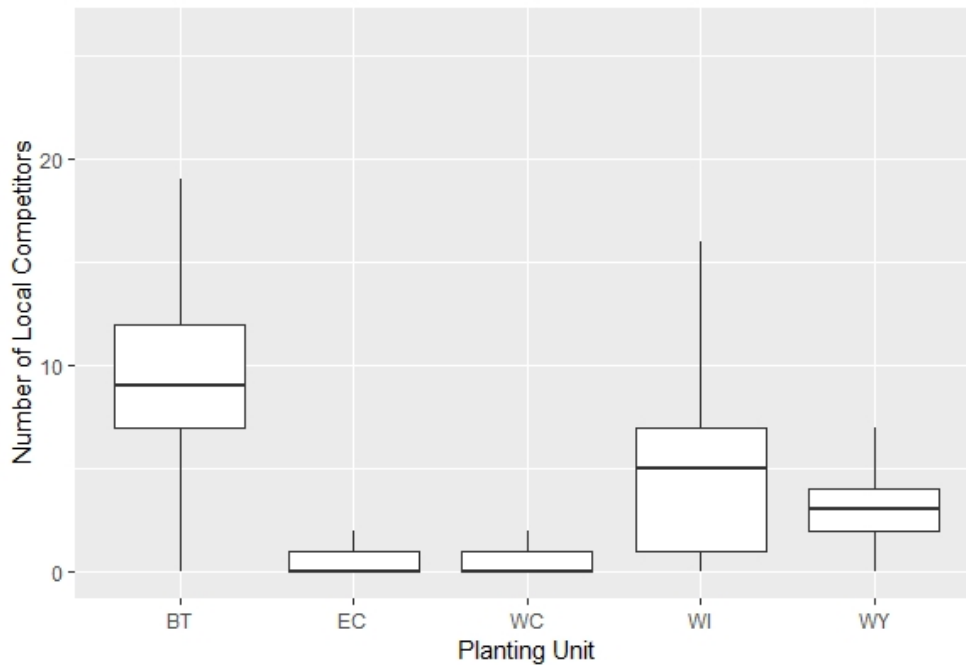


Figure 14. Mean number of local competitors for each unit.

Individual Growth Rate

Individual WBP growth rates ranged from 0.01 cm/year to 24.57 cm/year across all units. The West Yellowstone, Wind River, and Beartooth Planting Units had the highest mean and maximum growth rates, but there was a large amount of variation within all units (Figure 15). The East Centennial and West Centennial Planting Units had lower growth rates, but were also younger units (6 years post-planting relative to the mean of 15 years across all sites) and therefore did not have as many seasons to grow and exhibit variation in growth rate. Two sites showed a strong clustering pattern of seemingly lower growth rates (Figure 16; BT5 and WI3). Clark's nutcrackers were observed in higher numbers at these sites, and an active nutcracker nest was observed at the edge of BT5. Notably, WBP was also found at very high density in some areas at BT5, and both sites had higher present-day density than planting density (Figure 19).

Therefore, we believe that this clustering effect is a natural regeneration signal.

Additionally, this signal artificially deflates the growth rates calculated at these sites.

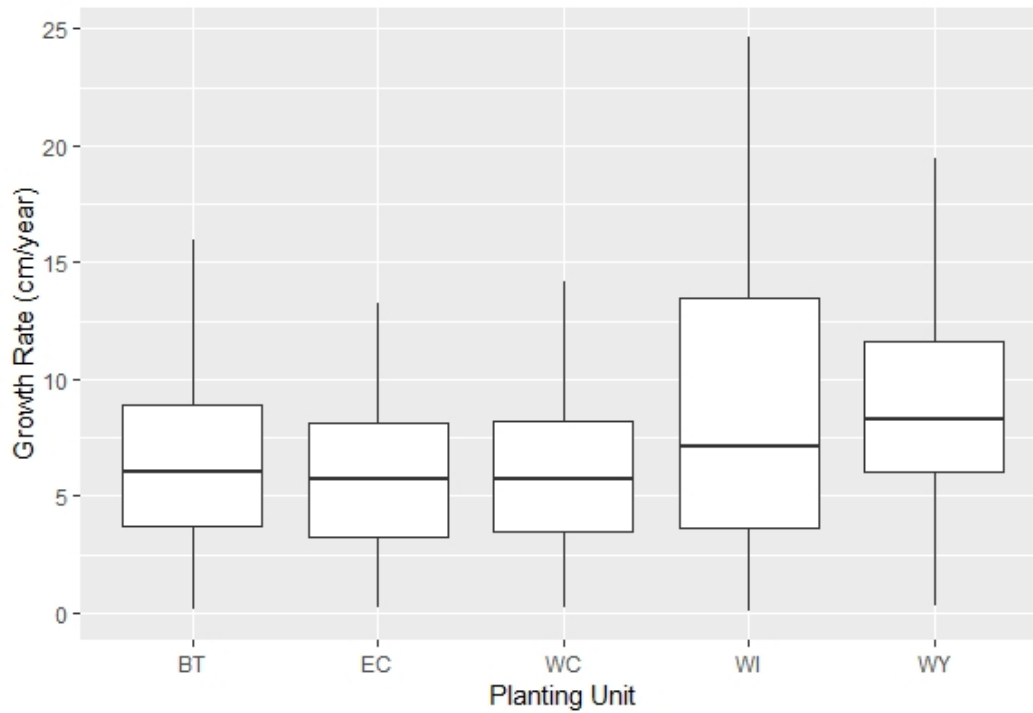


Figure 15. Adjusted growth rates (cm/year) across units (BT = Beartooth, EC = East Centennial, WC = West Centennial, WI = Wind River, WY = West Yellowstone).

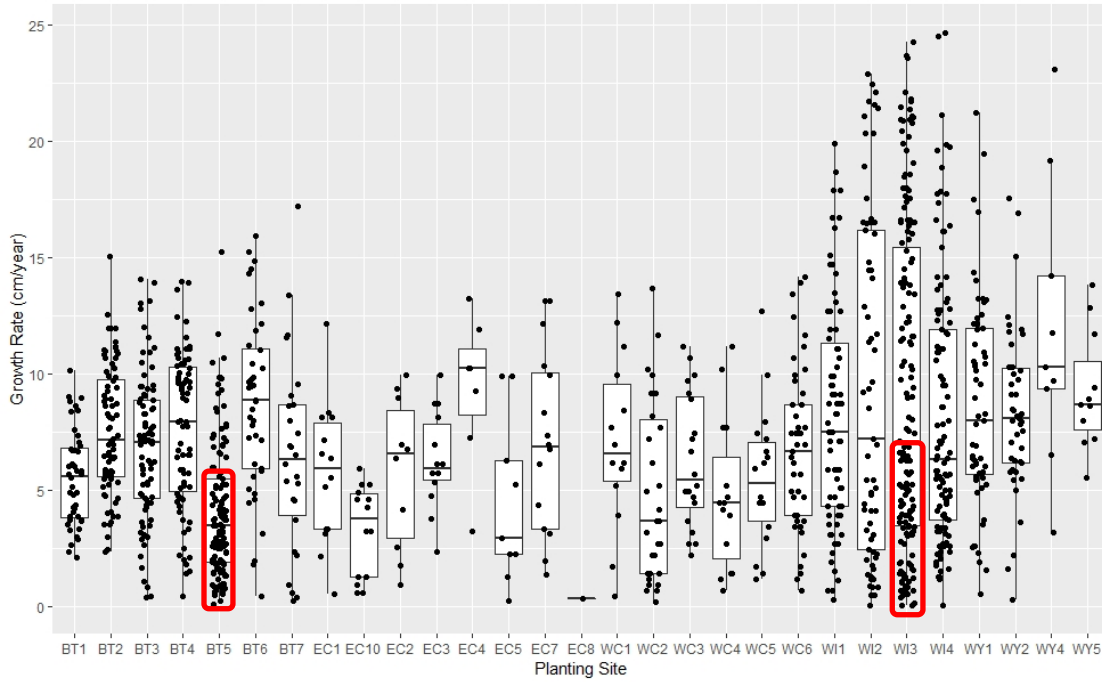


Figure 16. Adjusted growth rates (cm/year) across sites (BT = Beartooth, EC = East Centennial, WC = West Centennial, WI = Wind River, WY = West Yellowstone). Each black dot is an individual WBP. Likely natural recruitment (red boxes) at two sites.

The best supported model for individual growth rate ($AICc = 3154.32$, $K = 10$) included a cubic functional form for AET ($p\text{-value} = 0.005$) and number of competitors ($p\text{-value} = 0.038$; Table 4). Growth rate is positive at low levels of AET ($<200\text{mm}$), but the relationship essentially asymptotes from approximately $200\text{mm} - 300\text{mm}$ of AET, and then is once again positive when AET is greater than 300mm ($\hat{\beta}_{AET} = 3.59$, $SE = 1.65$; $\hat{\beta}_{AET^2} = 1.44$, $SE = 1.03$; $\hat{\beta}_{AET^3} = 2.40$, $SE = 0.97$; Figure 17). WBP growth rate is slightly positive at lower numbers of competitors, but at high numbers of competitors (>15 within $1/100^{\text{th}}$ acre) there is a negative relationship with growth rate of WBP ($\hat{\beta}_{comp} = 3.16$, $SE = 1.46$; $\hat{\beta}_{comp^2} = -0.70$, $SE = 1.21$; $\hat{\beta}_{comp^3} = -1.39$, $SE = 0.96$; Figure 17).

Individual Growth Rate Models	AICc	K	P-value
<u>Null Model</u>			
Log(growth_rate) ~ 1 + random(Site) + random(Unit)	3174.73	4	
<u>Full Model</u>			
Log(growth_rate) ~ AET + PET + PPT + T + Micro + Comp + PICO + PIEN + ABLA + random(Site) + random(Unit)	3243.05	13	
<u>Best Models</u>			
Log(growth_rate) ~ AET³ + Comp_number³ + random(Site) + random(Unit)	3154.32	10	0.005 0.038
Log(growth_rate) ~ AET ³ + random(Site) + random(Unit)	3163.55	5	0.015
Log(growth_rate) ~ Comp ³ + random(Site) + random(Unit)	3167.97	7	0.109

Table 4. Mixed effects models of individual growth rate (AET = actual evapotranspiration during the growing season, PET = potential evapotranspiration during the growing season, PPT = mean annual precipitation, T = mean annual temperature, Micro = microsite presence/absence, Comp = number of competitors within 1/100th acre plot, PICO = *Pinus contorta* presence or absence within plot, PIEN = *Picea Engalmanii* presence or absence within plot, ABLA = *Abies lasiocarpa* presence or absence within plot).

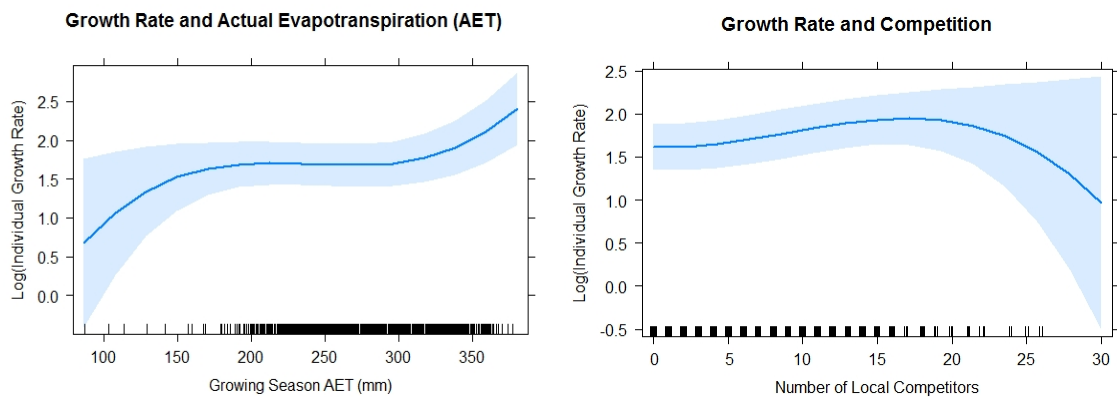


Figure 17. Plotted fixed effects of the best model for log(Individual Growth Rate) ~ AET³ + Number of Local Competitors³ + random(Site) + random(Unit) with confidence interval = 0.95 in light blue.

Site Density Change Ratio

Site density change ratios ranged from 0.1 to 4.2 across all units (Figure 18). The Wind River Planting Unit had the highest mean and maximum density change, and was the only unit with a higher present-day density of WBP relative to the initial planting density (ratio > 1). Notably, there was a large amount of variation between sites (Figure 19). Five sites exhibited likely natural regeneration (Figure 19; BT5, WI2, WI3, WI4, and WY2; ratio > 1), and seven of the top eight performing sites were from the Beartooth or the Wind River Planting Units.

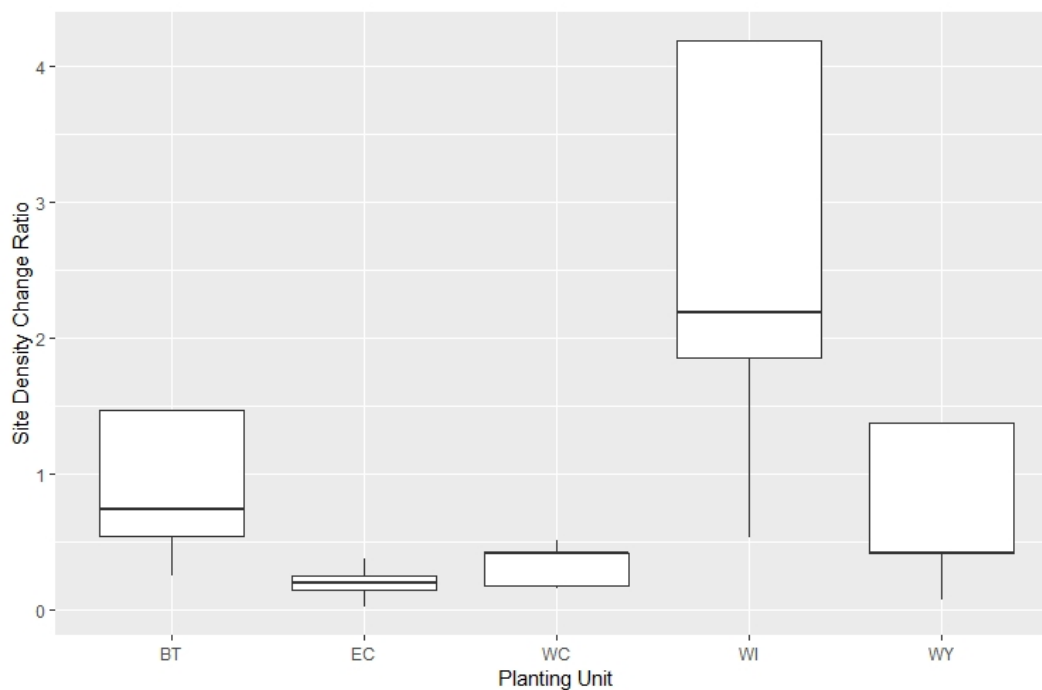


Figure 18. Density change ratio across all units.

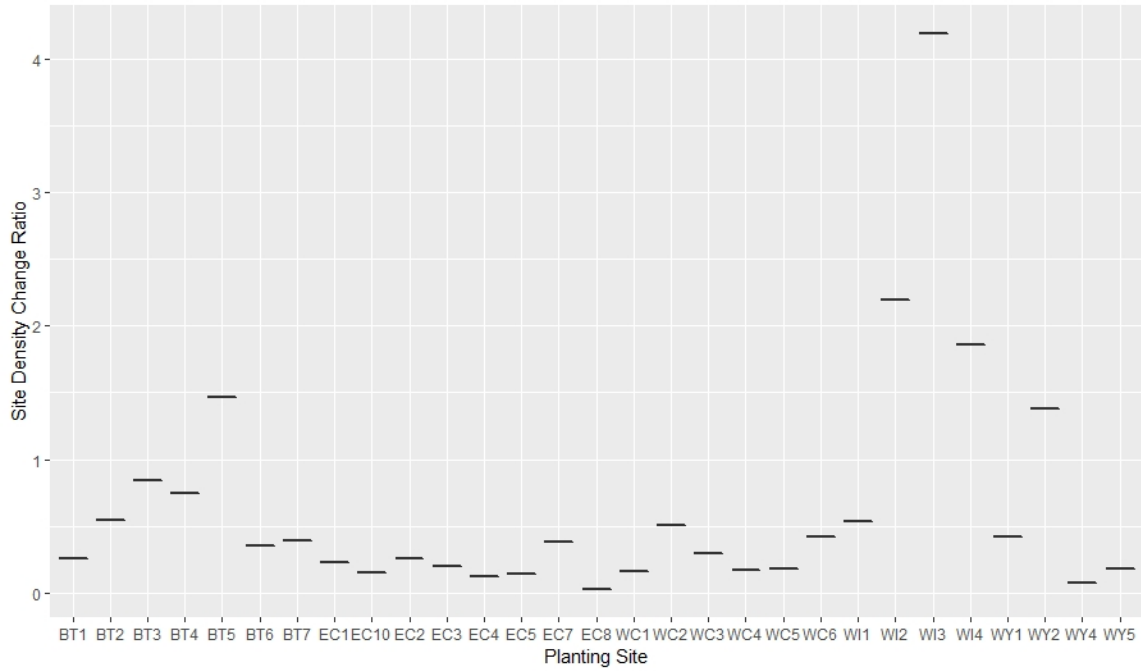


Figure 19. Density change ratio across all sites. Those sites with a ratio greater than 1.0 indicate sites with likely natural recruitment.

The best supported model for site density change ratio ($AIC_c = 72.42$, $K = 9$) included a cubic functional form for T_{max}^3 ($p\text{-value} = 0.45$) and number of competitors ($p\text{-value} = 0.25$; Table 5). At lower temperature maximums, the relationship with site density change ratio is positive, but as maximums increase a negative relationship develops ($\hat{\beta}_{T_{max}} = -2.49$, $SE = 1.19$; $\hat{\beta}_{T_{max}^2} = -0.71$, $SE = 1.00$; $\hat{\beta}_{T_{max}^3} = 0.62$, $SE = 0.93$; Figure 20). At low numbers of competitors, there is slightly positive relationship, but at higher numbers of competitors (>5 within $1/100^{th}$ acre) there is generally a negative relationship with site density change ratio of WBP ($\hat{\beta}_{Comp} = 2.34$, $SE = 1.28$; $\hat{\beta}_{Comp^2} = -2.16$, $SE = 1.00$; $\hat{\beta}_{Comp^3} = 1.35$, $SE = 1.11$; Figure 20).

Site Density Change Ratio Models	AICc	K	P-value
<u>Null Model</u>			
Log(density_change_ratio) ~ 1 + random(Unit)	83.72	3	
<u>Full Model</u>			
Log(density_change_ratio) ~ AET + WD _{max_month} + T _{max} + Micro _{ratio} + Comp + PICO + PIEN + ABLA + random(Unit)	93.33	11	
<u>Best Models</u>			
Log(density_change_ratio) ~ T_{max}³ + Comp³ + random(Unit)	72.42	9	0.45 0.25
Log(density_change_ratio) ~ WD _{max_month} ³ + Comp ³ + random(Unit)	74.15	9	0.78 0.30
Log(density_change_ratio) ~ Comp ³ + random(Unit)	76.00	6	0.14

Table 5. Mixed effects models of site density change ratio (AET = mean annual cumulative actual evapotranspiration, WD_{max_month} = maximum monthly water deficit, T_{max} = maximum monthly site temperature, Micro_{ratio} = ratio of microsite presence/absence, Comp = mean number of competitors within 1/100th acre plot, PICO = ratio of *Pinus contorta* presence or absence within plot, PIEN = ratio of *Picea Engelmanii* presence or absence within plot, ABLA = ratio of *Abies lasiocarpa* presence or absence within plot)

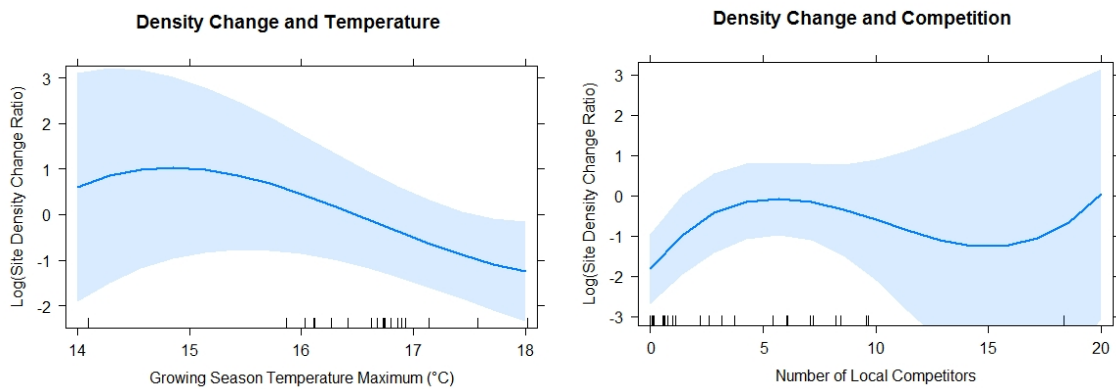


Figure 20. Plotted fixed effects of the best model for $\log(\text{Site Density Change Ratio}) \sim \text{Growing Season Temperature Maximum}^3 + \text{Number of Local Competitors}^3 + \text{random}(\text{Unit})$ with confidence interval = 0.95 in light blue.

Blister Rust

White pine blister rust (*Cronatium ribicola*) was confirmed at two of five planting units (Figure 21). Two trees in the Beartooths Planting Unit and one tree in the West Centennials Planting Unit.



Figure 21. Photo of blister rust “cankers” on a WBP sapling within the Beartooth Planting Unit (D. Laufenberg; May 2018).

The assessment of condition for each tree was not useful in the analysis, as very few trees ($n = 13$) were considered “unsatisfactory”.

Discussion

Actual Evapotranspiration, Competition, and Growth Rates

The leading model for growth rate was driven by mean annual growing season (April – October) AET since planting and the number of local competitors (within 1/100th acre). Models of WD and PET had similar strengths, and WD exhibited a positive relationship with WBP growth rates. These results are similar to other recent studies of

WBP performance associated with water balance metrics (Maher et al. 2018, Ford et al. 2017), and indicate that tree growth was likely more energy limited than water limited at our study sites since planting. We believe this positive effect is likely due to warm temperatures in years that cause a minimal amount of WD (not sufficient to kill or force seedlings to close their stomata for long periods during the growing season), even if higher temperatures during some years may have had a negative effect on seedlings. Rather, the warmth in those years that causes minimal WD is more beneficial than the negative effect of WD that accrues. Concurrently, our results also indicate that once a threshold of AET is reached (190mm – 300mm), there are diminishing returns for increasing AET until one reaches much higher levels (>300mm). At which point, these individuals are at greater risk of enduring higher WD when there are water shortages. Because of this, it is not prudent to attempt to plant in places with greater energy even though results suggest an energy limitation on growth rate for some individuals during some, but likely not all, seasons.

Notably, there is some support for silvicultural efforts to thin competitors at older sites with higher numbers of competitors (>15 competitors within 1/100th acre) in order to achieve a release of WBP growth similar to “closed-canopy” stands observed in another study (Maher et al. 2018).

Temperature, Competition, and Density Change

The leading model for site density change ratio was driven by the site summer monthly maximum temperatures and the site’s mean number of local competitors (within 1/100th acre) for each individual (aggregated as a ratio). This suite of models was much

less than those for individual growth rate, but the best supported model out-performed both the null and full by more than 10 AIC_c units. Both explanatory variables fit best as polynomials, and indicate a threshold associated with an initial increase in performance with increasing temperatures, but beyond 15°C (monthly mean) there is a cost to WBP site density. Similarly, a small number of competitors may actually be beneficial for young WBP trees because they provide some microsite advantages, but when more than five competitors are present, they likely outcompete WBP for finite resources (energy and water). This finding corroborates a recently developed species distribution model (SDM) for GYE WBP (Chang et al. 2014). Essentially, the site density change ratio is a reflection of WBP survival and recruitment rates since date of planting. In this sense, we would expect an SDM for GYE WBP to agree with the site trend of survival and recruitment rates because they are both rooted in a presence/absence analysis. Notably, there is only one site at the highest number of competitors, and it is nearly double the next highest. This lends to an artificial increase at the extreme tail (Figure 19). Additionally, greater exposure to sunlight (less shade, no microsite, and south or west-facing plantings) has been shown to increase water stress in young conifers, and inhibit their establishment (Germino et al. 2002).

Water Deficit

The West Yellowstone site is of particular interest because it experiences the greatest amount of precipitation, and the highest levels of WD. This is driven by two things in the water balance model: soils (poor and shallow) and southerly aspects. The

rhyolitic soils at the West Yellowstone unit holds less water and evaporates it more quickly than at other units following precipitation events.

Another study found that annual moisture deficits were significantly greater in 2000 – 2015 relative to the 1985 – 1999 period in the U.S. Rocky Mountains (Stevens-Rumann et al. 2018). This is believed to contribute to post-fire natural forest regeneration failure which has been noticed at higher levels in recent decades in the U.S. Rocky Mountains (Stevens-Rumann et al. 2018). This may also explain why north-facing aspects have been shown to exhibit greater regeneration than south-facing aspects within burned landscapes (Klutsch 2015).

A consistent interpretation of dryness is that it makes trees more susceptible to fire and MPB (Keane and Parsons 2010, Raffa et al. 2008). At the same time, WBP can survive dry sites where other trees cannot, and in these places fire keeps other competitors at low levels once WBP are mature (Keane et al. 2012). For these reasons, the concept of dryness as a driver of WBP life history and future distribution should be carefully considered in its management.

Forests that occur along the climatically dry periphery of their range are more susceptible to conversion to non-forest due to increasing trends in annual moisture deficits leading to decreases in tree regeneration post-wildfire (Stevens-Rumann et al. 2018). This is a major consideration for any planting efforts that plant seedlings that require a century of growth prior to production of seeds. Higher WD exhibited at the West Yellowstone Planting Unit is the likely “dry periphery” of WBP range. Indeed, a satellite-generated range map of GYE WBP indicates that this area is part of the species’

range edge (Landenberger et al. 2008). Notably, even in areas of high WD, convergent hillslope positions are often able to maintain shallow, subsurface water flows that augment water supply in otherwise dry climates (Hoylman et al. 2019). The climate portfolio is shifting and will continue to shift for the foreseeable future in the GYE (Sepulveda et al. 2015). Most notably, there is a strong warming trend with generally wetter springs, but greater water deficit by late summer (Chang et al. 2014).

Many climate niche and species distribution models assume that young individuals have similar tolerances as adult trees (Chang et al. 2014), but this is unlikely because seedlings with limited root systems, low carbon reserves, and reduced photosynthetic capacity will undergo mortality under conditions that present no difficulty for conspecific adults (Jackson et al. 2009). At some point in the past, these adult trees were young at the same site, so conditions were amenable to their development. Given climate change and forecasts for continued warming and drought events, it is possible that recruitment in historically favorable sites will no longer facilitate passage through early development demographic bottlenecks (Kueppers et al. 2017, Jackson et al. 2009). Perhaps, at these sites, microsites that enable lower WD experienced by the tree are the only viable options at a site.

Although the presence or absence of microsites did not perform well in our models, this is likely misleading because we were not able to track individual trees. We utilized the proportion of trees with microsites present at the site level to inform density changes at the site level. This is problematic because sites that appear to have lower densities (lower quality sites) have higher proportions of microsites. A benefit of our

study is that there are now 1,344 digitally-tagged trees across the GYE with known location, height, age, and presence/absence of microsite. These individuals could easily be tracked and visited in the future to provide a better understanding of long-term trends of planted GYE WBP.

Scope and Limitations

These results must be considered within the context of GYE WBP planting efforts. Although we were able to gather data from biophysically diverse sites (Appendix C), it is likely that natural conditions of WBP regeneration and establishment exist outside of this range. Additionally, we did not account for differences in the nursery stock of planted WBP, and each source population is likely to have some variation of genetics and therefore varied response to its environment. Some trees were planted in the spring months, whereas others were planted in the fall. Planting trees is a skill, and each individual planter likely had differences in their ability to successfully place trees within the earth so as to promote success in a young seedling. Additionally, different microsites have different qualities, but we did not take this into account in our analyses. While all plantings took place post-fire, the severity of the fire has implications for the remaining biota in the soil (seeds, fungi, bacterial communities, etc.), and also the rate at which competitors return to the site (*Pinus contorta* has serotinous cones). The volume of remaining dead at the site also changed from one area to another. It is possible that planting personnel did not update maps or shape files post-planting even if they only planted on a portion of the site. As noted earlier, we believe there was some degree of natural regeneration at some of the sites, but without more intrusive sampling there is no

way to find out which were planted and which individuals were not. Some sites have active grazing permits, and indeed we observed livestock at the Wind River Planting Unit. The possible browsing or trampling by livestock on seedlings may disrupt WBP planting efforts. Many managers pointed out that pocket gophers (*Thomomys* genus) are often deleterious to the health of WBP, and their abundance can change from site to site. Jenkins et al. (2018) also found that ectomycorrhizal communities have symbioses with young WBP that may promote growth and survival, but we did not investigate whether these communities were present. Finally, estimating temperature and precipitation in highly diverse topographic terrain is difficult, and weather instrumentation at higher elevations remains sparse (Oyler et al. 2014). Significantly, we did not measure vulnerability to drought directly. Although growth rate was used as a response variable, it should not be interpreted as an indicator of a tree's likelihood of longevity. Notably,

Policy and Management

Conservation Status

From a national perspective, it is important to recognize that federal policies regarding the environment initially assumed relatively stable climate, disturbance regimes, and biotic interactions (Spies et al. 2010). A vital question has arisen in the past couple of decades: is there enough flexibility inherent within historic policy to adapt to climate and land use change, and provide adequate flexibility in management options to optimize success under uncertain futures?

Endangered Species Act. The Natural Resources Defense Council first petitioned the United States Fish and Wildlife Service (USFWS) in December 2008 for listing whitebark pine as “endangered” under the federal Endangered Species Act (ESA; 16 U.S.C. § 1531 et seq.). Their position was that “the current extent of losses to whitebark pine populations and the combined synergistic effects of advancing succession from fire suppression, disease, and pests currently, and under future climate warming scenarios, threaten the continued existence of whitebark pine and qualify it for protection as endangered under ESA.” Per ESA stipulations, the petition triggered a 90 day review of WBP’s status, and a decision whether listing was warranted. The ESA requires the protection of a species as “endangered” if it “is in danger of extinction throughout all or a significant portion of its range.” 16 U.S.C. § 1532 (12). Following the review, there is a requirement of a second decision to list or defer listing within one year of the initial petition.

The USFWS (Katzenberger 2011) announced their decision in July 2011:

We determined the whitebark pine warrants protection under the Endangered Species Act (ESA), but that adding the species to the Federal List of Endangered and Threatened Wildlife and Plants is precluded by the need to address other listing actions of a higher priority.

We will add the whitebark pine to the list of candidate species eligible for ESA protection and review its status annually. If we propose the whitebark pine for listing in the future, the public will have an opportunity to comment. We have assigned the whitebark pine a listing priority number (LPN) of 2, which means we have determined the threats are of high magnitude and are imminent.

Threats to the whitebark pine include habitat loss and mortality from white pine blister rust, mountain pine beetle, catastrophic fire and fire suppression, environmental effects resulting from climate change, and the inadequacy of existing regulatory mechanisms.

Whitebark pine is experiencing an overall long-term pattern of decline, even in areas originally thought to be mostly immune from the above threats. Recent predictions indicate a continuing downward trend within the majority of

its range. While individual trees may persist, given current trends the Service anticipates whitebark pine forests will likely become extirpated and their ecosystem functions will be lost in the foreseeable future. On a landscape scale, the species appears to be in danger of extinction, potentially within as few as two to three generations. The generation time of whitebark pine is approximately 60 years.

WBP remains a “candidate” species under the ESA to this day, although an intent for a decision by 2019 was released by USFWS in January 2017. Notably, “candidate” designation translates to little or no additional considerations or requirements for management relative to any other organisms. Notably, Canada’s equivalent policy considers WBP endangered.

Custer Gallatin National Forest Plan Revision. Although the recent *Proposed Action-Revised Forest Plan* (2018) for Custer Gallatin National Forest (CGNF; the major federal land manager in the northern GYE) explicitly recognizes WBP as the only CGNF plant species that falls under the ESA, there is only one set of “Desired Conditions, Goals and Guidelines” mentioned for WBP. Notably, these are not enforced by law, but rather are a set of general directives for guiding “management activities in or near whitebark pine trees or stands identified for collection of scion, pollen, or seed; or areas identified as important for cone production; and whitebark pine plantations, project-level design criteria or wildland fire management strategies should protect them from potential loss to support the recovery or long-term persistence of this species.” Well beyond the geographical scope of a single national forest, the species is again under review by the USFWS for potential listing under the ESA, and a decision document is expected later this year.

Greater Yellowstone Coordinating Committee. The GYCC WBP coordinating committee is a collection of experts from the four GYE federal land management agencies that “help to ensure the long-term viability and function of whitebark pine in the GYE.” The GYCC was initially formed in 1964, and the WBP subcommittee was founded in 2000. Initially, the subcommittee only included three of the agencies, but in 2012, the BLM was also given a seat at the table. Notably, the subcommittee works hard to “collaborate extensively with the research community and partners”. This is a difficult undertaking given that they collectively manage over 20 million acres across many jurisdictions. Furthermore, members of the subcommittee are not able to forego their daily forest management responsibilities in order to focus on WBP, but rather, service on the subcommittee is in addition to daily operations. Because of this, there remains a need for greater funding to facilitate landscape level management of the species and GYE-wide collaboration between stakeholders. Funding opportunities could yield stakeholder workshops and paid professionals to focus exclusively on cohesive GYE WBP conservation efforts.

Current WBP management in the GYE is largely carried out by the GYCC – WBP subcommittee. Their activities include collecting seed cones from whitepine blister rust resistant individuals (PLUS trees), planting seeds and saplings, silvicultural treatments (thinning of competitors and Verbenone application), monitoring and inventory, and growing an “orchard” of diverse genetic stock in the Custer – Gallatin National Forest. The origin and subsequent planting locations of PLUS trees are coordinated by the region’s federal geneticist, Dr. Mary Francis Mahalavich, to ensure

appropriate diversity and PLUS-tree qualities are present in the planting efforts. Planting efforts have been ongoing for approximately three decades (over 1,500 treated acres to date) and will continue into the future. Very few records exist regarding GYE WBP management on private lands.

Conservation Recommendations

Similar to earlier attempts to inform environmental policy solutions in the GYE (Primm and Clark 1996, Clark et al. 1991, Greater Yellowstone Coordinating Committee 1990), I suggest that there remains a need for collaborative ecosystem and landscape-level management in the GYE. WBP is an ideal organism to serve as a central figure in coordinating ecosystem management, and our study of planting sites helps inform one of the major conservation strategies for GYE WBP. Ecosystem management goals include (Grumbine 1994):

- Maintaining viable populations
- Maintaining ecological process
- Protecting evolutionary potential of species and ecosystems
- Accommodating human use in light of the above short-term policy implications

Notably, “ecosystem management is not just about science nor is it simply an extension of traditional resource management; it offers a fundamental reframing of how humans may work with nature” (Grumbine 1994). Earlier attempts to manage at the ecosystem level have had limited success in the GYE. Although the “Vision” document

of the early 1990s was ultimately curtailed, the tenets and goals embedded within that effort are still in need today:

- Conserve the Sense of Naturalness and Maintain Ecosystem Integrity
- Encourage Opportunities that are Biologically and Economically Sustainable
- Improve Coordination

There are indications that national policy and management is beginning to encourage integrated approaches (Keiter 1998 and Groves et al. 2012) and sustainable forest management (SFM). Societal benefits are gained through ecosystem services (e.g. water conservation) and economics (e.g. recreational opportunities) where SFM is implemented (Hidayat 2018). A greater opportunity may be found in recent efforts to place more emphasis on the “stage” (Lawler et al. 2015) or abiotic landscape that many species collectively require. In this way, as climate continues to shift, conservationists can use species of concern (and the ESA) as a way to facilitate funds and collaboration, but also recognize the great value in supporting larger communities of organisms by protecting their “stage.” For instance, WBP’s subalpine “stage” supports species well beyond a single conifer (e.g. grizzly bears). Specific to the “stage”, our work indicates a need for better soils data to inform scientists and managers about the locations of higher quality planting sites.

Ultimately, policy and management determine the scope and objectives of conservation strategies for species of concern, and science helps inform the likelihood of success. Therefore, a balanced and holistic approach from all stakeholders is necessary in

planning efforts for successful conservation projects. There is evidence that citizens support use of public funds to conserve WBP (Naughton et al. 2018). WBP was first petitioned for listing under the Endangered Species Act in 2009, but has remained without a final decision due to the volume of other species of higher priority for listing. Often, poor communication (e.g. jargon, acronyms, etc.) of science by researchers does not translate to policy that reflects the science (Likens 2010). Strategies for forest conservation across landscapes is integrally tied to science, management, and policy (Noss 2001).

WBP affords potential GYE conservation collaborators the opportunity to engage in landscape-level management around an organism of conservation concern. Indeed, a major entity is already in place (GYCC WBP) that could serve as a model for conservation of other species in the GYE. Unfortunately, appointments to the committee and WBP objectives represent an additional workload to those individuals. If the GYE WBP population is seriously threatened, and the public already supports conservation of the species, an official listing of “endangered” status would help provide the necessary recognition, funds, expertise, and personnel explicitly focused on WBP to execute a cohesive conservation effort.

Planting and Monitoring Recommendations

1. Greatly consider increases in temperature and drought (Chang et al. 2014) in the region for this late to mature and long-lived species in future decades and centuries

- a. Higher elevation is generally better for decreasing competition and extreme levels of PET
 - b. Northeast aspects receive the least amount of energy (likely best survival for periods of drought, but not as good for tree growth). As the environment warms throughout the day, the afternoon sun delivers a greater heat load than earlier in the day. Therefore, a southeast aspect will receive substantially less PET than a southwest aspect. Notably, south and west aspects receive similar amounts of energy.
 - c. Concave hillslopes will offer buffers against general water scarcity (Davis et al. 2018)
 - d. High resolution water balance projections associated with potential WBP planting areas
 - e. Prioritize soil texture alongside aspect and elevation
 - f. Continue to utilize microsites that buffer seedlings from water-stress particularly at sites with higher likelihood of drought
2. Wait a few years in post-burn habitat to plant WBP due to bark slough falling and injuring young seedlings
 3. Measure annual height growth post-planting at stake rows (to nearest inch)
 4. Update planting files after planting to precisely reflect planted areas and concentration
 5. Directly measure drought stress (pressure chamber method or ^{13}C enrichment measurements via spectrometry)

6. In order to distinguish between artificially planted and naturally recruited individuals, it may be possible to confirm the plastic planting containers even decades post-planting in the field by a brief subterranean investigation near the base of each tree.

Notably, assisted migration of WBP to northern latitudes has shown that WBP seeds will germinate 800km northwest of the northern boundary of the current species range (McLane and Aitken 2012). Artificially planting WBP at higher elevations, instead of higher latitudes, in ecosystems where it already exists (i.e. the GYE) may provide opportunities to leverage nearby long-term viable habitats.

Conclusion

Although an organism must grow in order to eventually reach maturity (cone-bearing life stage), this long-lived and late to mature species must survive anticipated increases in drought frequency and severity in the GYE (Chang et al. 2014). Therefore, in order to be successful, WBP must tolerate periods of water stress in the coming decades and centuries. Our study only represents a small portion of the time it will take for planted WBP individuals to bear cones. With this in mind, if survival and reproduction is the basis for success or failure of planting efforts, it is prudent to prioritize localities buffered from intense and extended water stress. Our relatively simplistic water balance approach that quantitatively incorporates remotely-sensed and field-collected data can help inform future planting efforts.

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APPENDICES

APPENDIX A

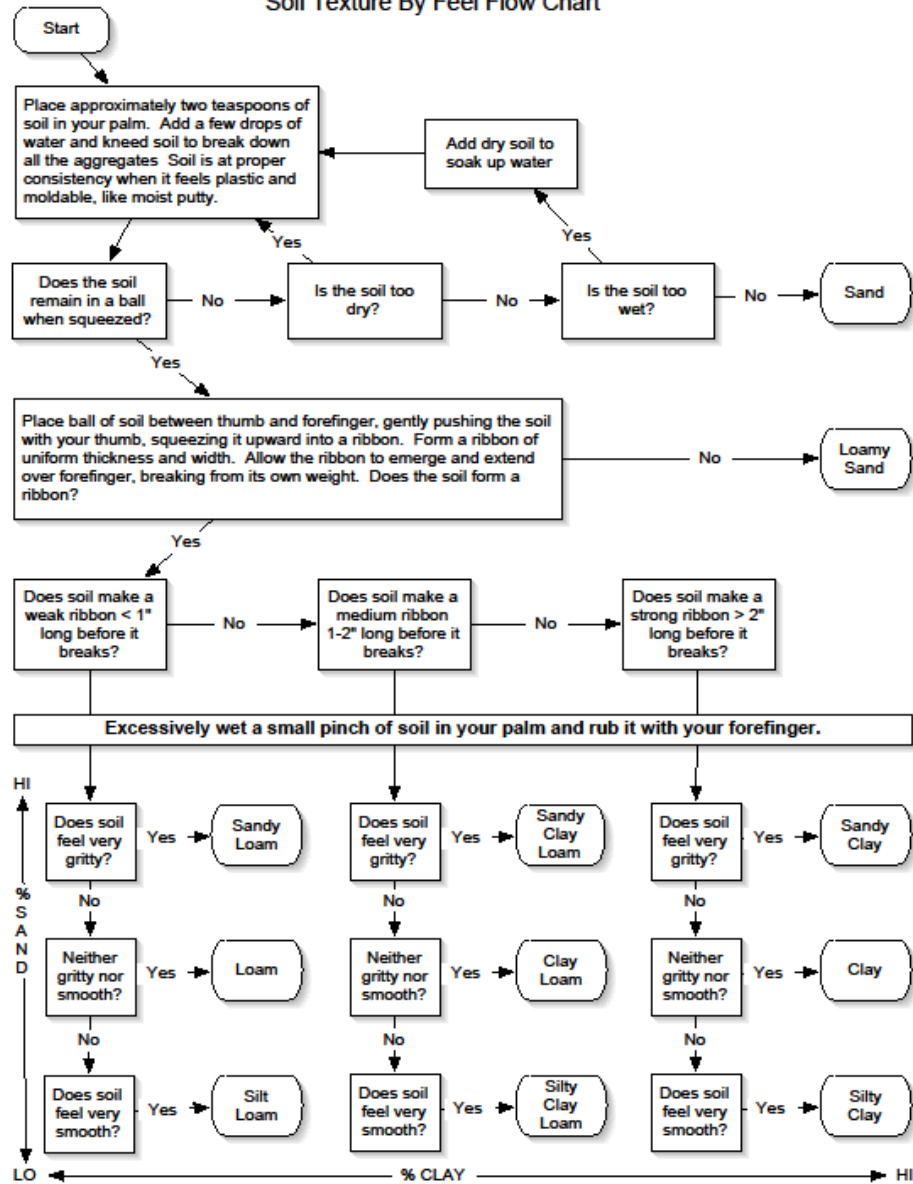
PRELIMINARY STUDY METHODOLOGY

1. Add relevant layers
 - a. Annual mean temperature low and high (800m; Prism)
 - b. Annual precipitation (800m; Prism)
 - c. Annual VPDmax (800m; Prism)
 - d. Elevation (1km; USGS)
 - e. Soil water holding capacity (1km; Penn. State Univ.)
2. Subset layers (specific to the GYE)
3. Transform projections for comparison (NAD83)
4. Add planting units
 - a. Utilize base map (National Agriculture Imagery Program; NAIP) in order to find planting unit locations
5. Extract layer data specific to each planting unit
6. Generate graphical and tabular representations of data

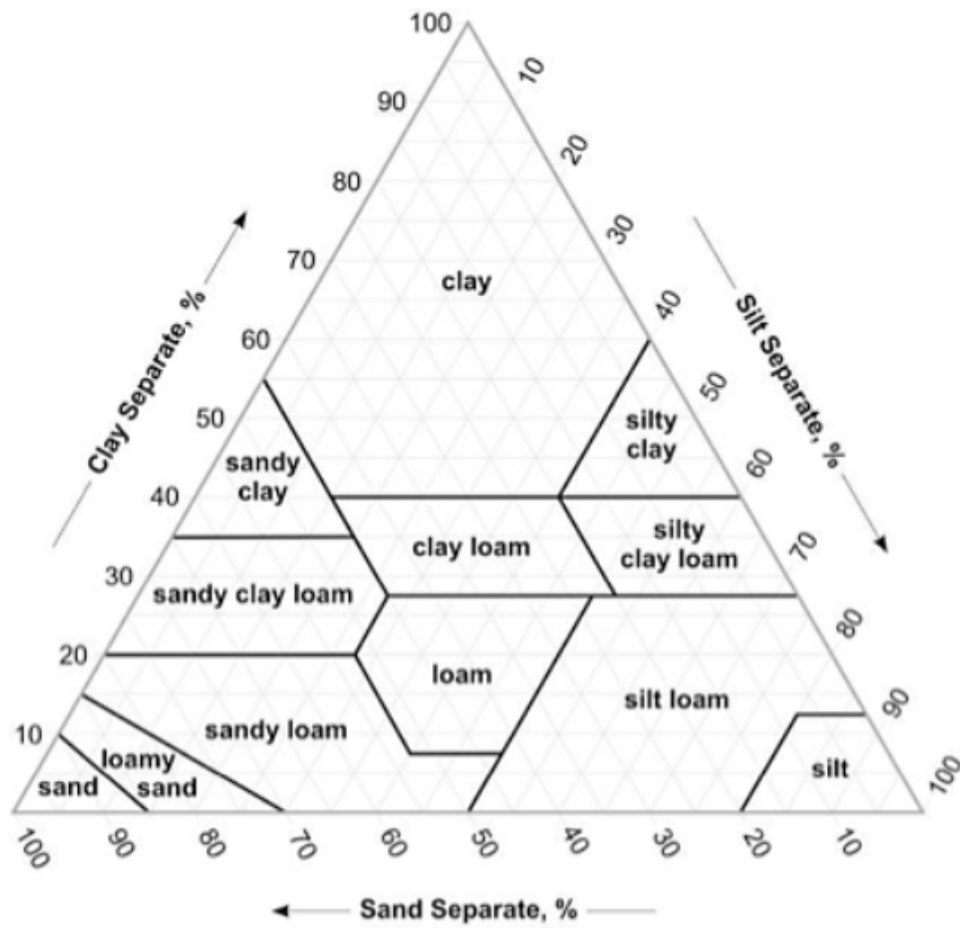
APPENDIX B

SOIL FIELD CAPACITY ESTIMATES

Soil Texture By Feel Flow Chart



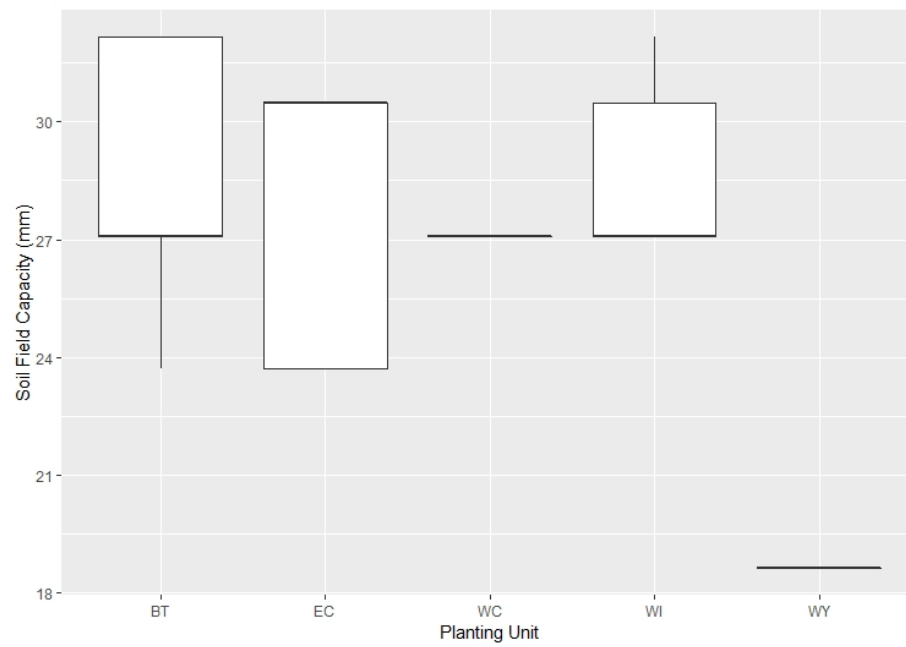
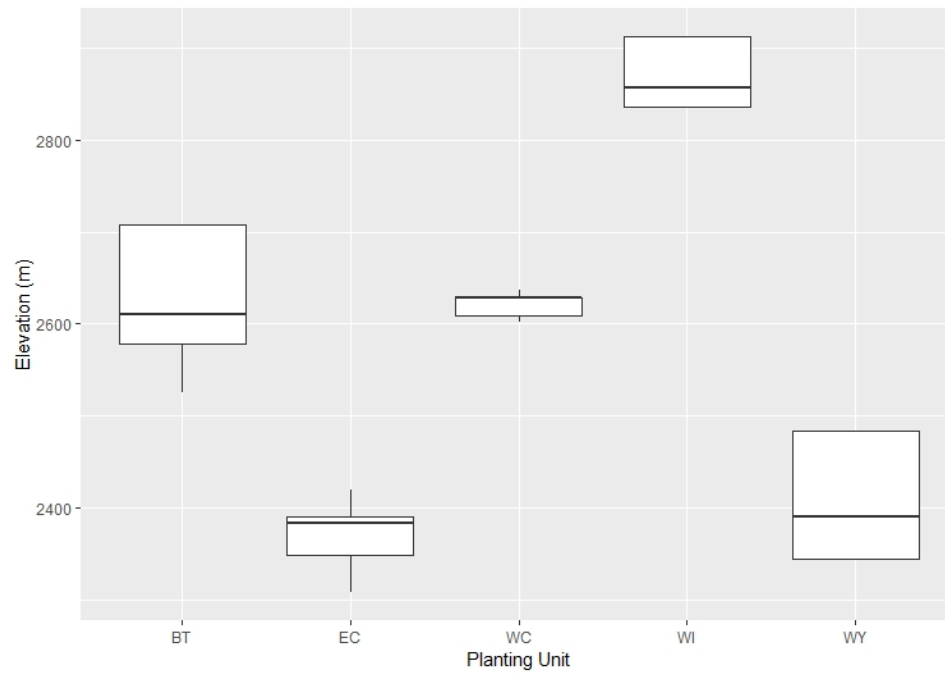
Soil Textural Triangle

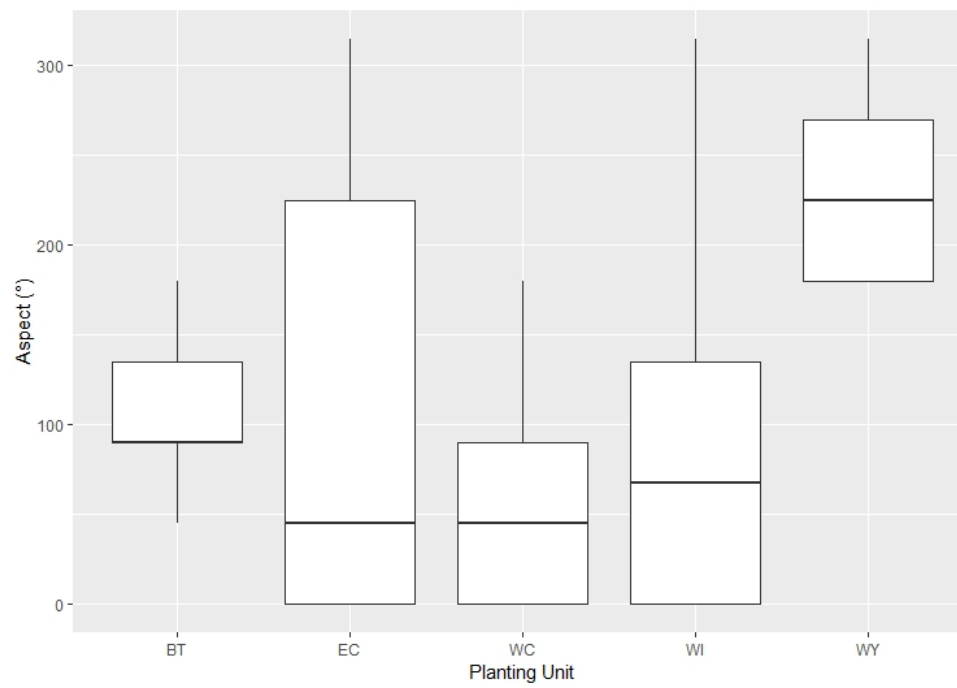
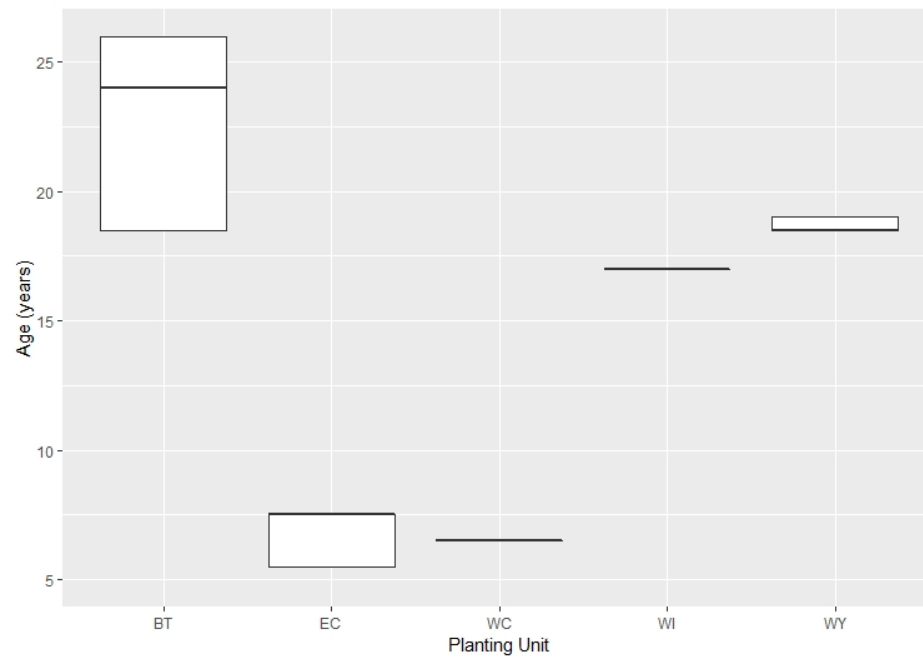


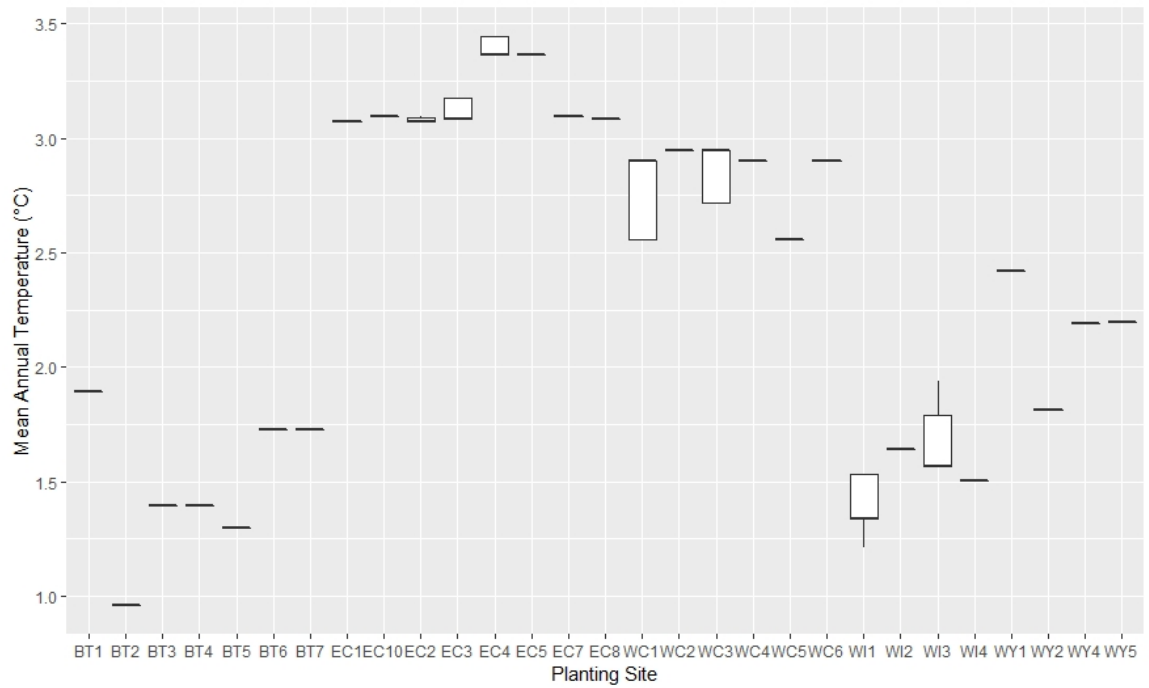
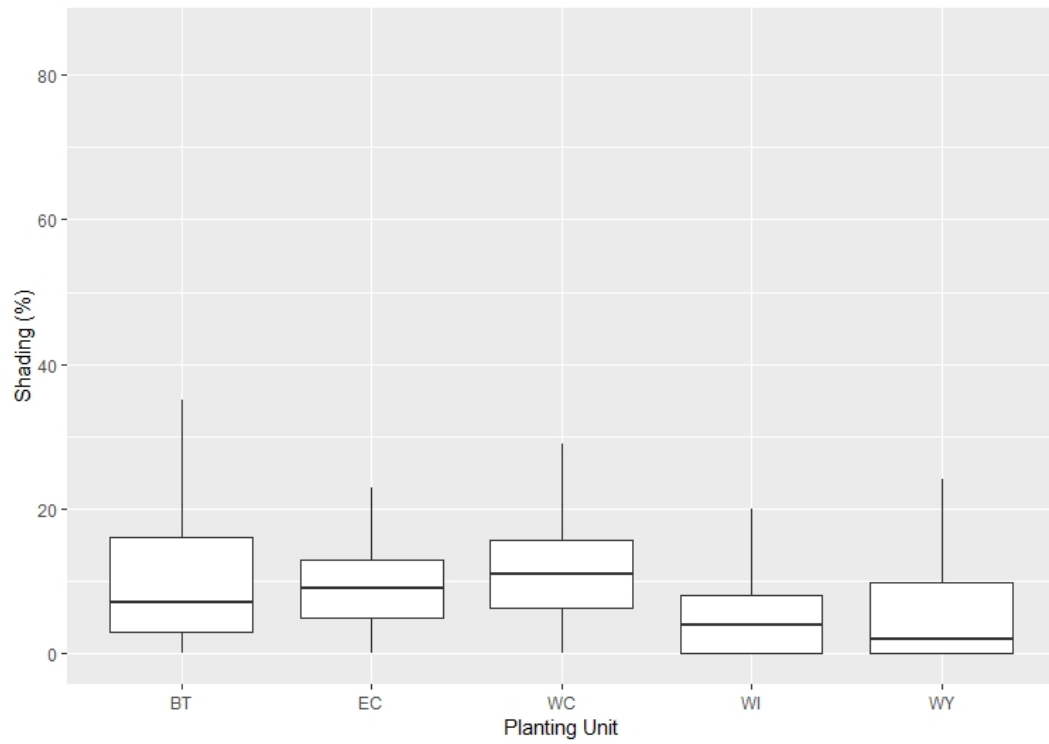
APPENDIX C

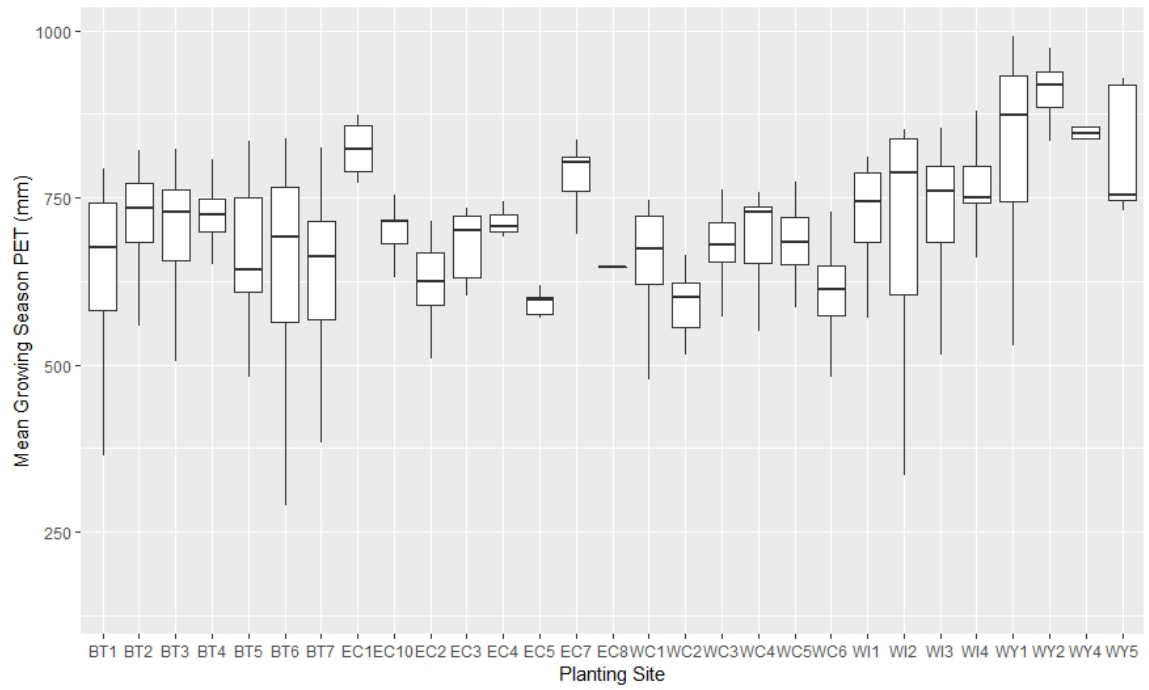
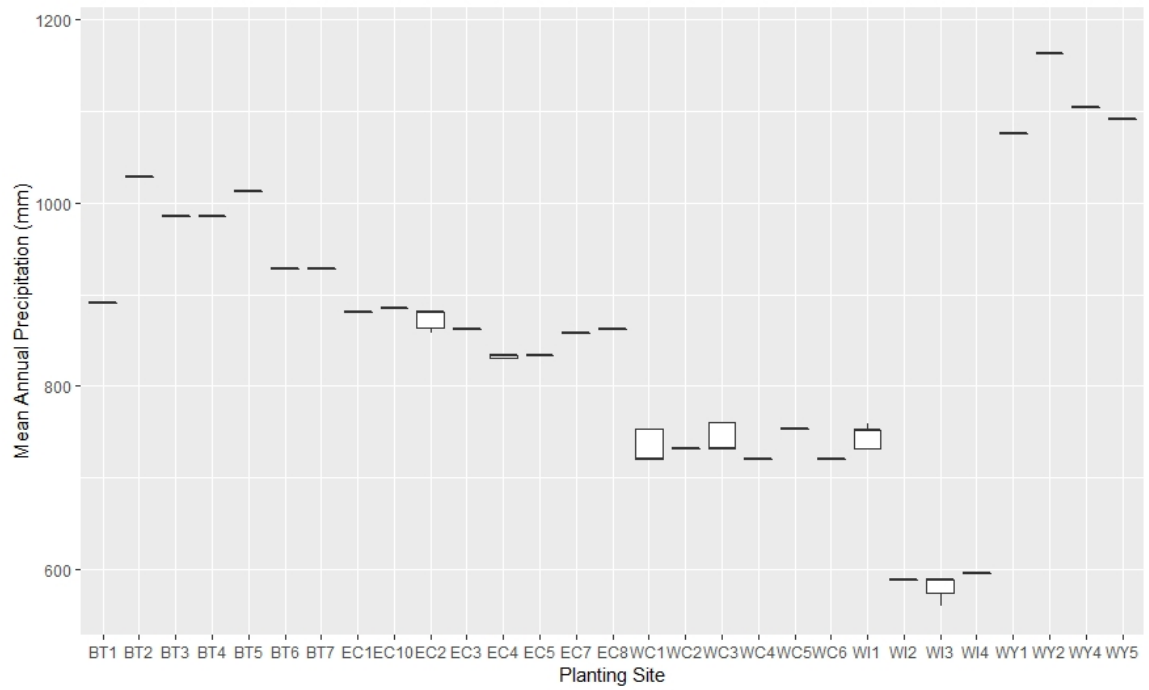
BIOPHYSICAL DATA PLOTS

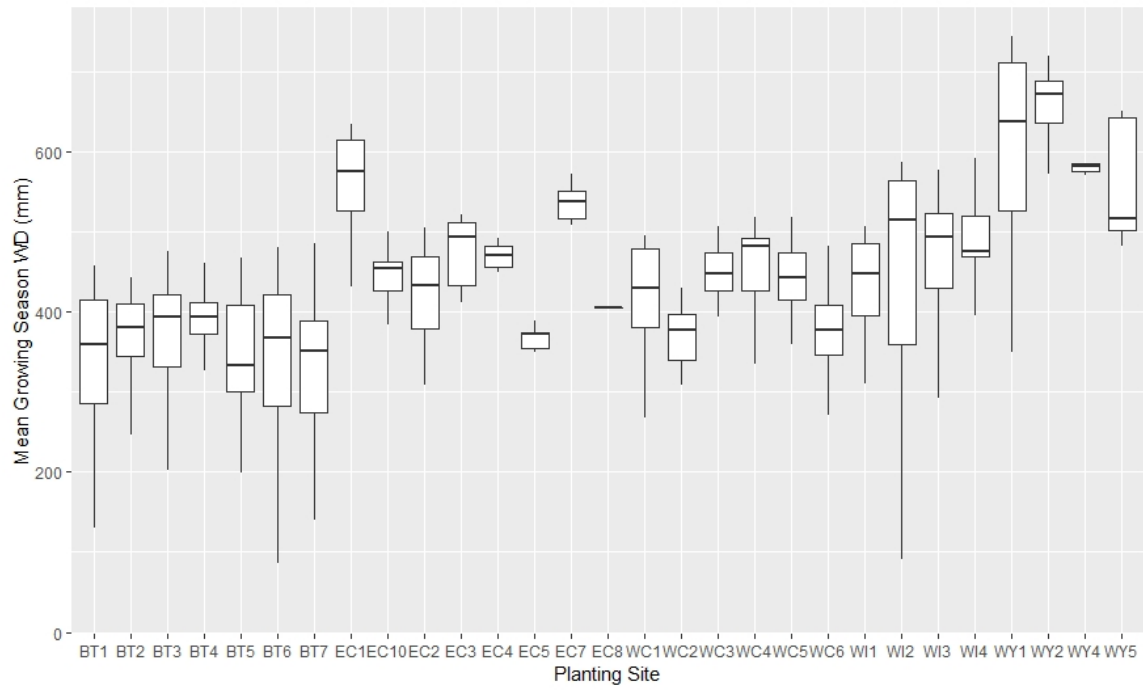
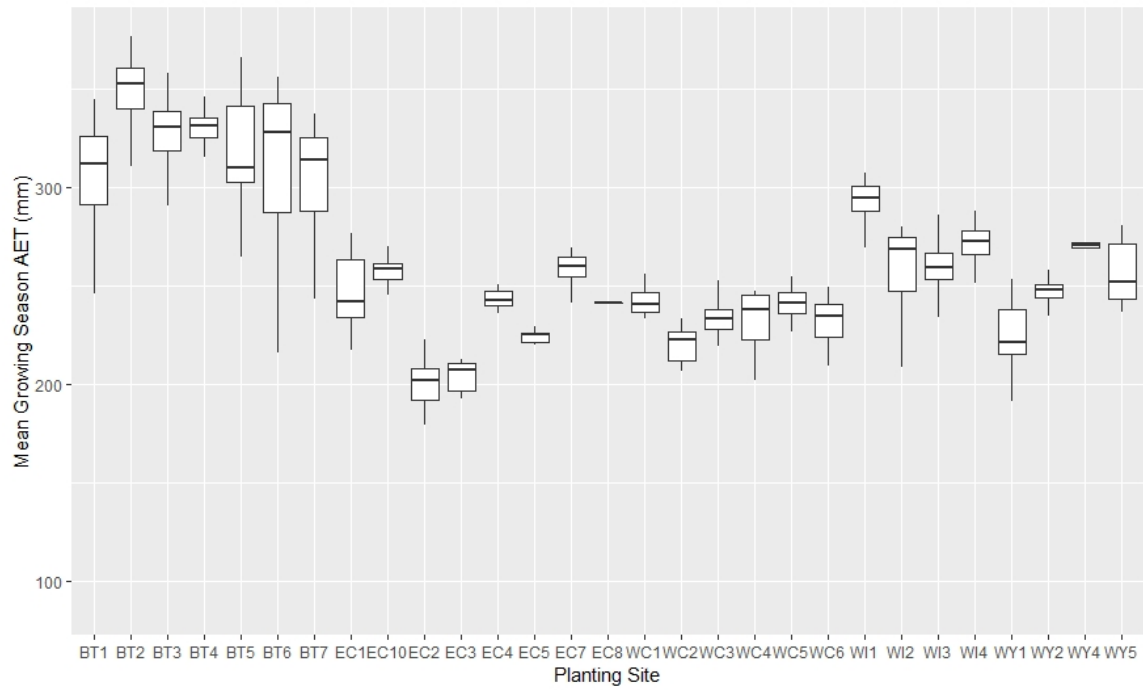
BT = Beartooth Unit, EC = East Centennial Unit, WC = West Centennial Unit,
WI = Wind River Unit, WY = West Yellowstone Unit





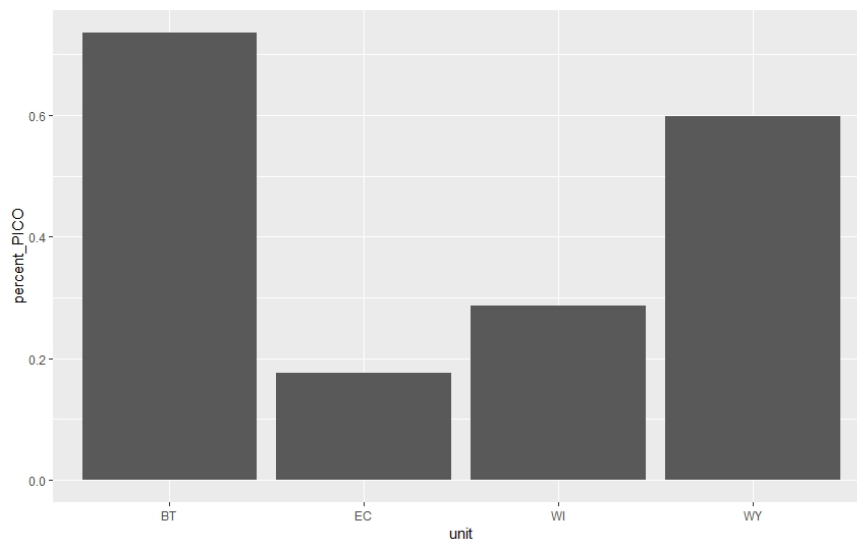
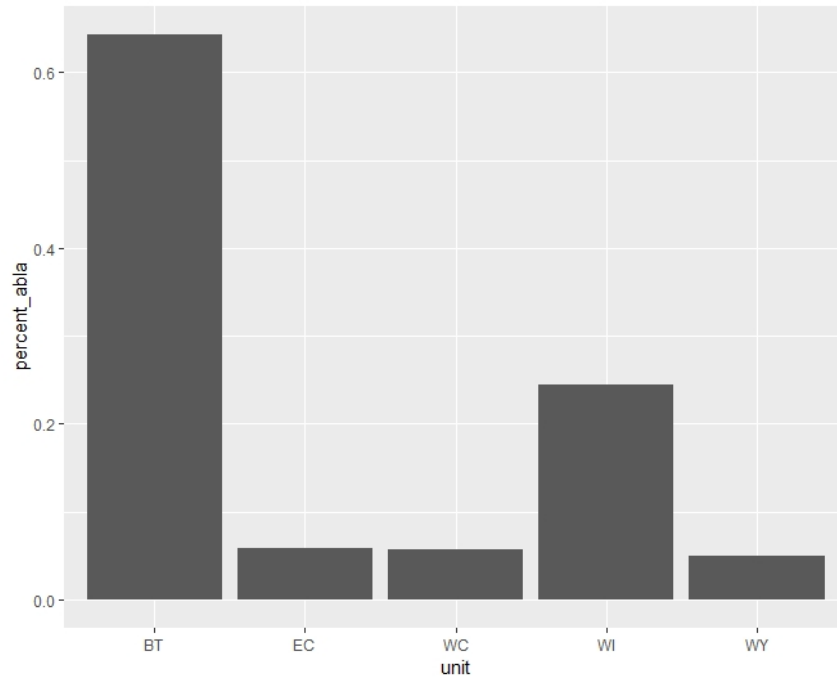


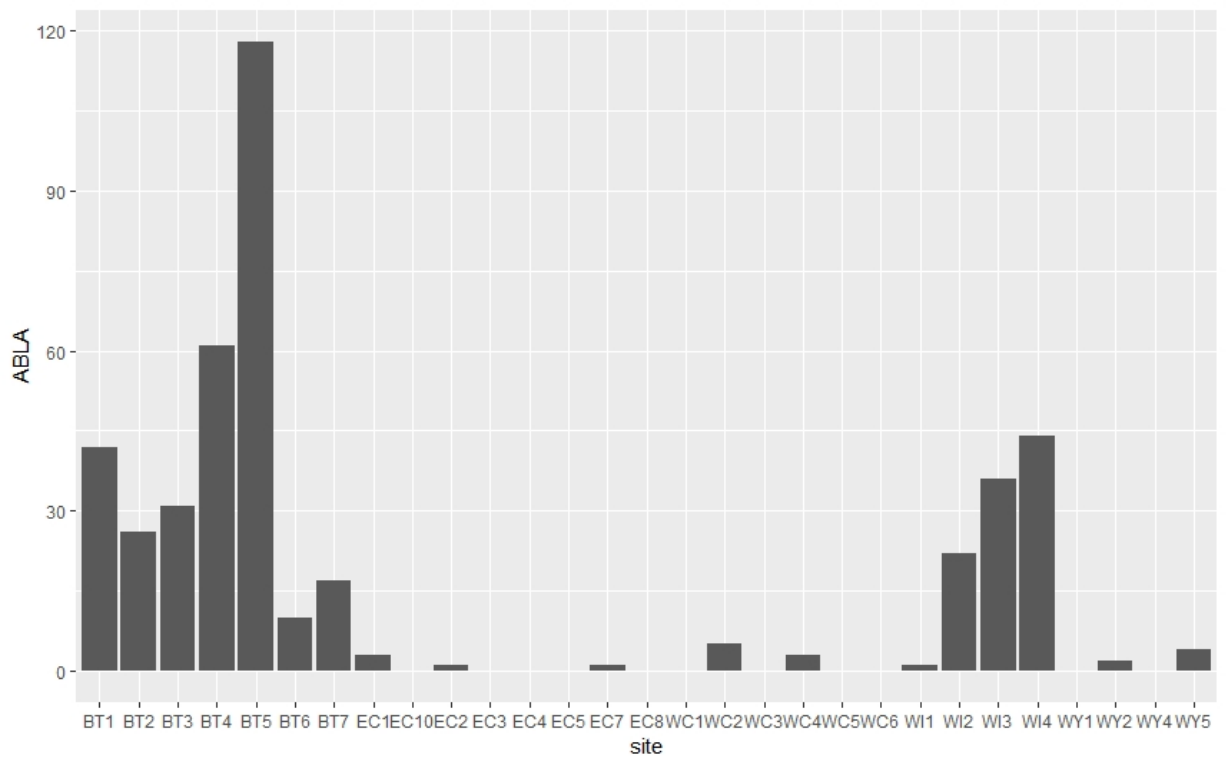
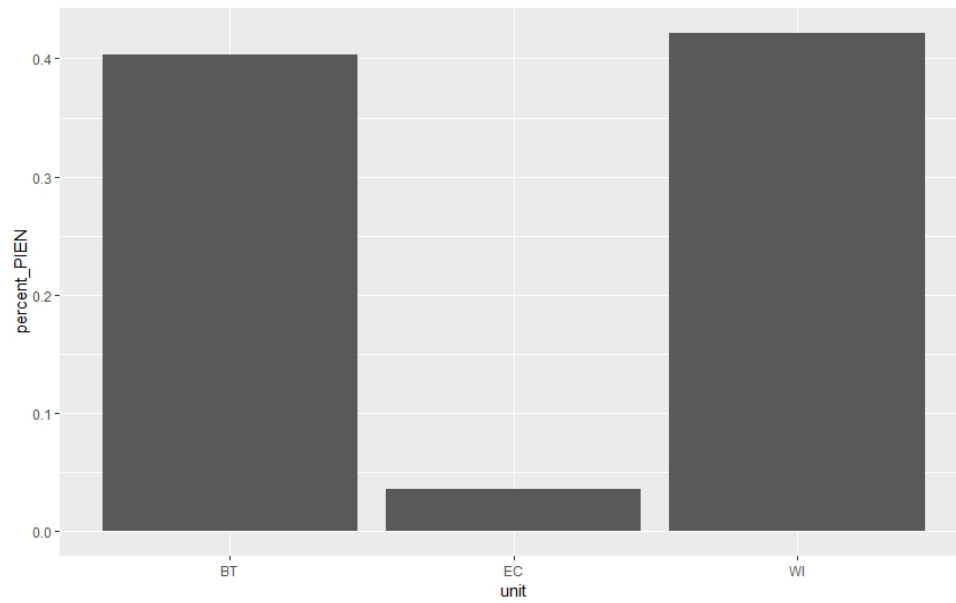


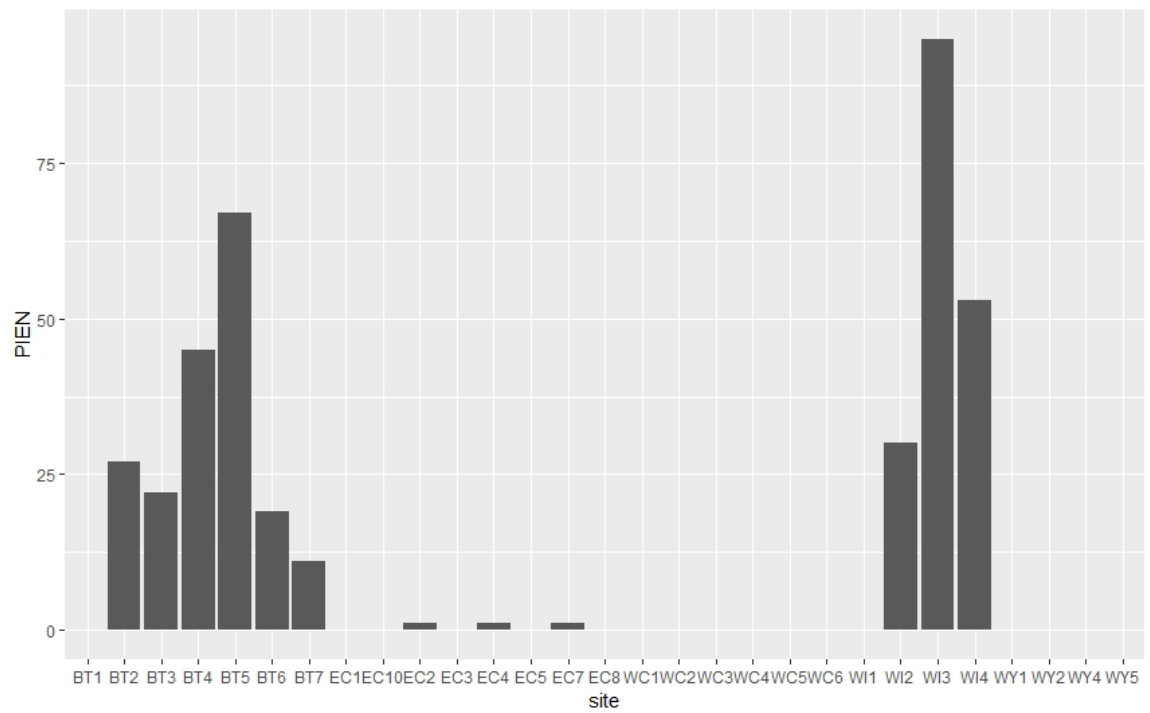
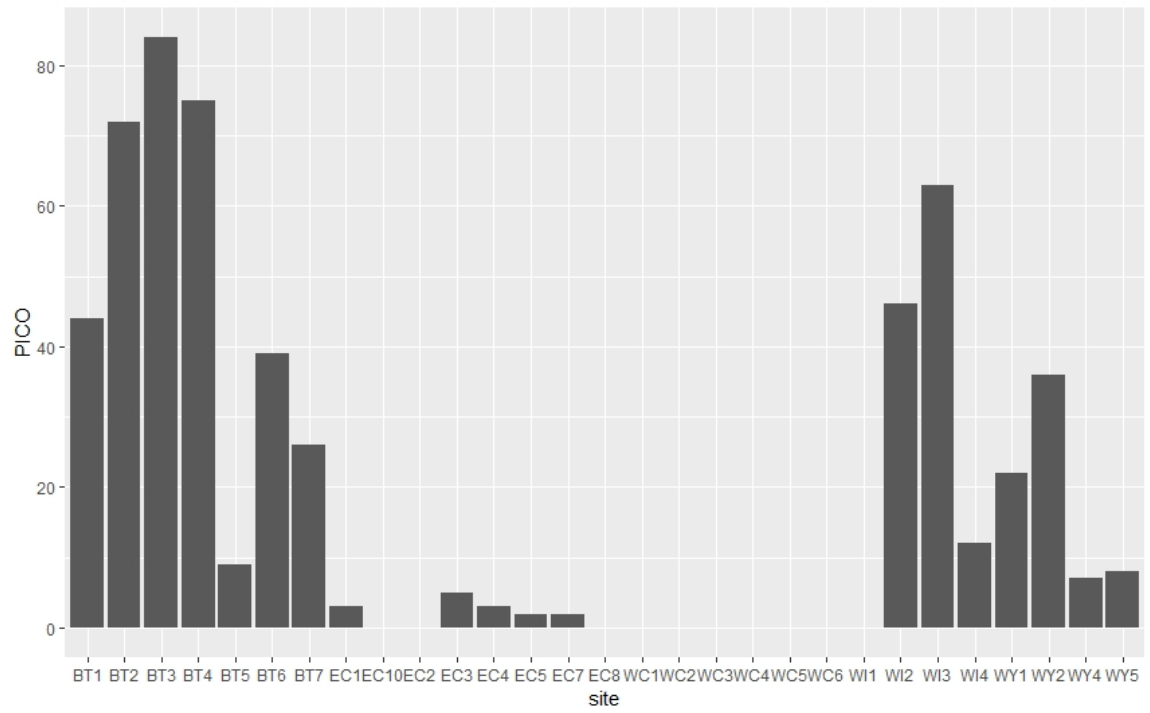


Competition Bar Graphs:

Similar to the box plots, we'll begin with an examination at the unit-level and then site-level. If a unit is not listed, then there were not any recorded competing individuals of that specific competing species at that unit. Units are in percent of WBP that had the competing species of interest present within a 1/100th acre plot. Sites are listed as counts and not percent of WBP with competitors.







APPENDIX D

SITE FIELD DATA TABLES

BT = Beartooth Unit, EC = East Centennial Unit, WC = West Centennial Unit,
 WI = Wind River Unit, WY = West Yellowstone Unit

	<u>BT-1</u>	<u>BT-2</u>	<u>BT-3</u>	<u>BT-4</u>	<u>BT-5</u>	<u>BT-6</u>	<u>BT-7</u>	<u>BT-ALL</u>
<u>Initial Planting Data</u>								
Year	1993	1993	1991	1991	1999	1991	1991	
Individuals	1700	1000	980	1000	8335	3110	1000	17125
Space (m ²)	15904	4097	8783	10603	78625	23917	11938	153867
Density (ind./m ²)	0.11	0.24	0.11	0.09	0.11	0.13	0.08	0.13
Space (acres)	3.93	1.01	2.17	2.62	19.43	5.91	2.95	38.02
Density (ind./acre)	432.57	987.83	451.6	381.68	429	526.2	339	506.84
<u>2018 Field Sampling Data</u>								
Grids	16	6	9	11	12	17	16	87
Individuals	44	80	85	77	187	79	52	604
Space (m ²)	1600	600	900	1100	1200	1700	1600	8700
Density (individuals/m ²)	0.028	0.133	0.094	0.07	0.156	0.046	0.033	0.08
Space (acres)	0.4	0.15	0.22	0.27	0.3	0.42	0.4	2.15
Density (individuals/acre)	111.3	539.6	382.2	283.3	630.6	188.1	131.5	323.8
<i>Density Change Ratio</i>	<i>0.257</i>	<i>0.546</i>	<i>0.846</i>	<i>0.742</i>	<i>1.470</i>	<i>0.357</i>	<i>0.388</i>	<i>0.639</i>
Percent of Site Sampled	0.1	0.15	0.1	0.1	0.02	0.07	0.13	0.1
Mean Height (cm)	134.4	178.2	173.9	195.6	81.1	224.9	169.2	165.3
Adjusted Mean Height (cm)	119.1	163.0	158.6	180.4	65.9	209.6	154.0	150.1
Summers Since Planted	24	24	26	26	18.5	26	26	24.36
Adjusted Establishment Period	21.5	21.5	23.5	23.5	16	23.5	23.5	21.86
<i>Growth Rate (cm/yr)</i>	<i>5.54</i>	<i>7.58</i>	<i>6.75</i>	<i>7.68</i>	<i>4.12</i>	<i>8.92</i>	<i>6.55</i>	<i>6.87</i>

	<u>EC-1</u>	<u>EC-2</u>	<u>EC-3</u>	<u>EC-4</u>	<u>EC-5</u>	<u>EC-7</u>	<u>EC-8</u>	<u>EC-10</u>	<u>EC-ALL</u>
<u>Initial Planting Data</u>									
Year	2010	2010	2010	2012	2012	2010	2010	2012	
Individuals	4835	999	2896	3603	1078	1839	3930	2590	22209
Space (m ²)	113433	23431	67947	43787	12829	43139	92187	33589	436818
Density (ind./m ²)	0.04	0.04	0.04	0.08	0.08	0.04	0.04	0.08	0.06
Space (acres)	28.03	5.79	16.79	10.82	3.17	10.66	22.78	8.3	107.94
Density (ind./acre)	172.5	172.5	172.5	333	340	172.5	172.5	312	235.83
<u>2018 Field Sampling Data</u>									
Grids	22	11	23	12	9	13	19	12	126
Individuals	21	12	20	12	11	21	2	14	113
Space (m ²)	2200	1100	2300	1200	900	1300	1900	1200	12600
Density (individuals/m ²)	0.01	0.011	0.009	0.01	0.012	0.016	0.001	0.012	0.009
Space (acres)	0.54	0.27	0.57	0.3	0.22	0.32	0.47	0.3	3.11
Density (individuals/acre)	38.63	44.15	35.19	40.47	49.46	65.37	4.26	47.21	36.08
Density Change Ratio	0.224	0.256	0.204	0.122	0.145	0.379	0.025	0.151	0.153
Percent of Site Sampled	0.02	0.05	0.03	0.03	0.07	0.03	0.02	0.04	0.04
Mean Height (cm)	40.86	45.17	43.05	37.67	28.18	51.14	10.5	25.07	31.29
Adjusted Mean Height (cm)	25.62	29.93	27.81	22.43	12.94	35.9	0	9.83	18.27
Summers Since Planted	7.5	7.5	7.5	5.5	5.5	7.5	7.5	5.5	6.61
Adjusted Establishment Period	5	5	5	3	3	5	5	3	4.11
Growth Rate (cm/yr)	5.12	5.99	5.56	7.48	4.31	7.18	0	3.28	4.44

	<u>WC-1</u>	<u>WC-2</u>	<u>WC-3</u>	<u>WC-4</u>	<u>WC-5</u>	<u>WC-6</u>	<u>WC-ALL</u>
<u>Initial Planting Data</u>							
Year	2011	2011	2011	2011	2011	2011	
Individuals	3610	1390	2182	2802	4833	6381	21198
Space (m ²)	70213	27033	42452	54511	94008	124117	412334
Density (ind./m ²)	0.05	0.05	0.05	0.05	0.05	0.05	0.05
Space (acres)	17.35	6.68	10.49	13.47	23.23	30.67	101.89
Density (ind./acre)	208.05	208.05	208.05	208.1	208.1	208.05	208.05
<u>2018 Field Sampling Data</u>							
Grids	17	13	13	18	19	22	102
Individuals	14	34	20	16	18	47	149
Space (m ²)	1700	1300	1300	1800	1900	2200	10200
Density (individuals/m ²)	0.008	0.026	0.015	0.009	0.009	0.021	0.015
Space (acres)	0.42	0.32	0.32	0.44	0.47	0.54	2.52
Density (individuals/acre)	33.33	105.84	62.26	35.97	38.34	86.46	60.37
Density Change Ratio	0.160	0.509	0.299	0.173	0.184	0.416	0.290
Percent of Site Sampled	0.02	0.05	0.03	0.03	0.02	0.02	0.03
Mean Height (cm)	43.64	32.15	40.3	33	37.28	41.17	37.92
Adjusted Mean Height (cm)	28.4	16.91	25.06	17.76	22.04	25.93	22.68
Summers Since Planted	6.5	6.5	6.5	6.5	6.5	6.5	6.5
Adjusted Establishment Period	4	4	4	4	4	4	4
Growth Rate (cm/yr)	7.1	4.23	6.27	4.44	5.51	6.48	5.67

	<u>WI-1</u>	<u>WI-2</u>	<u>WI-3</u>	<u>WI-4</u>	<u>WI-ALL</u>
<u>Initial Planting Data</u>					
Year	2013	2002	2002	2002	
Individuals	7434	5101	3728	3924	20187
Space (m ²)	124223	231773	163776	76941	596714
Density (ind./m ²)	0.06	0.02	0.02	0.05	0.04
Space (acres)	30.7	57.27	40.47	19.01	147.45
Density (ind./acre)	242.18	89.07	92.12	206.39	157.44
<u>2018 Field Sampling Data</u>					
Grids	27	17	22	13	79
Individuals	86	82	210	123	501
Space (m ²)	2700	1700	2200	1300	7900
Density (individuals/m ²)	0.032	0.048	0.095	0.095	0.068
Space (acres)	0.67	0.42	0.54	0.32	1.95
Density (individuals/acre)	128.9	195.2	386.29	382.9	273.32
Density Change Ratio	0.532	2.192	4.193	1.855	1.736
Percent of Site Sampled	0.02	0.01	0.01	0.02	0.01
Mean Height (cm)	35.9	211.85	174.28	145.85	141.97
Adjusted Mean Height (cm)	20.66	196.61	159.04	130.61	126.73
Summers Since Planted	5	17	17	17	14
Adjusted Establishment Period	2.5	14.5	14.5	14.5	11.5
Growth Rate (cm/yr)	8.26	13.56	10.97	9.01	11.02

	<u>WY-1</u>	<u>WY-2</u>	<u>WY-3</u>	<u>WY-5</u>	<u>WY-ALL</u>
<u>Initial Planting Data</u>					
Year	1999	1998	2002	2001	
Individuals	5000	1100	10000	2800	18900
Space (m ²)	46175	18009	111815	32860	208858
Density (ind./m ²)	0.11	0.06	0.09	0.09	0.09
Space (acres)	11.41	4.45	27.63	8.12	51.61
Density (ind./acre)	438.21	247.19	361.93	344.83	348.04
<u>2018 Field Sampling Data</u>					
Grids	13	7	14	7	41
Individuals	59	59	9	11	138
Space (m ²)	1300	700	1400	700	4100
Density (individuals/m ²)	0.045	0.084	0.006	0.016	0.038
Space (acres)	0.32	0.17	0.35	0.17	1.01
Density (individuals/acre)	183.67	341.09	26.02	63.59	153.59
Density Change Ratio	0.419	1.380	0.072	0.184	0.441
Percent of Site Sampled	0.03	0.04	0.01	0.02	0.03
Mean Height (cm)	153.68	143.17	176.11	144.82	154.44
Adjusted Mean Height (cm)	138.44	127.93	160.87	129.58	139.2
Summers Since Planted	18.5	19	16	16.5	17.5
Adjusted Establishment Period	16	16.5	13.5	14	15
Growth Rate (cm/yr)	8.65	7.75	11.92	9.26	9.28

<u>ALL SITES</u>	
<u>Initial Planting Data</u>	
Year	
Individuals	99619
Space (m ²)	1808591
Density (ind./m ²)	0.07
Space (acres)	446.91
Density (ind./acre)	298.02
<u>2018 Field Sampling Data</u>	
Grids	435
Individuals	1505
Space (m ²)	43500
Density (individuals/m ²)	0.038
Space (acres)	10.75
Density (individuals/acre)	155.37
<i>Density Change Ratio</i>	<i>0.521</i>
Percent of Site Sampled	0.05
Mean Height (cm)	95.07
Adjusted Mean Height (cm)	80.5
Summers Since Planted	13.17
Adjusted Establishment Period	10.67
<i>Growth Rate (cm/yr)</i>	<i>7.55</i>