ASPEN GROWTH RESPONSE IN THE PRESENCE OF INTER-ANNUAL CLIMATE FLUCTUATION AND DISTURBANCE IN THE LAKE TAHOE BASIN

By

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ABSTRACT

ASPEN GROWTH RESPONSE IN THE PRESENCE OF INTER-ANNUAL CLIMATE FLUCTUATION AND DISTURBANCE IN THE LAKE TAHOE BASIN

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In the western US, aspen forests tend to be small and rare, but have great ecological importance. There is much interest and concern over how aspen in the Sierra Nevada Mountains of the western USA will respond to a changing climate and future disturbances. Impacts from climate change create stress on aspen trees that further compound threats to aspen communities. This analysis assessed the radial growth response of aspen under previously recorded climate conditions to better understand how measurable climate variables affect aspen growth. Along with aspen's growth response to climate, this analysis also assessed the growth response of aspen within the vicinity of a wildfire by measuring growth from aspen stands above and below the 2002 Showers fire footprint. Increment cores were collected from aspen trees in 20 stands around Lake Tahoe, California and Nevada, USA, spanning different aspects, elevations, and species compositions. Tree ring widths were measured using WinDENDRO and the data were visually cross-dated through microscopic comparison. The relationship between aspen growth, climate, disturbance, and stand conditions were analyzed using linear mixed effects regression. The models incorporated random effects for time and space since the data exhibited temporal and spatial autocorrelation. The data were separated into northeast (NE) and southwest (SW) regions of the Lake Tahoe Basin based on the similarities of the stands' climate values revealed by a dendrogram. In both regions, the most influential climate variables were annual maximum temperature and annual precipitation. In the NE region, the highest aspen tree basal area increment (BAI) was measured in previously recorded years with a low temperature/high precipitation climate regime. For the SW region of the Lake Tahoe Basin, aspen tree BAI was higher under a low temperature/low precipitation climate regime. Along with climate, stand level variables such as canopy stratum (overstory/understory), elevation, and species composition (percent aspen presence) also influenced growth of aspen trees. The regression analysis indicated that aspen BAI was greater in areas with a higher proportion of aspen composition and for dominant trees in the canopy. However, aspen BAI declined with increases in elevation.

The post-wildfire analysis modeled how aspen responded when downstream of a wildfire compared to unaffected stands upstream, where downstream aspen could be influenced by added availability of water and nutrients, due to increased runoff and erosion from the fire. However, only the stand closest to the burned area exhibited a significant increase in aspen tree growth downstream from the wildfire. A response was not detected when stands further downstream were included in the analysis. Therefore, a wildfire could produce increases in aspen growth post-disturbance depending on proximity to the fire. In terms of growth response longevity, increased growth was detected in ratios of growth over a 3- and 5-year period from when the fire occurred.

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INTRODUCTION

Paradoxically, quaking aspen (*Populus tremuloides)* is the most widely distributed tree species in North America (Mitton & Grant 1996), yet it is threatened and becoming scarce in parts of the southwestern US where it has great ecological importance (Manley & Schlesinger 2001, Kuhn et al. 2011). The presence of aspen is particularly desirable in the Sierra Nevada Mountains of California and Nevada, where conifers are outcompeting aspen and dominate the landscape (Shepperd et al. 2006). Aspen communities are rare and have a disproportionately high importance for such attributes as their higher productivity rates from the decomposition of deciduous aspen foliage (King et al. 2001). This high productivity is one factor that allows increased diversity of both plant and animal life by providing favorable conditions for a high diversity of understory plant species (Kuhn et al. 2011). An example of plant diversity within the Lake Tahoe Basin measured counts of 1,308 vascular plants, 115 nonvascular plants, and 573 fungi and lichens (Manley & Schlesinger 2001). Much of this biodiversity resides within aspen stands which cover less than 2% of the Lake Tahoe Basin (Shepperd et al. 2006). Another factor promoting biodiversity could be the high soil moisture and humidity within the riparian aspen ecosystem (Potter 1998). Aspen stands play a protective role in these sensitive areas, and serve as an important foundation species that must be conserved or restored in order to foster biodiversity and numerous other values and services associated with aspen stands (Shepperd et al. 2006).

Due to the changes in Earth's climate, ecosystems may exhibit changes in composition, shifts in natural species range, or even potential extinction of the minority species due to the loss of habitat (Allen et al. 2010, Flanagan et al. 2016). Rehfeldt et al. (2009) studied aspen in relation to a changing climate from the Rocky Mountains extending the entire western US and found that, based on three general circulation models and two scenarios, aspen stands within the study area were predicted to suffer a 46-94% reduction by 2090. In the Lake Tahoe Basin, aspen comprise a small percentage of the forest composition and are found in isolated patches surrounded by mixed-conifer (pine and fir) forests (Shepperd et al. 2006). Climate within the Lake Tahoe Basin is expected to undergo a "minimum temperature rise of 4.3°C by 2100 under the [model] A2 emissions scenario" (Dettinger 2013). According to the study, the model A2 scenario was a projection for a worst case scenario; however, emission levels have already exceeded its estimated inputs. The continued fluctuation in climate is expected to impact aspen ecosystems by applying stress from years of consecutive drought (Hogg et al. 2008), along with increased competition from mixed-conifer species (Pierce & Taylor 2010). Hogg et al. (2008) assessed the health and mortality of aspen during drought conditions and concluded that during 2000-2002, drought conditions were associated with a doubling of mortality of aspen regeneration and reduced stand growth by 30%. Anderegg et al. (2012) found that climate conditions further facilitated mortality of aspen by increasing water stress, making the trees more susceptible to other disturbances. As with climate change, another stress inducing agent is defoliation by insects, which may facilitate the deaths of already stressed aspen trees (Hogg et al. 2002).

In addition to factors directly affecting aspen regeneration and growth, such as within-stand competition from conifers, changes in regional climate and disturbances outside aspen stands also have the potential to indirectly impact aspen. Sustained warming and drying causing regional drought could threaten riparian aspen by reducing or eliminating summer flows in small creeks that sustain aspen. Increasing densities of conifers further up the watershed may consume available soil moisture before it can move down the watershed. Conversely, disturbances such as harvesting or wildfire higher in the watershed could make more growth-limiting resources, such as water, available to aspen downstream (Johansen et al. 2001, Robichaud et al. 2013). Disturbances adjacent to aspen stands could liberate growing space and allow aspen to expand or migrate into the new area (Brewen 2019, Brewen et al. 2020).

Aspen is a light-demanding pioneer species (wind dispersed pollen and seed) that favors open areas with low competition and cool moist summers for successful seedling establishment (Turner et al. 2003). Aspen also regenerate *in situ* after disturbances that promote vegetative regeneration via root suckering (Perala 1990). Fire as a disturbance has been suppressed from the Lake Tahoe Basin over the past century due to the risk of high severity fire within the wildland urban interface. The lack of disturbance has long added stress to aspen by increasing competition with coniferous trees that cast shade on the shade intolerant aspen (Shepperd et al. 2001, Pierce & Taylor 2010). Berrill & Dagley (2012, 2014) and Berrill et al. (2016) studied aspen growth in mixed aspen-conifer stands and pure aspen stands finding that aspen showed a growth reduction of up to 30% in mixed stands when compared to those in pure aspen stands. Berrill et al. (2017) also measured reduced growth in Sierra Nevada aspen regeneration during drought years, and found that conifer removal enhanced understory light availability and the growth of young aspen. Jones et al. (2005) also reported benefits associated with the removal of conifers competing with aspen.

Conifers outcompeting aspen in mixed stands have become a major concern, and climate conditions that favor conifer, or impact aspen, may accelerate the process of succeeding aspen with a mixed-conifer forest. With a re-introduction of disturbances, such as fire, it is hypothesized that fire could favor aspen by removing conifers and promoting root sucker regeneration (Krasnow et al. 2012). Fire can trigger a hormonal response in aspen to begin sprouting from their intact root system (Frey et al. 2003). Yang et al. (2015) measured aspen coverage based on simulation scenarios and reported increased aspen cover post-fire in areas experiencing a high fire frequency. Wildfire also allows aspen to expand and cover larger areas (Brewen 2019, Brewen et al. 2020). Smith et al. (2011) recorded ranges of 500 to 228,000 aspen stems per hectare post-fire. Thinning and pile burning of cut conifers also promoted aspen regeneration (Dagley et al. 2020). These studies highlight the potential for fire use as a restoration tool that promotes aspen regeneration and growth. Furthermore, the influence of disturbances, stand conditions, and geographic location on aspen growth must be accounted for in analyses of aspen growth-climate relationships.

Rapid tree growth and successful regeneration and recruitment to the overstory indicate that a species has adequate access to resources and growing space. The radial growth of aspen trees is linked to aspen vigor, in terms of crown ratio, where aspen with larger crowns exhibit more rapid radial growth (Berrill & Dagley 2012). It follows that rapid radial growth of aspen trees is a useful indicator of performance and success. Furthermore, radial tree growth is the lowest priority for carbon allocation, indicating that a tree with increasing stem diameter also has enough energy to perform necessary maintenance, growth and defense functions. As such, radial growth is the first facet of tree growth to slow or stop under adverse or resource-limited conditions (Oliver & Larson 1996). Short-term reductions in radial growth of aspen can be caused by many factors including drought or otherwise inhospitable growing season climate (Hogg et al. 2008) or re-allocation of carbon to defense or foliage replacement after insect defoliation (Berrill et al. 2017). Short-term increases in radial growth could also be indicative of disturbances within or outside aspen stands that somehow favored aspen by providing limiting resources (e.g., light or soil moisture), such as loss or removal of trees competing with aspen (Bates & Davies 2006) or enhanced soil moisture resulting from changes upstream (Cavus et al. 2019).

Given that plants require sunlight and water to photosynthesize, the most important climate variables associated with growth would likely be a form of interaction between precipitation and temperature. Dudley et al. (2015) studied growth-climate relationships throughout Colorado and Wyoming, consistently finding that aspen radial tree growth correlated with temperature and precipitation. Each climate variable within this analysis was dependent, in part, on these two variables. Vapor pressure deficit (VPD) is the difference between the moisture in the air and how much moisture the air can hold. Hogg & Hurdle (1997) studied the VPD relationship with growth of aspen and its relation to stomatal conductance during transpiration, and its effect on net photosynthesis. Dew point temperature (dp) is the temperature of the air when water saturates in 100% humidity. The dew point temperature uses relationships of temperature, water molecules in the air, and pressure to estimate the point at which water forms around leaves (Roberts 2003). The Palmer drought severity index (PDSI) is a measure of dryness and drought conditions of the soil which also accounts for precipitation and temperature fluctuation (Alley 1984). Identifying the relationship between aspen radial growth and influential climate variables would provide a better understanding of which climate variables most strongly correlate with the growth of aspen. This would contribute to a mechanistic understanding of how climate fluctuations alter aspen growth.

The primary objective of this study was to examine the relationship of aspen growth rates to measurable climate variables from 1991-2011 in the Lake Tahoe Basin, USA. Climate variables expected to influence tree growth were chosen based on *a priori* knowledge and variables used in previous studies: temperature, precipitation, vapor pressure deficit (VPD), dew point temperature (dp), snowfall, and Palmer drought severity index (PDSI). I hypothesized that aspen radial growth would correlate with a different suite of climate variables and their interactions at different locations around the Lake Tahoe Basin. As a secondary objective, the presence of the 2002 Showers fire within our study area provided an opportunity to study aspen growth upstream and downstream of a burned area. Understanding aspen growth response downstream of a wildfire may support re-introduction of fire on the landscape as a forest restoration tool.

The hypothesis being that more nutrients and/or water could become available downstream of a burned area, leading to greater aspen radial growth.

METHODS

Study Area

The Lake Tahoe Basin (N 39°05 W 120°02) is located in the central Sierra Nevada Mountains of California and Nevada, USA (Figure 1). The climate in the area consists of warm dry summers, followed by cold winters. During the summer, the average maximum temperature is around 25.9°C and the average minimum temperature is around 4.3°C. During the winter, the average maximum temperature is around 5.0°C and the average minimum is around -9.4°C. Annual precipitation averages around 690 mm on the northeastern region of the Lake Tahoe Basin, and 1135 mm on the southwestern region. Most of the precipitation in the Lake Tahoe Basin falls as snow in the winter averaging around 510 cm of snowfall (https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca8758).

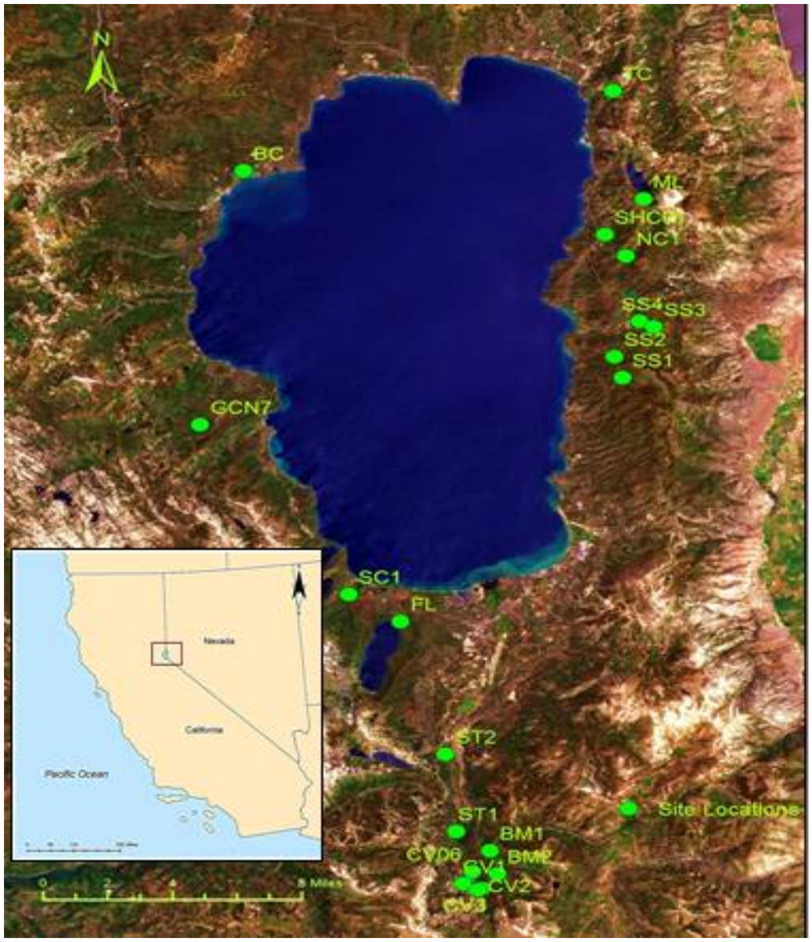


Figure 1. Study sites around Lake Tahoe, California and Nevada, USA.

Data Collection

Twenty aspen stands were sampled to represent the range of geographic locations and elevations occupied by aspen within the Lake Tahoe Basin (Figure 1). Up to 10 aspen trees were selected for sampling in each of the 20 stands. Sample trees covered a wide range of sizes, and were selected to cover a range of individual stand densities and species compositions within the immediate vicinity of each sampled tree (Berrill &

Dagley 2012). For each aspen tree, measurements of diameter at breast height (dbh), stratum, crown height, vicinity basal area (VBA), percent aspen presence, and location in respect to Lake Tahoe were recorded. Bark-to-pith cores were collected at breast height for each aspen tree. Stems >20 cm dbh were cored twice, at right angles beginning with the uphill side, and stems <10 cm dbh were cored once on the uphill side.

Annual climate data for temperature (mean, minimum, maximum), precipitation, VPD (minimum and maximum), and dew point temperature were extracted using the PRISM website (http://prism.oregonstate.edu). The PRISM dataset provided annual average values from 1991-2011 for each aspen stand sampled. The PDSI and snowfall values were collected from the Western Regional Climate Center that partner with the National Oceanic and Atmospheric Administration (NOAA) to cover all of Lake Tahoe at lake level (~1906 m elevation). The PDSI was measured on a scale of weekly values which were converted to annual averages (ftp://ftp.cpc.ncep.noaa.gov/htdocs/temp2/). Snowfall estimates were recorded as annual averages (https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca8758), and unlike the other climate variables, snowfall data were only available basin wide as opposed to site-specific.

Data Analysis and Modeling

Dendrochronology

Increment cores were dried and mounted to boards using standard dendrochronological techniques (Speer 2010). To ensure the accuracy of ring detection, cores were sanded down using 1000 grit sandpaper. This method was chosen due to the difficulty of examining ring-porous hardwood cores. Annual ring widths were measured using a high resolution (1200 dpi) flatbed scanner and WinDENDRO software (Regent Instruments Inc.). Cross-dating of the rings was done visually and any anomalies to the overall trend were cross checked visually using a microscope. Visual cross-dating was used instead of software, such as COFECHA, due to the small sample size which would have produced misleading intercorrelation estimates. The software is typically used for chronologies that span hundreds of years. Since aspen >20 cm dbh were cored twice, the ring width data for each year were averaged when both cores had a complete ring record spanning 1991-2011; otherwise the core with the longest ring record was selected for analysis.

Growth-Climate Analysis

Using the increment core data, measurements of ring width and dbh were used to reconstruct estimates of aspen tree growth for each year (1991-2011). Firstly, subtracting two times the bark thickness from the diameter produced a diameter inside the bark (dib) measurement. The dib was then subtracted from two times each year's incremental growth width and these values were used to convert from diameter measurements to tree basal area (BA). Estimates of tree BA increment (BAI) were obtained by subtracting the previous year’s BA from the current BA. BAI was chosen to represent growth instead of dbh increment because BAI reduced the influence of tree size on growth. Differencing of the growth variable was performed to reduce short-term cyclical trends within the sample.

The data were analyzed using linear mixed effects models within R's 'nlme' package to include random effects for sites, tree ID, and years (R Core Team 2017). The random effects were used to aid in structuring the error in the model to account for breaches in the assumption of independence of a linear model as the data contained multiple values from a single source. A correlation matrix of the climate variables was used to check for multicollinearity within variables selected in the models. Selection of the best candidate set of models was based on small-sample size corrected Akaike Information Criterion (AICc), which accounts for the penalty associated with the increase in the number of parameters used in the model, along with a penalty for small sample sizes (Burnham & Anderson 2003).

Post-Wildfire Analysis

Data from 4 sites upstream and 2 sites downstream of the 2002 Showers fire were used to test for an effect wildfire could produce on the growth of aspen trees downstream. The aspen tree BAI were summed for 3-, 4- and 5-year periods pre- and post-2002 Showers fire. The values were then divided (Σpost-fire/Σpre-fire) to create a ratio of differences in aspen growth before and after the wildfire. A linear mixed effects model incorporated tree-level variables dbh, crown ratio, vicinity basal area (VBA), canopy stratum (overstory/understory), and presence of disturbance (yes/no) as fixed effects; along with a random effect for the different site locations. AICc statistics were used to determine the best model among candidate models predicting growth response as a ratio of pre- and post-fire BAI.

RESULTS

Aspen Growth-Climate Relationship

Sampled aspen trees covered a wide range of tree sizes and growth rates, and experienced a wide range of climatic conditions over the 20-year study period (Table 1).

Table 1. Summary data for aspen tree size, growth, and climate variables for 155 aspen trees at 20 study sites around the Lake Tahoe Basin over a 20 year period 1991-2011.

Code	Variable	Unit	Mean	St.Dev	Min	Max
dbh	Diameter at Breast Height	Millimeters (mm)	202.89	104.27	60.00	555.00
BAI	Basal Area Increment	mm^2 $year^{-1}$	759.92	582.30	2.43	5061.84
Elev	Elevation	Meters (m)	2191.90	163.94	1904.00	2405.00
Precip	Precipitation	Millimeters (mm)	919.95	359.50	385.86	2085.43
Tmin	Minimum Temperature	Celcius (°C)	0.02	0.98	-2.40	2.00
Tmean	Average Temperature	Celcius (°C)	6.22	0.96	3.30	7.90
Tmax	Maximum Temperature	Celcius (°C)	12.43	1.23	9.10	15.60
dp	Dew point	Celcius (°C)	-4.99	1.44	-8.60	-1.30
VPDmin	Minimum Vapor Pressure Deficit	HectoPascal (hPa)	2.33	0.56	0.62	3.58
VPDmax	Maximum Vapor Pressure Deficit	HectoPascal (hPa)	11.92	1.28	8.88	14.96
PDSI	Palmer Drought Severity Index	-	-1.36	2.42	-5.28	3.37
Snowfall	Snowfall	Centimeters (cm)	510.41	140.22	209.55	848.36
VBA	Vicinity Basal Area	m^2 ha^{-1}	41.45	22.65	9.18	156.11
PctAsp	Percent Aspen	Proportion (%/100)	0.76	0.28	0.11	1.00
CrHt	Crown Height	Meters (m)	6.15	3.92	0.80	23.30

Due to the wide ranging values, the growth-climate data had non-normal residuals that violated the assumptions of a linear model. Due to this violation, a transformation of the BAI response variable was implemented to normalize the residuals and create a constant variance. Unfortunately, even with a square root transformation, there remained a noticeable departure from the assumptions required within a normal distribution model (Appendix A). These errors were associated with the structure of the data and the increased variability of the sample ranges used within the model. Therefore, in order to reduce to the variability, samples were tested for cluster recognition within a dendrogram. A dendrogram, in the form of a heatmap, was created revealing how the site locations could be grouped based on climate data for each site (Figure 2). From the clustering of climate variables within the different sites, grouped sites were created with similar climate attributes. One clear determining factor of how the similar sites might be grouped was based on the similarities in precipitation values for each site location around Lake Tahoe (Figure 2). The data were then split into NE and SW regions based on site climate similarities. After the data were grouped, the assumptions of a linear model were better fit after applying the square root transformation to the BAI (Appendix B, Appendix C).

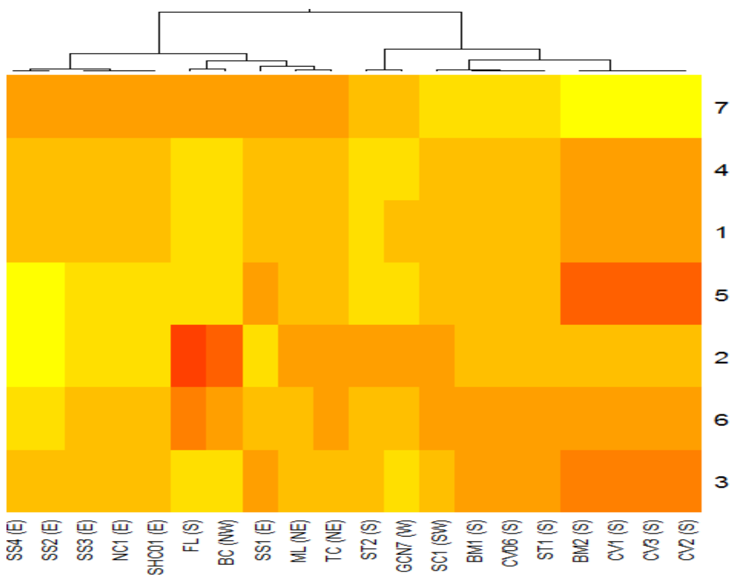


Figure 2. Heatmap dendrogram of the 20 aspen study sites and their position around Lake Tahoe (N, NE, S, SW, E, W) grouped by climate variables. 1: VPDmax, 2: VPDmin, 3: dp, 4: Tmax, 5: Tmean, 6: Tmin, 7: Precipitation.

NE Region Analysis

There were variations among tree-level, stand-level, and climate variables among sample aspen stands located on the northern and eastern regions of the Lake Tahoe Basin (Table 2).

Table 2. Summary data for aspen tree size, growth, and climate variables for 71 aspen trees at 9 study sites located on the northern and eastern shores of the Lake Tahoe Basin over a 20 year period from 1991-2011.

Code	Variable	Unit	Mean	St.Dev	Min	Max
dbh	Diameter at Breast Height	Millimeters (mm)	202.70	98.59	68.00	470.00
BAI	Basal Area Increment	mm^2 $year^{-1}$	637.36	465.15	10.06	3611.28
Elev	Elevation	Meters (m)	2230.87	117.04	1963.00	2405.00
Precip	Precipitation	Millimeters (mm)	690.54	212.72	385.86	1388.00
Tmin	Minimum Temperature	Celcius (°C)	0.50	0.93	-2.10	2.00
Tmean	Average Temperature	Celcius (°C)	6.64	0.68	4.30	7.90
Tmax	Maximum Temperature	Celcius (°C)	12.78	0.84	10.10	15.20
dp	Dew point	Celcius (°C)	-4.68	1.15	-7.20	-1.50
VPDmin	Minimum Vapor Pressure Deficit	HectoPascal (hPa)	2.41	0.63	0.62	3.58
VPDmax	Maximum Vapor Pressure Deficit	HectoPascal (hPa)	12.12	1.12	9.28	14.52
PDSI	Palmer Drought Severity Index	-	-1.36	2.42	-5.28	3.37
Snowfall	Snowfall	Centimeters (cm)	510.41	140.22	209.55	848.36
VBA	Vicinity Basal Area	m^2 ha^{-1}	41.90	22.66	9.18	110.19
PctAsp	Percent Aspen BA	Proportion (%/100)	0.74	0.30	0.14	1.00
CrHt	Crown Height	Meters (m)	6.16	4.02	1.50	21.40

After analyzing the data with a series of aspen growth-climate models for the NE region, there were similar likelihood values among the models (Table 3). The two best models included precipitation and temperature variables (i.e., Tmax or Tmin). Between these two models, the best model included the interaction between maximum temperature and precipitation, along with stand elevation, canopy stratum and percent aspen presence

(Table 4). The high uncertainty associated with the Tmax:Precip interaction is noteworthy; nevertheless the best model with maximum temperature and precipitation has a 0.46 AICc weight meaning there is a 46% chance it is the best model describing the data given the candidate set of models (Table 4).

Table 3. Best candidate models for the NE region Lake Tahoe Basin aspen growth-climate analysis with number of parameters (K), AICc scores, change in AICc scores (Delta_AICc), and log likelihood (LL).

	K	AICc	Delta_AICc	AICcWt	LL
Tmax*Precip+Elev+Stratum +PctAsp	10	9134.43	0	0.46	-4557.13
Precip*Tmin+Elev+Stratum +PctAsp	10	9135.25	0.82	0.30	-4557.54
VPDmax+VPDmin+Precip+ PDSI+Elev+Stratum+PctAsp	11	9136.94	2.52	0.13	-4557.37
VPDmin+Precip+PDSI+Elev+ Stratum+PctAsp	10	9137.47	3.04	0.10	-4558.65
Precip*VPDmin+Elev +Stratum+PctAsp	10	9141.37	6.94	0.01	-4560.65
Null model with RandomEffects	4	9491.82	357.39	0	-4741.90

By holding all stand level variables constant at their mean, climate effects on aspen growth could be modeled (Figure 3). According to the best model, the NE region aspen growth rates were estimated to be highest in years receiving high precipitation with cooler maximum temperatures and lowest in years experiencing the highest maximum temperature values (Figure 3A & 3B). Based on the estimates from Figure 3A, the measured ranges of maximum temperature were the greatest determining factor in aspen BAI. The only scenario where growth increased with increasing precipitation amounts was when maximum temperature was held at its minimum value within the range of data.

By holding climate variables constant at the mean, stand level variables that influence aspen BAI could be modeled. The best growth was measured in pure aspen stands regardless of elevation (Figure 3C) and growth was greater in stands located in lower elevation ranges (Figure 3D).

Table 4. Aspen tree growth-climate model for the NE region of the Lake Tahoe Basin. Coefficients and fit statistics for fixed effects in the generalized linear mixed effects model fitted to the grouped data from 1991-2011 (n=1331).

	Estimate	Std. Error	DF	t-value	p-value
Intercept	55.25558	15.25	1125	3.62	0.0003
Tmax	0.35361	0.980	1125	0.36	0.7100
Precip	0.01755	0.010	1125	1.21	0.2200
Elev	-0.01636	0.002	1125	-6.98	< 0.0001
StratumC	-7.85942	0.430	1125	-18.23	< 0.0001
PctAsp	6.46807	0.750	1125	8.61	< 0.0001
Tmax:Precip	-0.00149	0.001	1125	-1.32	0.1800

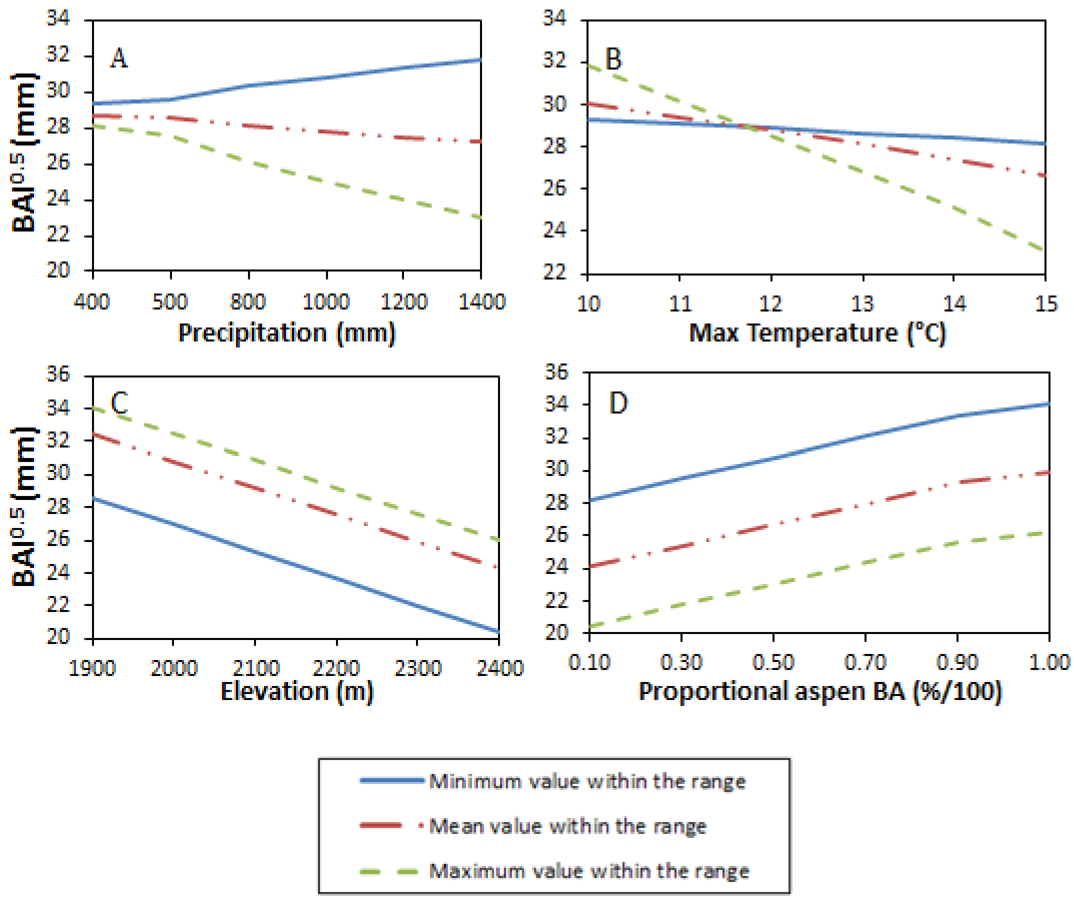


Figure 3. Relationship between aspen tree basal area increment (BAI; square root transformed) and measured climate variables located on the northeastern side of the Lake Tahoe Basin including: (A) BAI and precipitation relationship with maximum temperature values held constant, (B) BAI and maximum temperature relationship with precipitation held constant, (C) BAI and elevation relationship with species composition in terms of percent aspen BA held constant, and (D) BAI and aspen as a proportion of total BA relationship with elevation held constant.

SW Region Analysis

Although stand conditions and snowfall estimates were recorded as similar to the NE region climate data (Table 2), precipitation amounts were 64% greater on average in the SW region (Table 5).

Table 5. Summary data for aspen tree size, growth, and climate variables for 84 aspen trees for 11 study sites grouped on the SW side of the Lake Tahoe Basin over a 20 year period from 1991-2011.

Code	Variable	Unit	Mean	St. Dev	Min	Max
dbh	Diameter at Breast Height	Millimeters (mm)	203.06	109.42	60.00	555.00
BAI	Basal Area Increment	mm year	875.05	653.59	2.43	5061.84
Elev	Elevation	Meters (m)	2155.30	191.06	1904.00	2379.00
Precip	Precipitation	Millimeters (mm)	1135.44	335.09	495.24	2085.43
Tmin	Minimum Temperature	Celcius (°C)	-0.43	0.79	-2.40	1.50
Tmean	Average Temperature	Celcius (°C)	5.84	1.02	3.30	7.80
Tmax	Maximum Temperature	Celcius (°C)	12.10	1.43	9.10	15.60
dp	Dew point	Celcius (°C)	-5.29	1.61	-8.60	-1.30
VPDmin	Minimum Vapor Pressure Deficit	HectoPascal (hPa)	2.25	0.48	0.93	2.96
VPDmax	Maximum Vapor Pressure Deficit	HectoPascal (hPa)	11.73	1.38	8.88	14.96
PDSI	Palmer Drought Severity Index	-	-1.36	2.42	-5.28	3.37
Snowfall	Snowfall	Centimeters (cm)	510.41	140.22	209.55	848.36
VBA	Vicinity Basal Area	m^2 ha^{-1}	41.02	22.65	9.18	156.11
PctAsp	Percent Aspen BA	Proportion (%/100)	0.77	0.26	0.11	1.00
PctCon	Percent Conifer BA	Proportion (%/100)	0.23	0.26	0.00	0.89
CrHt	Crown Height	Meters (m)	6.14	3.83	0.80	23.30

The best model of aspen BAI in the SW region included the same predictor variables as the model for the NE region: the interaction of maximum temperature and precipitation along with stand elevation, stratum, and percent aspen presence (Table 6).

Table 6. Best candidate models for the SW region Lake Tahoe Basin aspen growth-climate analysis with number of parameters (K), AICc scores, change in AICc scores (Delta_AICc), and log likelihood (LL).

	K	AICc	Delta_AICc	AICcWt	LL
Tmax*Precip+Elev+Stratum +PctAsp	10	9919.73	0	0.49	-4949.79
Precip*VPDmin+Elev+Stratum +PctAsp	10	9919.97	0.25	0.43	-4949.91
dp+Precip+Tmax+Snowfall +Elev+Stratum+PctAsp	10	9923.90	4.17	0.06	-4951.87
Tmax*Snowfall+Elev +Stratum+PctAsp	10	9927.87	8.15	0.01	-4953.86
dp*Tmax+Elev+Stratum +PctAsp	10	9929.18	9.45	0	-4954.51
Null model with RandomEffect	4	10523.99	604.26	0	-5257.98

According to the best model, the estimates of aspen growth in the SW region (Table 7) were greater than those in the NE region (Table 4). In the SW region, the climate regime modeled to maximize BAI was during years experiencing a low precipitation/low maximum temperature climate (Figure 4A & 4B). In scenarios with high precipitation/low temperature climate, and vice versa, modeled estimates of BAI were lower. As with the NE analysis, the stand conditions for elevation, stratum and percent aspen presence were held constant at the mean to assess the temperature and precipitation interaction. When the climate values were held constant at the mean, trees located in pure aspen stands had higher growth values than those with coniferous species occupying a greater percentage of the stand BA (Figure 4C). Increases in elevation produced a decrease in the aspen growth in both regional models (Figure 4D).

Table 7. Aspen tree growth-climate model for the SW region of the Lake Tahoe Basin. Coefficients and fit statistics for fixed effects in the generalized linear mixed effects model fitted to the grouped data from 1991-2011 (n=1417).

	Estimate	Std. Error	DF	t-value	p-value
Intercept	81.87175	10.1500	1211	8.06	< 0.0001
Tmax	-2.52390	0.5600	1211	-4.47	< 0.0001
Precip	-0.01937	0.0050	1211	-3.85	0.0001
Elev	-0.00882	0.0020	1211	-4.37	< 0.0001
StratumC	-11.8704	0.4400	1211	-26.91	< 0.0001
PctAsp	4.22580	0.8400	1211	5.01	< 0.0001
Tmax:Precip	0.00154	0.0004	1211	3.72	0.0002

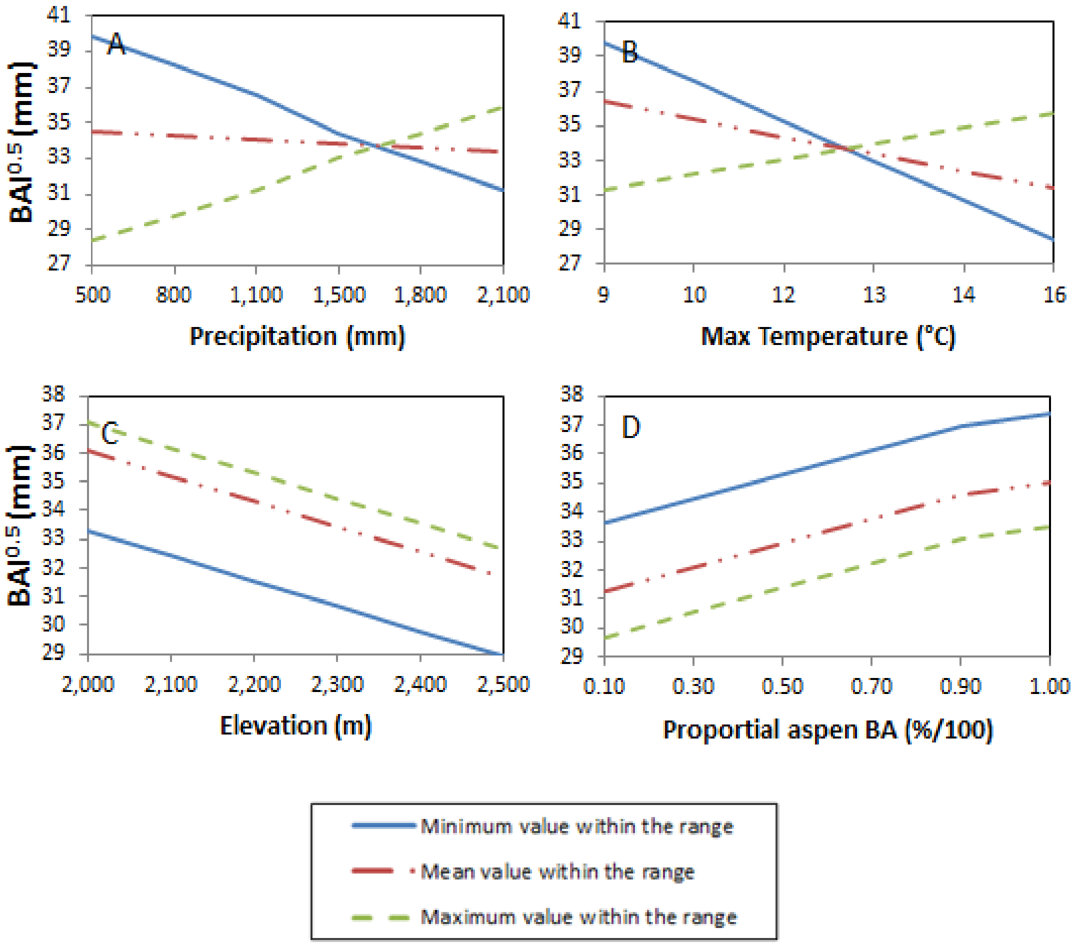


Figure 4. Relationship between aspen tree basal area increment (BAI; square root transformed) and measured climate variables located on the southwestern side of the Lake Tahoe Basin including: (A) BAI and precipitation relationship with maximum temperature values held constant, (B) BAI and maximum temperature relationship with precipitation held constant, (C) BAI and elevation relationship with species composition in terms of aspen as a proportion of total BA held constant, and (D) BAI and percent aspen BA relationship with elevation held constant.

Aspen Post-Wildfire Analysis

The analysis of aspen tree growth before and after a wildfire included two downstream stands (ST1 & ST2) located at different distances from the fire. When the analysis included aspen tree growth data for both downstream stands, there was no distinction between growth above or below the fire (Appendix D). However, after excluding the more distant stand (ST2), a significant temporary increase in aspen tree growth was detected downstream of the burned area. The effect of fire became marginally statistically significant by increasing the best model's maximum likelihood while still accounting for the penalties of added parameters and a small sample size according to the AICc (i.e., ~2 AICc points lower than the null model). Two models had greater AICc weights than the "Random Effect" null model, including the simplest and best model with categorical variable for location downstream of a wildfire (yes/no), and another plausible model that also included a variable representing stand density in terms of vicinity basal area (Table 8). The simplest model had the highest AICc weight, and was selected as the best model. This model indicated that aspen downstream of the fire exhibited greater tree growth over a three year post-wildfire period. The second-best model that also accounted for stand density indicated that the growth response of individual aspen stems depended on VBA. This model had the second-highest AICc weight, and was more informative insofar as it predicted that aspen stems with lower VBA exhibited an even greater positive growth response to upstream fire in terms of the ratio of growth pre- and post-wildfire among trees in close proximity to the burned area

(Table 9). For an aspen tree of average DBH in a stand of average VBA, the model predicts a 3-year response ratio of 1.52 & 1.06 with and without a burned area upstream. These ratios indicate that aspen trees downstream of the fire enjoyed a temporary enhancement in growth of around 43%.

Table 8. Best candidate models for southern Lake Tahoe Basin for the 3-year post-wildfire aspen BAI response ratio, without the more distant ST2 site with number of parameters (K), AICc scores, change in AICc scores (Delta_AICc), AICc weights, and loglikelihood (LL).

	K	AICc	Delta_AICc	AICcWt	LL
Fire	4	39.16	0	0.43	-14.71
Fire+VBA	5	40.37	1.21	0.23	-13.82
Null with RandomEffect	3	41.12	1.96	0.16	-17.06
VBA	4	42.78	3.62	0.07	-16.52
Fire+DBH+VBA	6	43.20	4.04	0.06	-13.6
DBH	4	43.57	4.41	0.05	-16.92
DBH+Fire+VBA+CrHt	7	46.65	7.49	0.01	-13.52
Full	10	59.34	20.18	0	-13.2

Table 9. 3-year post-wildfire aspen BAI response ratio model, without the more distant ST2 site, for the southern Lake Tahoe Basin. Coefficients and fit statistics for fixed effects in the generalized linear mixed effects model fitted to the grouped data from 1991-2011 (n=28). Vicinity BA (VBA) is metric BA (m^2 ha^{-1}) divided by the constant 4.356.

	Estimate	Std.Error	DF	t-value	p-value
Intercept	1.310270	0.209	22	6.26	<0.0001
Fire	0.454006	0.194	3	2.33	0.1017
VBA	-0.00130	0.001	22	-1.27	0.2139

Along with a 3-year analysis, 4- and 5-year analyses were conducted to measure additional persistence of the fire's effect (Appendix E & F). Growth in the 4-year range was not significantly different, even with the subtraction of the further distant ST2 stand

(Appendix E). However, the ratio of growth post-/pre-wildfire became significant for the 5-year analysis with similar results as the 3-year, where fire enhanced the growth ratio of pre- and post-wildfire growth after accounting for the negative effect of VBA (Appendix F). Therefore, the duration of the increased growth is unknown as there are many other factors that could have led to higher or lower growth ratios that were not included within this analysis.

DISCUSSION

Aspen Growth-Climate Relationship

The growth of aspen trees was linked to climate, and climate fluctuations influenced radial growth of aspen in different ways on the NE versus SW sides of the Lake Tahoe Basin. Maximum temperature and precipitation were the most influential climate variables. Within this analysis, precipitation and temperature functioned as an interactive variable. In the NE region of the Lake Tahoe Basin, water availability played a major role in supporting aspen growth. The NE region receives, on average, less precipitation than the SW region and the best radial growth was measured in years that received higher annual precipitation. Conversely, the SW region of the Lake Tahoe Basin received, on average, more precipitation and exhibited the best radial growth during low precipitation years. Aspen exhibited greater growth in cooler years (lower max. temperature) in both regions.

Unknown is whether cooler temperatures were correlated with greater soil moisture availability and thus better aspen tree growth on the more xeric sites of the NE region. Carroll et al. (2019) measured aspen leaf osmotic potential in the presence of changing temperatures and the effect on BA growth, resulting in decreased growth efficiency when temperatures either increased or decreased beyond the site’s ‘normal’ temperature regime. They also identified a strong relationship between leaf osmotic potential and soil moisture, with decreases in water conductance during increases in temperature. Understanding that water potential plays a major role in aspen BAI, there were similar results found within this analysis where temperature may have influenced water availability. Although soil moisture wasn’t taken into account, the interaction variable for temperature and precipitation was able to represent how increases in the maximum temperature were accompanied by slower aspen growth regardless of location around Lake Tahoe. The limiting variable between the NE and SW analysis then became water availability in the form of annual precipitation amounts.

Available soil moisture plays an influential role in the potential for aspen radial growth, however, changes in climate also influence growing season durations. White et al. (1999) studied growing season length in eastern deciduous forests and reported findings of longer growing seasons based on cooler surface temperature values. Although this analysis did not include growing season duration, the results are consistent with a lower maximum temperature value providing the means of increased aspen growth, possibly by increasing the growing season duration.

Water availability and temperature can vary according to site level differences (i.e. topography, slope, aspect, etc.). Leonelli et al. (2008), in the Canadian northeast, reported instances of increased aspen growth based on different site specific qualities, such as sites with greater water holding capacity and nutrient richness. Consistent with the finding of this analysis, the differentiation of site locations within the Lake Tahoe Basin (NE/SW) created a distinct difference between the two regions in regards to their climate and its influence on aspen growth.

Other factors or events that may have influenced aspen growth that were not represented in this study include insect infestation and mast seed years. Hogg et al. (2002) used climate moisture index (CMI), in the northwest region of Canada, to quantify the influence of soil moisture on the reduced growth and dieback of aspen. Although, their results did show reductions in growth in low moisture years, there was an additional factor of insect damage that influenced the already stressed aspen trees. During mast seeds years, trees are expected to have slower radial growth as they reallocate their resources to prioritize reproduction (Morelli et al. 2009).

Aspen tree rings exhibited visible and statistically significant differences in growth in accordance with fluctuating climate variables, but these effects may not persist under sustained climate changes because trees may adapt under stress in order to survive. The NE region analysis produced lower slope coefficient estimates indicating reduced sensitivity of aspen growth to inter-annual climate variations. This could represent an adaptation within the genome of aspen growing on a consistently water-limited site. Alberto et al. (2013) and Griffin et al. (1991) reported findings that aspen may have adaptations within their genome to react differently in the presence of a changing climate. Thus, the estimated fluctuations in climate could have less impact on aspen in the xeric NE region, where aspen may be more drought-adapted, as opposed to aspen in the mesic SW region that may be more sensitive to declining annual precipitation (Dolanc et al. 2013).

The analysis of the aspen climate-growth relationship, and the comparison of aspen growth upstream and downstream of one wildfire footprint, had limitations. Two limitations of the climate-growth study were the short time period of 20 years and the paucity of snowfall and snow pack data. A large proportion of annual precipitation falls as snow in the Lake Tahoe Basin. However, site-specific snowpack data were not available for our 20 study sites. A major limitation concerning both the climate-growth study and the wildfire response study arose from the clonal habit of aspen where many stems (or indeed all stems) within one stand could be genetically identical. Many of these stems may remain interconnected belowground via root grafts or among stems originating from root suckers along shared lateral roots, but the extent of resource sharing among established stems is unknown (Jelinkova et al. 2009). This relatedness complicates any analysis because stems cored for growth data within the same stand lack assumptions of true biological or statistical independence. To mitigate this problem, we only cored stems that were far apart from each other and hence experiencing different localized stand and site conditions, and we used linear mixed-effects regression analysis with random effects to account for the spatial autocorrelation of data from aspen stems within the same stand.

Future studies should attempt to analyze longer ring records and increase the sample size given the amount of variability in the growth-climate relationship. The incorporation of more core samples that date further back in time will improve, or at least facilitate, the cross-dating of aspen within the dendrochronology. The incorporation of longer ring records would also facilitate the use of a time series analysis to better account for the temporal autocorrelation within the data. Future studies at Lake Tahoe should also test for additional variables such as snow or growing season length that may influence the growth of aspen in a changing climate.

Aspen Response to Wildfire Disturbance

To our knowledge, downstream effects of fire on forest communities has not been studied, but fire within aspen stands has known benefits: the species is capable of rapid post-fire regeneration by root suckers and fire can also reduce or eliminate conifer trees and their regeneration competing with aspen (Yang et al. 2015, Frey et al. 2003). However, fire that kills conifers will also kill aspen trees which may have various ecosystem values such as cavities for nesting. Any restoration treatments performed outside aspen stand boundaries without disturbance to aspen or its many associate species would be welcome.

The detection of growth differences among aspen located above and below a wildfire highlights need for more research into the causes, magnitude, and distance over which fire can influence growth within downstream stands by providing additional water and nutrition. Johansen et al. (2001) and Robichaud et al. (2013) studied water runoff and different sediment yield rates from post-fire erosion. Johansen et al. (2001) studied sediment yields and found that burned areas had an increase in sediment deposition 25 times that of unburned land cover area. Robichaud et al. (2013) tested different mulch treatments on runoff rates post-wildfire and concluded that 3-4 years after fire, within the control section (no treatment), sediment rates stabilized to near zero values. The results of their runoff duration coincide with our findings of a short-term growth difference post-wildfire, suggesting that sediment runoff may be affecting growth of downstream vegetation.

This study of aspen response to nearby wildfire disturbance was opportunistic and would benefit from replication. Unfortunately, having only one aspen stand exhibiting significant positive growth response to wildfire upstream meant that this result could be confounded by other variables. Therefore, we recommend additional coring of aspen trees upstream and downstream of two or more additional wildfires to rigorously test our hypothesis and validate our initial observation that wildfire disturbances enhance growth of aspen downstream. Nevertheless, the comparison of growth pre- and post-wildfire showing a consistent positive response among aspen stems within that single downstream stand was in direct contrast to nearby aspen upstream of the same wildfire footprint that did not show enhanced growth during the same climate years. These results suggest there may be a benefit to re-introducing prescribed fire into areas above important aspen communities to improve aspen tree growth by making nutrients available, and mobile (Robichaud et al. 2013, Johansen et al. 2001), by burning vegetation and/or by increased water made available by greater snowpack accumulation inside burned areas (Stevens 2017) and/or lower transpiration after trees were culled by fire, allowing more water to move down the watershed into aspen stands below (Ford et al. 2011). To better understand these processes and the benefit to aspen downstream, I recommend further testing, by measuring nutrient and soil moisture availability, and collecting additional data for aspen trees to assess the magnitude and duration of improvements in site quality and tree growth. Given the potential for restoration inside and outside aspen stands to benefit aspen, especially in drier areas or dry years, the interaction of climate, site, and restoration activities also merits further research.

CONCLUSION

Based on the climate values represented within our 20 year study, the greatest influence that climate had on aspen growth was represented by an interaction between maximum temperature and precipitation. Aspen stands at different locations around Lake Tahoe exhibited different growth patterns and climate-growth relationships. Aspen grew best at low elevations, within pure aspen stands receiving ample precipitation in lower temperature portions of the Lake Tahoe Basin.

The positive influence of wildfire on aspen located downstream needs to be verified at other sites within stands close enough to the fire footprint to receive its benefits. Future studies should include assessment of factors and mechanisms explaining measured increases in aspen tree growth.

REFERENCES

Alberto, F. J., Aitken, S. N., Alía, R., González-Martínez, S. C., Hänninen, H., Kremer, A., & Savolainen, O. (2013). Potential for evolutionary responses to climate change–evidence from tree populations. *Global Change Biology*, *19*(6), 1645-1661.

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., et al. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259(4), 660-684.

Alley, W. M. (1984). The Palmer drought severity index: limitations and assumptions. *Journal of Climate and Applied Meteorology*, *23*(7), 1100-1109.

Anderegg, W. R. L., Berry, J. A., Smith, D. D., Sperry, J. S., Anderegg, L. D. L., & Field, C. B. (2012). The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *Proceedings of the National Academy of Sciences*, *109*(1), 233–237.

Bates, J. D., Miller, R. F., & Davies, K. W. (2006). Restoration of quaking aspen woodlands invaded by western juniper. *Rangeland Ecology & Management*, *59*(1), 88-97.

Berrill, J-P., & Dagley, C. M. (2012). Geographic patterns and stand variables influencing growth and vigor of *Populus tremuloides* in the Sierra Nevada (USA). *International Scholarly Research Network ISRN Forestry*, *2012*, 1- 9.

Berrill, J-P., & Dagley, C. M. (2014). Regeneration and recruitment correlate with stand density and composition in long-unburned aspen stands undergoing succession to conifer in the Sierra Nevada, USA. *Forest Research,* 3, 119.

Berrill, J-P., Dagley, C. M., & Coppeto, S. A. (2016). Predicting treatment longevity after successive conifer removals in Sierra Nevada aspen restoration. *Ecological Restoration*, *34*(3), 236-244.

Berrill, J-P., Dagley, C. M., Coppeto, S. A., & Gross, S. E. (2017). Curtailing succession: Removing conifers enhances understory light and growth of young aspen in mixed stands around Lake Tahoe, California and Nevada, USA. *Forest Ecology and Management*, *400*, 511-522.

Brewen, C. (2019). Multidecadal change in Aspen experiencing long-unburned, mixed-severity wildfire, and reburn disturbance regimes [Unpublished Master's thesis]. Humboldt State University.

Brewen, C. J., Berrill, J-P., Ritchie, M. W., Boston, K., Dagley, C. M., Jones, B., Coppoletta, M., & Burnett, C. L. (2020). Multidecadal decline and recovery of aspen experiencing contrasting fire regimes: long-unburned, infrequent and frequent mixed-severity wildfire. *PlosOne Preprint* https://doi.org/10.1101/2020.04.28.065896

Burnham, K. P., & Anderson, D. R. (2003). Model selection and multimodel inference: a practical information-theoretic approach. *Springer Science & Business Media*.

Carroll, C. J., Martin, P. H., Knapp, A. K., & Ocheltree, T. W. (2019). Temperature induced shifts in leaf water relations and growth efficiency indicate climate change may limit aspen growth in the Colorado Rockies. *Environmental and Experimental Botany*, *159*, 132-137.

Cavus, I., Kalin, L., & Kara, F. (2019). Changes in stream morphology protected by best management practices under effects of upstream disturbances. *Environmental Earth Sciences*, *78*(16), 526.

Dagley, C. M., Berrill, J-P., Coppeto, S. A., & Eschtruth, A. K. (2020). Understory responses to restoration in aspen-conifer forests around the Lake Tahoe Basin: residual stand attributes predict recovery. *Restoration Ecology*, *28*(3), 603-611.

Dettinger, M. D. (2013). Projections and downscaling of 21st century temperatures, precipitation, radiative fluxes and winds for the Southwestern US, with focus on Lake Tahoe. *Climatic Change*, *116*(1), 17-33.

Dolanc, C. R., Westfall, R. D., Safford, H. D., Thorne, J. H., & Schwartz, M. W. (2013). Growth–climate relationships for six subalpine tree species in a Mediterranean climate. *Canadian Journal of Forest Research*, *43*(12), 1114-1126.

Dudley, M. M., Negron, J., Tisserat, N. A., Shepperd, W. D., & Jacobi, W. R. (2015). Influence of climate on the growth of quaking aspen (*Populus tremuloides*) in Colorado and southern Wyoming. *Canadian Journal of Forest Research*, 45(11), 1546-1563.

Flanagan, S. A., Hurtt, G. C., Fisk, J. P., Sahajpal, R., Hansen, M. C., Dolan, K. A., Sullivan, J. H., Zhao, M. (2016). Potential vegetation and carbon redistribution in northern North America from climate change. *Climate*, *4*(1), 2.

Ford, C. R., Laseter, S. H., Swank, W. T., & Vose, J. M. (2011). Can forest management be used to sustain water-based ecosystem services in the face of climate change? *Ecological Applications*, *21*(6), 2049-2067.

Frey, B. R., Lieffers, V. J., Landhäusser, S. M., Comeau, P. G., & Greenway, K. J. (2003). An analysis of sucker regeneration of trembling aspen. *Canadian Journal of Forest Research*, *33*(7), 1169–1179.

Griffin, D. H., Schaedle, M., DeVit, M. J., & Manion, P. D. (1991). Clonal variation of *Populus tremuloides* responses to diurnal drought stress. *Tree Physiology*, *8*(3), 297-304.

Hogg, E. H., Brandt, J. P., & Kochtubajda, B. (2002). Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects. *Canadian Journal of Forest Research*, *32*(5), 823-832.

Hogg, E. H., Brandt, J. P., & Michaelian, M. (2008). Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. *Canadian Journal of Forest Research*, *38*(6), 1373–1384.

Hogg, E. H., & Hurdle, P. A. (1997). Sap flow in trembling aspen: implications for stomatal responses to vapor pressure deficit. *Tree Physiology*, *17*(8-9), 501-509.

Jelinkova, H., Tremblay, F., & DesRochers, A. (2009). Molecular and dendrochronological analysis of natural root grafting in *Populus tremuloides* (Salicaceae). *American Journal of Botany 96*:1500–1505.

Johansen, M. P., Hakonson, T. E., & Breshears, D. D. (2001). Post-fire runoff and erosion from rainfall simulation: contrasting forests with shrublands and grasslands. *Hydrological Processes*, 15(15), 2953-2965.

Jones, B. E., Rickman, T. H., Vazquez, A., Sado, Y., & Tate, K. W. (2005). Removal of encroaching conifers to regenerate degraded aspen stands in the Sierra Nevada. *Restoration Ecology*, *13*(2), 373-379.

King, J. S., Pregitzer, K. S., Zak, D. R., Kubiske, M. E., Ashby, J. A., & Holmes, W. E. (2001). Chemistry and decomposition of litter from *Populus tremuloides* Michaux grown at elevated atmospheric CO2 and varying N availability. *Global Change Biology*, *7*(1), 65-74.

Krasnow, K. D., Halford, A. S., & Stephens, S. L. (2012). Aspen restoration in the eastern Sierra Nevada: effectiveness of prescribed fire and conifer removal. *Fire Ecology*, *8*(3)

Kuhn T. J., Safford, H. D., Jones, B. E., & Tate, K. W. (2011). Aspen (*Populus tremuloides*) stands and their contribution to plant diversity in a semiarid coniferous landscape. *Plant Ecology*, *212*, 1451-1463.

Leonelli, G., Denneler, B., & Bergeron, Y. (2008). Climate sensitivity of trembling aspen radial growth along a productivity gradient in northeastern British Columbia, Canada. *Canadian Journal of Forest Research*, *38*(5), 1211-1222.

Manley, P. N., & Schlesinger, M. D. (2001). Riparian biological diversity in the Lake Tahoe basin. Final report for the California Tahoe Conservancy and the US Forest Service.

Mitton, J. B., & Grant, M. C. (1996). Genetic Variation and the Natural History of Quaking Aspen. *BioScience*, *46*(1), 25–31.

Morelli, T. L., Millar, C. I., Delany, D. D., & Westfall, R. D. (2009). The status of quaking aspen (*Populus tremuloides*) in the Sierra Nevada. *Report. USDA Forest Service, Pacific Southwest Research Station, Sierra Nevada Research Center, Albany, California, USA.*

Oliver, C. D., & Larson, B.C. (1996). *Forest stand dynamics. Update edition*. John Wiley and Sons, New York, NY.

Perala, D.A., 1990. Quaking aspen (*Populus tremuloides Michx*.). In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America: II. Deciduous. *United States Department of Agriculture Handbook no.* 654, pp. 555–569.

Pierce, A. D., & Taylor, A. H. (2010). Competition and regeneration in quaking aspen-white fir (*Populous tremuloides-Abies concolor*) forests in the Northern Sierra Nevada, USA. *Journal of Vegetation Science*, 21(3), 507-519.

Potter, D.A. (1998). Forested communities of the upper montane in the central and southern Sierra Nevada. PSW-GTR-169. Albany, CA: *U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station*. 319 p.2353–64.

PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu.

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rehfeldt, G. E., Ferguson, D. E., & Crookston, N. L. (2009). Aspen, climate, and sudden decline in western USA. *Forest Ecology and Management*, *258*(11), 2353–2364.

Roberts, J. S. (2003). Dew point temperature. *Encyclopedia of Agricultural, Food, and Biological Engineering.* D.R. Heldman, eds., CRC Press, Boca Raton, FL, 186-191. http://doi.org/10.1081/E-EAFE120007052

Robichaud, P. R., Lewis, S. A., Wagenbrenner, J. W., Ashmun, L. E., & Brown, R. E. (2013). Post-fire mulching for runoff and erosion mitigation: Part I: Effectiveness at reducing hillslope erosion rates. *Catena*, 105, 75-92.

Shepperd, W. D., Bartos, D. L., & Mata, S. A. (2001). Above-and below-ground effects of aspen clonal regeneration and succession to conifers. *Canadian Journal of Forest Research*, *31*(5), 739-745.

Shepperd, W. D., Rogers, P. C., Burton, D., & Bartos, D. L. (2006). Ecology, biodiversity, management, and restoration of aspen in the Sierra Nevada. *Gen. Tech. Rep. RMRS-GTR-178. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station 122 p.*, *178*.

Smith, E. A., O'Loughlin, D., Buck, J. R., & Clair, S. B. S. (2011). The influences of conifer succession, physiographic conditions and herbivory on quaking aspen regeneration after fire. *Forest Ecology and Management*, *262*(3), 325-330.

Speer, J. H. (2010). Fundamentals of tree-ring research. *University of Arizona Press.*

Stevens, J. T. (2017). Scale-dependent effects of post-fire canopy cover on snowpack depth in montane coniferous forests. *Ecological Applications*, *27*(6), 1888-1900.

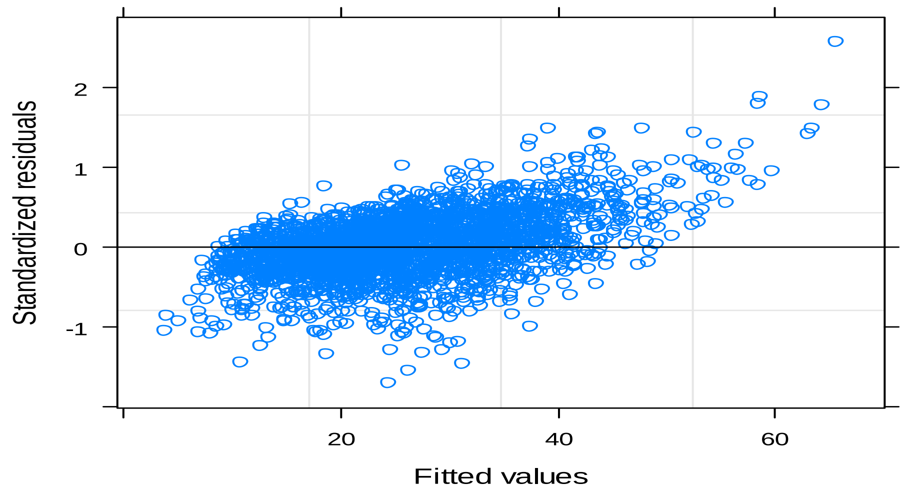
Turner, M. G., Romme, W. H., Reed, R. A., & Tuskan, G. A. (2003). Post-fire aspen seedling recruitment across the Yellowstone (USA) landscape. *Landscape Ecology*, *18*(2), 127-140

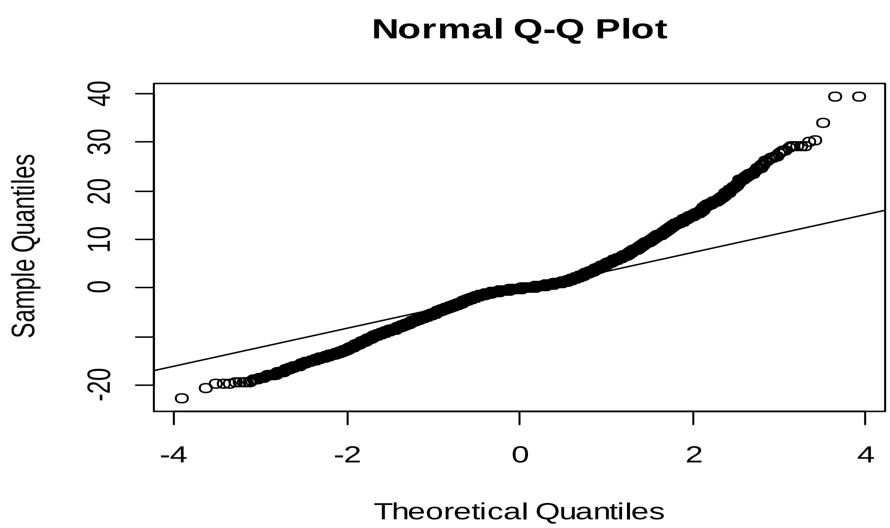
White, M. A., Running, S. W., & Thornton, P. E. (1999). The impact of growing-season length variability on carbon assimilation and evapotranspiration over 88 years in the eastern US deciduous forest. *International Journal of Biometeorology*, *42*(3), 139-145.

Yang, J., Weisberg, P. J., Shinneman, D. J., Dilts, T. E., Earnst, S. L., & Scheller, R. M. (2015). Fire modulates climate change response of simulated aspen distribution across topoclimatic gradients in a semi-arid montane landscape. *Landscape Ecology*, *30*(6), 1055-1073.

APPENDIX A

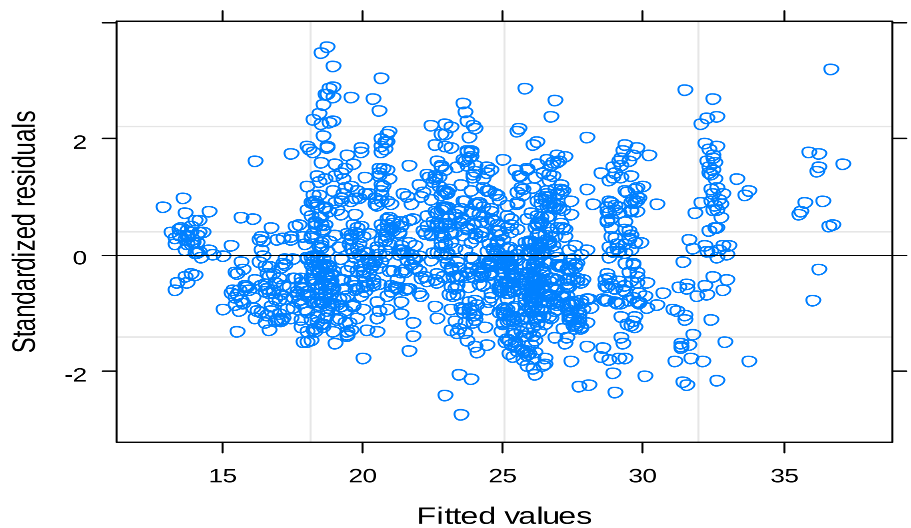
Appendix A. Full sample growth-climate analysis. Failure of the best model (with square root transformation) to meet linear regression assumptions: (above) the assumption of constant variance of the standardized residuals; and (below) assumption of normality of the residuals.

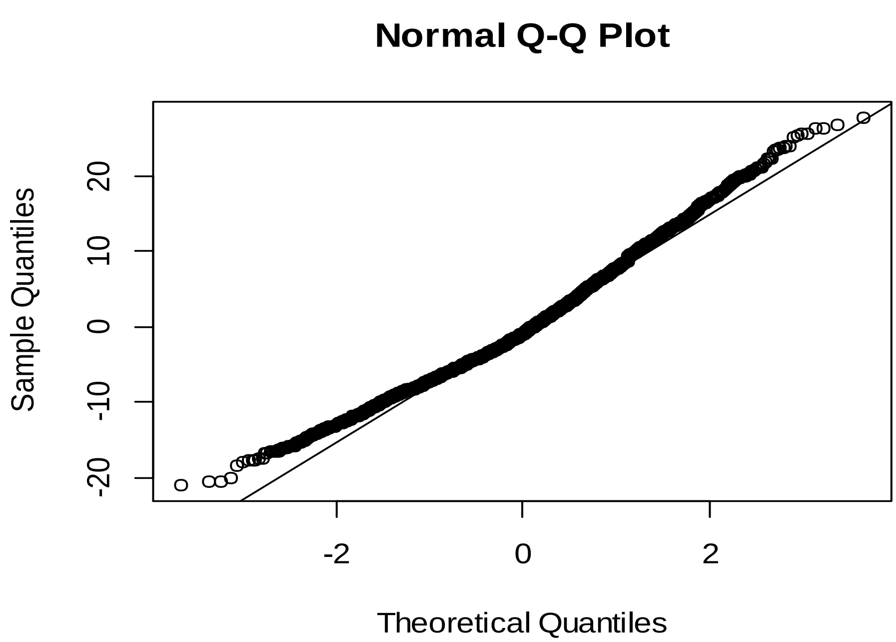




APPENDIX B

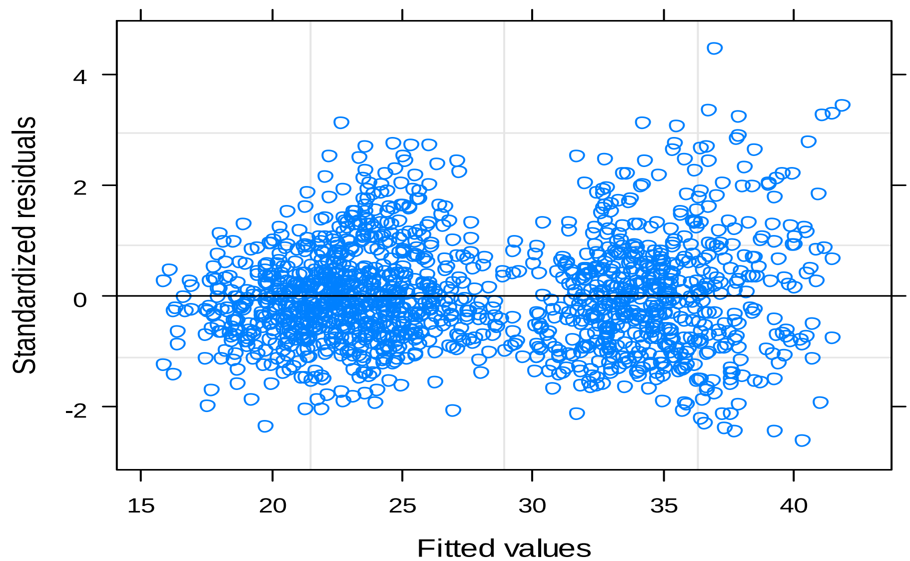
Appendix B. Checking the assumptions of the linear model in the growth-climate NE region analysis; both of which are assumed to be passing as there is no discernible pattern in the variance and passes the assumption of normality of the residuals.

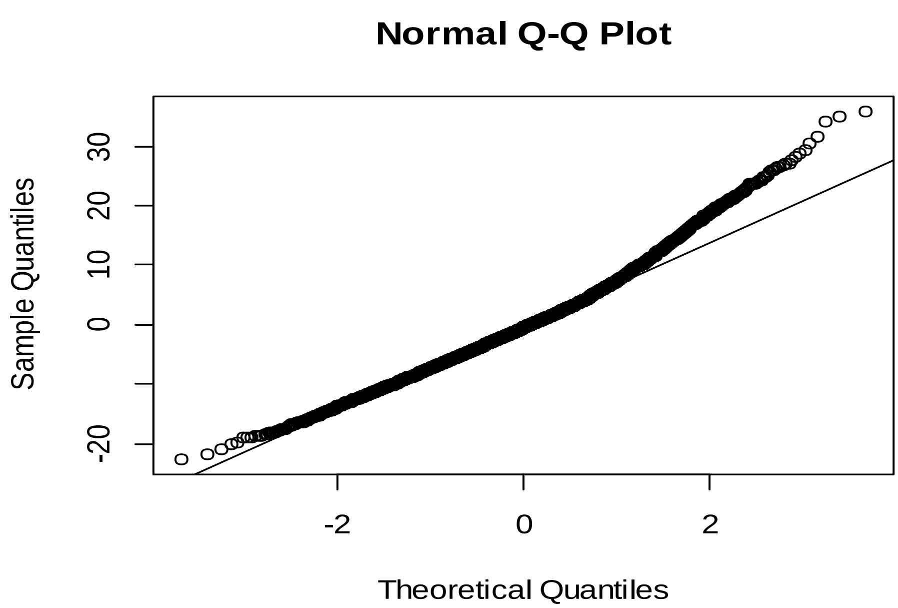




APPENDIX C

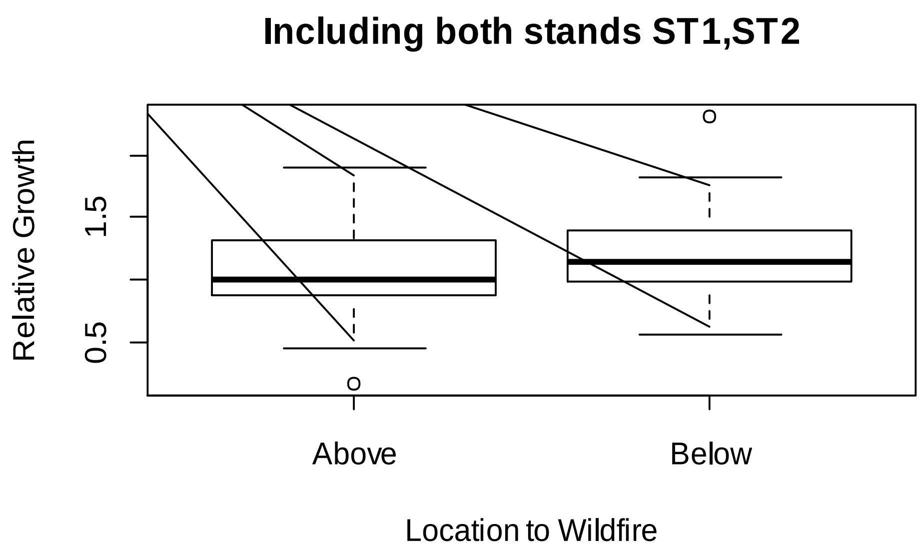
Appendix C. Checking the assumptions of the linear model in the growth-climate SW region analysis; showing passing of the assumption of normality and a recognized clustering in the variance.





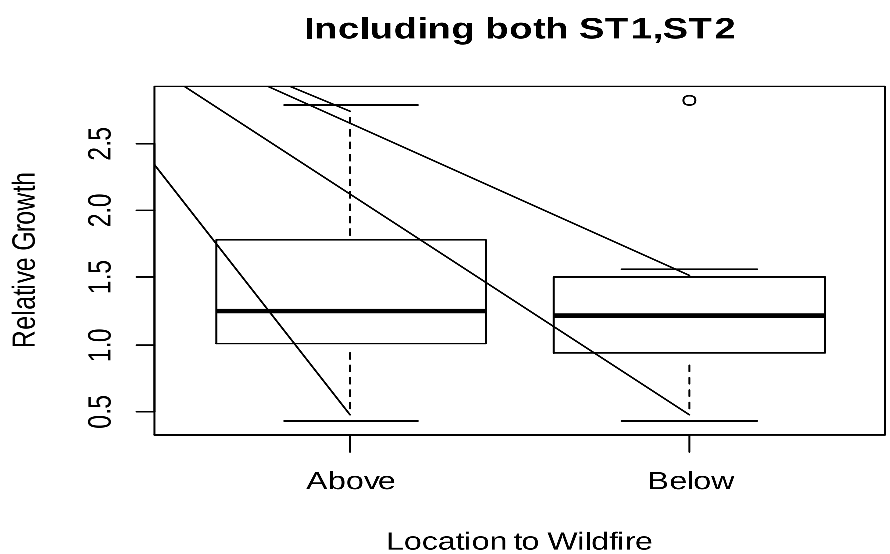
APPENDIX D

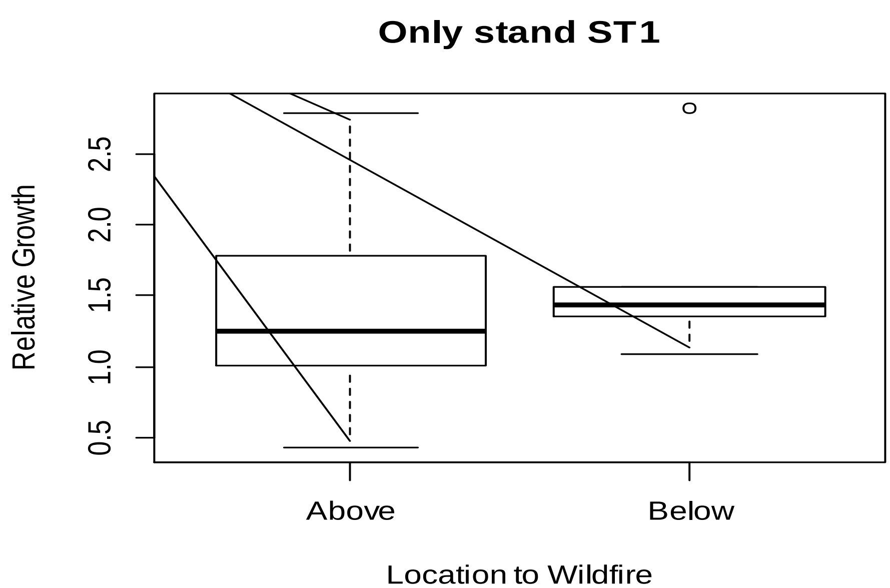
Appendix D. Box-plot comparison of the difference in 3-year post-wildfire relative growth analysis including both stands (ST1, ST2) and only one stand (ST1) measuring the effect of distance from the wildfire with estimates located above and below the 2002 Showers fire.



APPENDIX E

Appendix E. Box-plot comparison of the difference in 4-year post-wildfire relative growth analysis including both stands (ST1, ST2) and only one stand (ST1) measuring the effect of distance from the wildfire with estimates located above and below the 2002 Showers fire.

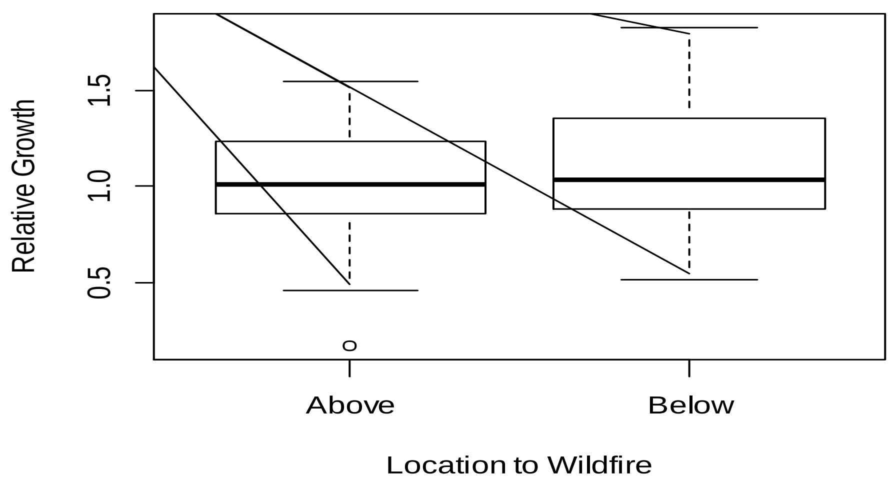




APPENDIX F

Appendix F. Box-plot comparison of the difference in 5-year post-wildfire relative growth analysis including both stands (ST1, ST2) and only one stand (ST1) measuring the effect of distance from the wildfire with estimates located above and below the 2002 Showers fire.

Including both stands ST1,ST2



Only stand ST1