INFLUENCES OF STAND DEVELOPMENT AND CLIMATE ON

ABOVE-GROUND BIOMASS IN SUBALPINE FOREST

PERMANENT PLOTS IN THE COLORADO FRONT RANGE

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Influences of stand development and climate on above-ground biomass in subalpine forest permanent plots in the Colorado Front Range.
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Understanding the factors that influence above-ground biomass (AGB) in subalpine forests is important for predicting the vulnerability of these ecosystems to variations in climate. Utilizing ten permanent forest plots containing >5000 tagged trees, we examined changes in tree diameter distribution, mortality, and AGB estimates from 1982 to 2016, to address the following questions: 1) How is change in stand-level tree biomass influenced by stand age, species composition, and initial stand structure? 2) How is change in stand-level tree biomass influenced by site-level differences in topoclimatic conditions which influence moisture availability? 3) How do changes in stand-level tree biomass reflect climate variability? In addition to a total 6.5% AGB gain across all permanent plots over the period of study, we found all stands were able to accrue biomass had they not been affected by disturbance. Sites not limited by moisture obtained the highest increases in AGB. The lack of annual census data made it difficult to interpret the response each variable had to climate. However, differentiating between expected successional trajectories of each variable and trends coinciding with climate variability allowed for ecologically meaningful interpretations. Overall, we found measures of tree population structures in all stands to be sensitive to climate variations. This was evident in the increase and subsequent decrease in tree mortality rates that coincided with increases and decreases in precipitation deficits. Hence, mortality rates increased in each successive mortality census (1982-1994, 1995-2007, 2008-2013) until the latest census period (2014-2016) when mortality rates show a decline in nearly all permanent plots, which corresponds with the increasing moisture deficits that lasted until 2011 followed by periods of higher precipitation.
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INTRODUCTION

Forest biomass is an important ecological indicator of potential productivity within a given area. Most importantly, it can reflect the capability of an ecosystem to cycle and store carbon. Variations in above-ground biomass (AGB) are vital to the carbon cycle through ecosystem productivity and decomposition processes (Guobin et al. 2008). Changes in AGB over time are directly impacted by stand structural attributes and site characteristics through tree recruitment, growth, and mortality. In the context of climate change, potential changes in forest biomass are both important indicators of ecosystem response to climate change as well as possible sources of negative or positive feedbacks of carbon into the atmosphere (Bonan 2008). Recent increases in tree mortality have been documented in forests all across the world, which potentially can affect AGB and therefore carbon storage in forests (van Mantgem et al. 2009, Allen et al. 2010, Brando et al. 2013, Peng et al. 2011, Williams 2013). Widespread evidence of rising tree mortality rates with climate warming has raised concerns about the ability of tree recruitment and growth to compensate for these higher rates of mortality. Additionally, higher tree mortality rates may lead to significant declines in forest biomass and carbon storage in forest ecosystems.

Given that projected temperature increases are expected to be among the most rapid in the high elevation areas due to a variety of feedback mechanisms (Pepin et al. 2015), warming effects on tree demographic processes and forest biomass potentially may be extreme in subalpine forests. Specifically, for the Colorado Rocky Mountain region, the recent warming trend appears to be among the largest in the contiguous United States (Saunders et al. 2008, McGuire et al. 2012). Previous research has documented earlier snowmelt in the Colorado Rockies and warmer and drier summers in the subalpine zone of the Colorado Front Range.
(Clow 2010, McGuire et al. 2012, Kittel et al. 2015), similar to patterns across the U.S. West (Stewart 2009, Pederson et al. 2011). Previous research conducted in subalpine forests of the Colorado Front Range has also linked increases in tree mortality rates and decreased primary productivity to earlier snowmelt and warmer and drier summers (Smith et al. 2015, Hu et al. 2010). Likewise, both radial tree growth and seedling survival in some Front Range subalpine forest habitats have been shown to be limited by moisture availability associated with higher temperatures (Villalba et al. 1994, Moyes et al. 2013, Kueppers et al. 2016). Thus, it is reasonable to expect that subalpine forest biomass in the Colorado Front Range may already be altered in response to warming climate trends of the late 20th to early 21st centuries and that it is likely to be more significantly altered under continued climate change.

There are two simplified and non-mutually exclusive scenarios for subalpine forest biomass changes under continued climate change. The first--termed the slow demographic change pattern--is the relatively direct effect of warmer and drier conditions on tree populations by altering background tree mortality rates, as well as recruitment rates into larger size classes (e.g. radial growth rates) and rates of new recruitment (e.g. seedling establishment and initial survival). Substantial empirical evidence as well as modeling simulations indicate that changes in the subalpine forests of the Colorado Front Range imply the demographic change pattern is already underway (e.g. Smith et al. 2015, Kueppers et al. 2016, Conlisk et al. 2017). While evidence of increased background tree mortality is available across a broad range of stand types and site conditions (Smith et al. 2015), experimental demonstration of seedling survival by moisture limitation is limited to a small range of site and stand types (Moyes et al. 2103, Kueppers et al. 2016) and does not include the most abundant conifer of the subalpine zone (subalpine fir).
The second scenario – termed *abrupt climate-induced disturbance pattern*-- involves climate-related disturbance events such as insect outbreaks or fire which result in massive tree mortality (in contrast to the typically low rates of background mortality) and may or may not result in new tree seedling establishment and recruitment of small tree sizes into larger size classes. This scenario is illustrated by abrupt increased tree mortality of subalpine tree populations caused by a recent severe spruce beetle (*Dendroctonus rufipennis*) outbreak in the Front Range (Derderian et al. 2016) which in turn is linked to warmer and drier climatic conditions (Hart et al. 2014). In addition, multi-century fire history records demonstrate the likelihood of increased fire activity in subalpine Front Range forests under a future warmer and drier climate (Sibold and Veblen 2006). Again, simulation modeling that integrates climate-driven changes in spruce beetle populations with fire responses demonstrates the sensitivity of subalpine forest biomass to future climate scenarios (Temperli et al. 2015).

The slow demographic and the abrupt disturbance patterns of climate-induced forest change are likely to simultaneously affect the subalpine forests of the Colorado Front Range and together will result in significant changes in forest biomass, carbon sequestration and other ecosystem services (Rocca et al. 2014). However, assessment of the carbon storage implications of climate-induced changes under either of the two scenarios requires better understanding of how AGB varies spatially across the subalpine landscape in relation to abiotic site factors and temporally in response to time since severe disturbance. In the Central Rocky Mountains (i.e. southern Wyoming and Colorado), there have been few studies of how AGB (or a proxy for it such as total stemwood volume) vary spatially across the landscape or vary over time based on re-measurement of permanent plots. The existing studies of AGB in subalpine forests in Colorado have resulted in conflicting conclusions about the degree and importance of spatial
variability of stand-level AGB. For example, previous research based on sampling forest structure in plots located in 1 km² landscapes in three subalpine landscapes in the Central Rocky Mountains of varying abiotic site factors and stand ages concluded that the AGB carbon pools were relatively similar; thus for purposes of assessment and modeling of carbon, the entire subalpine zone of the Central Rocky Mountains can be treated as a single forest type (Bradford et al. 2006). Analogously, comparison of stemwood biomass across a chronosequence of subalpine forest stands ranging in age from c. 125 to 700 years revealed relatively little variability in stemwood biomass (Aplet et al. 1989).

In contrast to the studies concluding that AGB in subalpine forests of the Central Rocky Mountains varies relatively little in relation to site factors and stand age, are several other studies indicating wide ranges of AGB across the subalpine forest landscape. Studies conducted in old (> 200 years) subalpine forests in Colorado have found a two- to three-fold range in total AGB across elevation ranges of < 500 m (Arthur and Fahey 1992, Binkley et al. 2003, Kueppers and Harte 2005). These existing studies were conducted in a relatively narrow range of forest composition (i.e. stands exclusively of Engelmann spruce [Picea engelmannii] and subalpine fir [Abies lasiocarpa], in some cases including lodgepole pine [Pinus contorta var. latifolia]) and topographic positions relevant to moisture availability. Considered as whole, these existing studies capture only a small portion of variability in stand composition (e.g. excluding pure lodgepole pine stands as well as stands with a significant component of limber pine [Pinus flexilis]) and clearly under represent the presence of young (< 130 years) stands.

The existing literature on AGB in subalpine forests in the Colorado Front Range leads to the contrasting conclusions that forest biomass is relatively homogeneous within the subalpine zone and the opposing view that site conditions and stand ages result in ecologically important
spatial variability in stand-level forest biomass in subalpine forests. Thus, the current study examines both spatial variation and temporal variation in AGB across a range of diverse stand ages and compositions in a subalpine forest in the Colorado Front Range. Stands range from young (122 years) pure post-fire stands of lodgepole pine to old growth stands of Engelmann spruce and subalpine fir. Sites range from dry south-facing slopes populated by limber pine mixed with Engelmann spruce and subalpine fir to permanently waterlogged sites of bog forests of Engelmann spruce and subalpine fir. Re-measurement of 10 permanent plots allowed the detection of changes in AGB over a 34-year period (1982-2016) across a complex subalpine forest landscape in the Colorado Front Range, southern Rocky Mountains, USA. The research addresses the following three questions: 1) How is change in stand-level tree biomass influenced by stand age, species composition, and initial stand structure (i.e. tree sizes and densities at the initiation of monitoring)? 2) How is change in stand-level tree biomass influenced by site-level differences in topoclimatic conditions which influence moisture availability? 3) How do changes in stand-level tree biomass reflect climate variability?
METHODS

STUDY AREA

Research was conducted at Niwot Ridge located in the Roosevelt National Forest on the eastern slope of the Colorado Front Range (40° 3’20”N, 105° 35’22”W). This area is characterized by a steep elevation gradient with a wide range of climate variables. Subalpine forests occur at an elevation range of roughly 2500 m to 3800 m above sea level. Dominant tree species are limber pine (*Pinus flexilis*), lodgepole pine (*Pinus contorta var. latifolia*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*). The mid-latitude, continental location of Niwot Ridge contributes to the large range in air temperatures from summer to winter (Greenland 1989). From 1982 through 2016 average annual temperature was -5 °C, with a maximum average temperature of 36 °C and a minimum average temperature of -46 °C (Climate Station C-1 at 3048 m). A trend of increasing mean annual air temperature has been recorded for climate stations at 2591 m and 3048 m elevations in this region over the 56 years from 1953-2008 (McGuire et al. 2012). The C1 station has recorded significant increases in monthly maximum air temperatures through 1953 to 2008 (McGuire et al. 2012). Over the period of 1989-2008, significant increases in July maximum temperatures, and June through August minimum temperatures, have been recorded (McGuire et al. 2012). At these high elevations, precipitation occurs predominately as snow. Average annual precipitation is 707 mm (C-1 climate data, 1982-2016). Between 1952-2010 there was a trend towards declining precipitation during summer months of May through September at the C-1 climate station (Kittel et al. 2015).

Between 1982 and 1986 ten large permanent forest inventory plots were installed by Dr. Thomas Veblen across a range of subalpine stand types (Fig.1). These plots were established with the intent of including a maximum range of stand ages and topographic positions while
avoiding areas that had been logged (Veblen 1986a). Individual plots initially contained 215 to 834 live trees; plot size was varied to adjust for stand densities and to the size of homogeneous forest patches free of cut stumps (Table 1). The six largest plots (BW2, BW3, MRS4, MRS5, BL6, MRS7) are older stands each including two to three common conifer species and spanning a range of site moisture conditions from hydric through mesic to xeric (Table 1). Successional status of each old stand ranged from c. 257 to 377-year-old post-fire successional stands (as interpreted from tree age data) to stands considered to be in compositional equilibrium with maximum tree ages > 450 years (Veblen 1986a; Table 1). The four smaller stands (MRS1, 8, 9, and 10) are relatively young (c. 122 years) post-fire xeric stands composed almost exclusively of lodgepole pine.

Although bark beetle activity in the Front Range became elevated in the mid-1990s, bark beetles were an insignificant agent of mortality in these plots prior to 2008 (Smith et al. 2015). The bark beetles which more recently have affected the permanent plots are: the mountain pine beetle (MPB, *Dendroctonus ponderosae*), affecting lodgepole pine and limber pine; spruce bark beetle (SBB, *Dendroctonus rufipennis*) affecting Engelmann spruce; and western balsam bark beetle (WBBB, *Dryocoetes confusus*) affecting subalpine fir. The 2007 mortality census preceded any local effects of the regional MPB event that has massively affected nearby forests since 2004 (Chapman et al., 2012). During the 2007 mortality census, only one limber pine was observed to have been killed by MPB and two others were under attack, whereas in the 2010 and 2013 mortality censuses 17 and 44 trees, respectively, were killed by bark beetles of different types (mostly WBBB).
Fig. 1. Map of the study area showing the location of permanent plots along a wide-ranging elevation gradient.

Table 1. Descriptors of the ten permanent plots.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Plot size (sq. m)</th>
<th>Initial population size</th>
<th>Present population size</th>
<th>Live basal area (sq. m/h)</th>
<th>Stand age (yrs.)</th>
<th>Topographic position</th>
<th>Successional status</th>
</tr>
</thead>
<tbody>
<tr>
<td>Old stands</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BW2</td>
<td>2592</td>
<td>374</td>
<td>356</td>
<td>41.24</td>
<td>267</td>
<td>xeric</td>
<td>Successional from limber pine to Engelmann spruce and subalpine fir</td>
</tr>
<tr>
<td>BW3</td>
<td>810</td>
<td>282</td>
<td>261</td>
<td>87.41</td>
<td>257</td>
<td>mesic</td>
<td>Successional with Engelmann spruce, subalpine fir and lodgepole pine</td>
</tr>
<tr>
<td>MRS4</td>
<td>1944</td>
<td>515</td>
<td>490</td>
<td>68.06</td>
<td>357</td>
<td>xeric</td>
<td>Successional with Engelmann spruce, subalpine fir and lodgepole pine</td>
</tr>
<tr>
<td>MRS5</td>
<td>2916</td>
<td>425</td>
<td>444</td>
<td>52.81</td>
<td>556</td>
<td>hydric</td>
<td>Compositional equilibrium with Engelmann spruce and subalpine fir</td>
</tr>
<tr>
<td>BL6</td>
<td>1944</td>
<td>416</td>
<td>351</td>
<td>56.33</td>
<td>464</td>
<td>mesic</td>
<td>Compositional equilibrium with Engelmann spruce and subalpine fir</td>
</tr>
<tr>
<td>MRS7</td>
<td>2916</td>
<td>496</td>
<td>524</td>
<td>50.75</td>
<td>377</td>
<td>xeric</td>
<td>Successional with Engelmann spruce, subalpine fir and limber pine</td>
</tr>
<tr>
<td>Young stands</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MRS1</td>
<td>1134</td>
<td>834</td>
<td>653</td>
<td>59.79</td>
<td>122</td>
<td>xeric</td>
<td>Lodgepole pine dominated, stem-exclusion phase</td>
</tr>
<tr>
<td>MRS8</td>
<td>648</td>
<td>396</td>
<td>341</td>
<td>31.05</td>
<td>122</td>
<td>mesic</td>
<td>Lodgepole pine dominated, stem-exclusion phase</td>
</tr>
<tr>
<td>MRS9</td>
<td>324</td>
<td>215</td>
<td>179</td>
<td>14.96</td>
<td>122</td>
<td>xeric</td>
<td>Lodgepole pine dominated, stem-exclusion phase</td>
</tr>
<tr>
<td>MRS10</td>
<td>432</td>
<td>257</td>
<td>245</td>
<td>17.31</td>
<td>122</td>
<td>xeric</td>
<td>Lodgepole pine dominated, stem-exclusion phase</td>
</tr>
</tbody>
</table>
Considering the large variability in stand structural characteristics and topoclimatic conditions throughout the sites, inferences will be made on a plot-by-plot basis. With each plot being treated as its own case study, results will be presented as such.

PERMANENT PLOT RE-MEASUREMENT

In the summer of 2016, a complete census of all permanent plots was conducted. This procedure followed the original installation measurements taken in 1982 (Veblen 1986a). To allow for calculation of basal area increment and biomass, all live and dead standing trees > 4 cm dbh were measured at diameter at breast height (dbh). Height class was established for each tree and classified into 3 categories; (1) canopy, (2) intermediate and (3) subcanopy (Veblen 1986a) for use as a model parameter in interpolating non-measured heights. In the summer of 2016, height was measured using a laser rangefinder, for a subset of 25 to 88 trees within each plot for use in allometric equations predicting biomass.

A mortality census of newly dead trees (i.e. trees that had died since the previous census) was previously conducted for each plot at three-year intervals since plot installation until 1994 (i.e. 1985, 1988, 1991, and 1994), and then again in 2007, 2010, and 2013 (Smith et al. 2015). For the current study, mortality was measured in 2016. Thus, in comparison to the Smith et al. (2015) study, new mortality data were obtained for the 2014-2016 period. Newly dead trees were identified by species and tag number, and recorded as standing or fallen (if fallen, orientation was also taken). Decomposition status was then identified as an estimate of tree decay after mortality where categorization is based on the remaining woody material as follows: (1) needles, (2) twigs, (3) branches, or (4) bole. In cases where there was evidence of a cause of tree death, mortality agents were recorded as wind damage or insect attack. The types of insect attack were: MPB, SBB, WBBB, and FEB (Fir Engraver Beetle, Scolytus ventralis).
ANALYTICAL METHODS

*Above-ground biomass*- Utilizing the relationship between dbh and height from data that was collected during the summer of 2016, estimates of non-measured tree heights and heights for the plot establishment year were calculated using a nonlinear regression model for each species within a specific plot. The established height estimates were then applied to species-specific allometric equations for each full census year (1982 and 2016) in conjunction with dbh to compute total above-ground tree biomass. Such equations have been developed for most subalpine tree species located in the permanent plots. For quaking aspen, we used a single equation from a study conducted in Alberta (Appendix A; Singh 1982). Engelmann spruce, subalpine fir, and lodgepole pine required separate equations for wood, bark, foliage and branches to estimate total biomass (Appendix A; Ung 2007). Equations for the closely related white bark pine was used to calculate biomass of limber pine (Appendix A; Jenkins et al 2004). Height computations were performed in R, and AGB computations were performed in Microsoft Excel.

*Mean annualized mortality*- Mortality measurements were conducted at three year intervals until 1994 and then began again in 2007. Periods of mortality were given a numeric representation of the period with which a tree was observed to have died (Table 2).
Table 2: Mortality census intervals by plot.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Mortality intervals</th>
</tr>
</thead>
</table>

Most commonly, mortality is represented as the number of survivors at the start of each age interval. This is impacted by both natality and mortality (Kimmins 1987). Thus, previous computations of tree mortality divide number of tree deaths by the initial live tree count at time of plot installation (Smith 2015). However, we lacked data on in-growth into the > 4 cm dbh size class for each of the dates at which a mortality census was performed. Hence, we computed annualized % mortality (M) using the following equation:

\[(dT/TC)/P * 100 = M\]

where \(dT\) is the number of trees that died, in the number of years included in the given time period \(P\), and \(TC\) represents the number of live trees at the start of the mortality period being computed, ignoring the number of trees that may have newly recruited into the > 4 cm dbh class.

To compare annualized mortality rates with climatic conditions, four periods were defined according to their common climatic conditions and the appearance of significant bark beetle activity. The first two periods, 1983-1994 and 1995-2007, are of equal length and lack bark beetle outbreak (Smith et al. 2015). The final two periods, 2008-2013 and 2014-2016, were shorter periods that exhibited significant bark beetle activity compared to the absence of bark.

MOISTURE INDICES

To characterize climatic conditions during the four *a priori* defined time periods of measured tree mortality (i.e. 1983 to 1994, 1995-2007, 2008-2013, 2014-2016) we used three parameters: precipitation deficit, standardized precipitation evapotranspiration index (SPEI), and daily temperatures. Data collected from the Niwot Ridge C-1 climate station were used to compute all indices. This station is located at a central location for all plots and is believed to be an accurate indicator for climate affecting the permanent plots.

**Precipitation deficit.** Average monthly mean, maximum, and minimum temperatures in Celsius along with monthly precipitation accumulation in millimeters were computed in Microsoft Excel using the daily climate measurements at Niwot Ridge C-1 climate station. Monthly values of temperature were then applied to the Thornthwaite function “thornthwaite” in R package “ClimClass”, to calculate potential evapotranspiration (PET) reported in millimeters. Total annual precipitation deficits are expressed as PET minus precipitation. Values were then scaled using the “scal” function in R, where R calculates the mean and standard deviation (sd) of the entire vector, and ‘scales’ each element by subtracting the mean and dividing by the sd. Positive values of the precipitation deficit indicate moisture were removed through evapotranspiration and not replaced by precipitation whereas negative values indicate there was more precipitation than evapotranspiration.
**Standardized Precipitation Evapotranspiration Index (SPEI).** SPEI is a climate index used for quantifying drought and is defined as the sensitivity of Palmer Drought Severity Index (PDSI) in combination with changes in evaporation demand (caused by fluctuations and trend in temperature) (Vincente-Serrano et al. 2009). It can be calculated on a range of timescales but for our purpose in identifying contributions to mean annualized mortality, it was computed for each calendar year from 1982-2016. For our calculations we used the “spei” function in R that was applied to the equation, precipitation minus potential evapotranspiration (previously calculated for precipitation deficit). Drier periods are indicated by negative values and wetter periods are indicated by positive values of SPEI.

**Temperature.** To examine changes in frequency of high daily temperatures in Celsius, for the summer months of June-September we calculated the mean maximum daily temperature and standard deviations for the period 1952-2016. We then represent the number of days where maximum temperature was greater than one standard deviation on a scatter plot and fit a simple loess curve using the R package ‘ggplot2’, which displays the conditional mean, to visualize the pattern in changes of frequencies over time.
RESULTS

CHANGES IN FOREST STRUCTURE AND COMPOSITION FROM 1982 TO 2016

*Plot BW2.*

BW2 is a relatively xeric site on a rocky convex moraine with a high degree of wind exposure. BW2 is a c. 290-year old post-fire stand dominated by limber pine in which the more shade-tolerant subalpine fir and Engelmann spruce are successionality replacing the shade-intolerant limber pine (Veblen 1982a). The small number of tree deaths as well as the overall basal area increase from 1982 to 2016 may reflect the open canopy exhibited throughout this site. The two shade tolerant tree species approximately doubled their basal areas and substantially increased the number of trees > 10 cm dbh (Fig.2). The relatively small population of lodgepole pine (20 trees) did not change in quantity or total basal area over the 34-year period. While the total basal area for limber pine only slightly declined, there was a substantial decline in the total population size from 253 to 213 trees. Overall, we found the increase in dominance by larger Engelmann spruce and subalpine fir and the decline in number of limber pine < 20 cm dbh is consistent with a slow successional displacement of the shade intolerant limber pine by the two shade-tolerant species.

*Plot BW3.*

BW3 is a mesic site, adjacent to BW2 but located in a slight depression (i.e. water gathering topography) and is less exposed to the wind. Its stand density in 2016 is far greater than BW2 with 3222 trees h⁻¹ and a basal area of 87cm h⁻¹ (APPENDIX B). Tree populations have shown a 7% decline since the original measurement, 3481 trees h⁻¹. This decline has not been evident in basal area increment as a 10% increase was shown over 34 years. Tree
population decline is primarily attributed to the loss in lodgepole pine. Despite this decline in numbers of lodgepole pine, its basal area has increased as trees have grown into the larger size classes. The approximately bell-shaped curve with few trees < 20 cm dbh (Fig. 3) indicates no new recruitment into small dbh classes as expected for this shade-intolerant species.

Subalpine fir was the only other species to decline in population size which prompted the only decline in basal area for a species in this plot. This 17% loss in tree population was associated with a 31% loss in basal area. In contrast, Engelmann spruce was the only species to exhibit both an increase in number of trees and basal area. Trees for this species increased by only 4% in tree count but 14% in basal area. Both these shade tolerant species display negative exponential (“reverse J”) diameter distributions, indicating there is constant mortality and continuous recruitment/growth into the larger size classes. Without disturbance, a shift in dominance from lodgepole pine to Engelmann spruce is likely as lodgepole pine populations continue to decline and Engelmann spruce increases.
Fig. 2. Diameter at breast height (DBH) distribution in centimeters for each species at BW2. Bins are in increments of 5, starting at a dbh of 4.

Fig. 3. Diameter at breast height (DBH) distribution in centimeters for each species at BW3. Bins are in increments of 5, starting at a dbh of 4.
Plot MRS4.

Initial establishment of MRS4 was dominated by lodgepole pine and Engelmann spruce. However, gradual shifts in stand dominance are being observed through a 24% loss in lodgepole pine basal area and increase in both Engelmann spruce and subalpine fir basal area by 7% and 26%. This is also apparent in the bell-shaped curve of lodgepole pine where there is a decrease in all size class quantities below 20 cm dbh, and the reverse J curve of subalpine fir that shows an increase in almost all diameter size classes (Fig. 4). Although the number of subalpine fir trees is greater, lodgepole pine remains dominant in basal area which likely resulted from faster growth (Veblen, 1986a). Through increase in diameter size classes, shade-tolerant spruce and fir are likely to continue replacing lodgepole and limber as canopy dominants, as long as there is no disturbance.

MRS4 is one of two sites to display a loss in total basal area (-1.8%). This is most likely attributed to the recent high mortality caused by a wind blow down event which knocked down numerous trees in MRS4 in the winter of 2011-12 and affected an extensive area of subalpine forests in the Front Range (Wohl, 2013).

Plot MRS5.

MRS5 is the only hydric site among the permanent plots; it a bog forest located in an area of low relief characterized by long-lasting snow and poor drainage. This is a compositional equilibrium stand with Engelmann spruce and subalpine fir existing in dense patches that are separated by poorly drained meadow. The reverse J-curve is evident in both figures and indicates subalpine fir and Engelmann spruce are maintaining a consistent residual distribution of sizes (Fig. 5). With warmer temperatures, trees in this site are not moisture limited and there is not only a 5% increase in tree population but a 19% increase in basal area. This can be explained
primarily by the 38% increase of subalpine fir basal area while Engelmann spruce had a 12% increase in basal area. Most likely attributed to the lack of moisture limitation, this site showed the highest increase in basal area of all permanent plots.

Fig. 4. Diameter at breast height (DBH) distribution in centimeters for each species at MRS4. Bins are in increments of 5, starting at a dbh of 4.

Fig. 5. Diameter at breast height (DBH) distribution in centimeters for each species at MRS5. Bins are in increments of 5, starting at a dbh of 4.
Plot BL6.

BL6 also is a compositional equilibrium stand with Engelmann spruce and subalpine fir represented in all size classes. This site has experienced an overall loss in basal area and tree population. The 15% loss in tree population can be attributed to mortality in both species but more predominately in subalpine fir. Subalpine fir experienced an 11% decline in numbers of trees and a 5% loss in basal area for the entire plot (Fig. 6). Some of the decline in tree population is related to the 2011-12 wind event (Wohl 2013) that significantly impacted MRS4, but a more common agent of tree mortality in BL6 is the combined influence of WBBB and Armillaria root rot which together are characterized as subalpine fir decline (Reich 2016). There is a greater abundance of young subalpine fir (diameter < 10) but it is not increasing its share of the canopy dominance at the expense of Engelmann spruce possibly due to the greater longevity of Engelmann spruce (Veblen 1986b).

Plot MRS7.

MRS7 is a well-drained, relatively xeric stand, located on a south-facing slope making it more exposed to solar radiation. Once dominated by limber pine and Engelmann spruce as indicated by tree ages (Veblen 1986a), this old post-fire stand canopy dominants are now Engelmann spruce and subalpine fir. Of the xeric and mesic sites, this is the only plot to increase in total tree population. The 5% increase in total tree population is primarily the result of subalpine fir recruitment into all size classes (Fig.7). Basal area gain is relatively uniform for all species with a ~16% increase in subalpine fir and Engelmann spruce, and a 14% increase in lodgepole pine. The decline in number of trees from the already small population of limber pine has resulted in its 50% loss in basal area. Thus, the overall pattern of change in MRS7 is
consistent with the slow successional replacement of the early post-fire dominant (limber pine) in the main canopy by Engelmann spruce and subalpine fir.

Fig. 6. Diameter at breast height (DBH) distribution in centimeters for each species at BL6. Bins are in increments of 5, starting at a dbh of 4.

Fig. 7. Diameter at breast height (DBH) distribution in centimeters for each species at MRS7. Bins are in increments of 5, starting at a dbh of 4.
**Plots MRS1,8,9,10.**

MRS 1, 8, 9 and 10 are young post-fire, lodgepole pine-dominated stands in the stem-exclusion phase. These plots exhibited the largest declines in populations of all permanent plots not caused by biotic disturbance. MRS1 had the greatest loss of 21%, while MRS 8, 9, and 10 lost 13%, 16%, 4% of their populations. While competing for sunlight, the decline in trees has allowed the remaining trees to fill in available canopy space. Excluding MRS5, these plots showed the highest percent gain in basal area with relatively uniform increases of 8.6, 16.8, 15.3, 16.8, respectively (Fig. 8).

![Graphs showing DBH distribution for MRS1, MRS8, MRS9, MRS10](image)

**Fig. 8.** Diameter at breast height (DBH) distribution in centimeters for each species at the young post-fires stands; MRS1, MRS8, MRS9, MRS10. Bins are in increments of 5, starting at a dbh of 4.
CHANGE IN ABOVE-GROUND BIOMASS FROM 1982 TO 2016

Trends in basal area increment (Appendix B) were consistent with above-ground biomass. In most of the permanent plots AGB increased from 1982 to 2016. Of the six old-growth stands, BW3 and MRS5 had the highest increases; 12.3% and 15.3% (Fig. 9). For all young lodgepole pine-dominated stands (MRS1, MRS8, MRS9, MRS10), AGB increased from 1982 to 2016 (Fig. 9). This is expected, as these stands are in the stem exclusion stage where growth of the smaller diameter trees into the larger size classes has resulted in 9.9 to 21.2% increases in AGB. Two sites displayed no gain in biomass; MRS4 (-1%) and BL6 (-2%). Both these stands experienced high mortality, attributed to wind damage and to subalpine fir decline, respectively.

The six graphs in Fig. 10 show trends in biomass by species in each permanent plot scaled to Mg ha\(^{-1}\). In BW2, a decline in the biomass of limber pine is offset by gains for Engelmann spruce and subalpine fir (Fig. 10). Contrarily, in BW3, both lodgepole pine and Engelmann spruce increased in biomass. The decrease in subalpine fir biomass in BW3, which is also seen in plot BL6, was the result of subalpine fir decline (i.e. the complex of WBBB, *Armillaria* root rot and FEB). Subalpine fir, Engelmann spruce and limber pine all gained biomass in MRS4 but there was a 25% loss in lodgepole pine biomass at least partially explained by the 2011-12 wind storm which resulted in a small reduction in the total biomass in this stand (Fig. 9). Hydric site, MRS5, increased biomass of fir by ~50% and spruce by 7%. Similar to BW2, the low percent increase in MRS7 is attributed to the increase in both spruce and fir, combined with the decrease in canopy dominants, lodgepole and limber pine.
Fig. 9. Change in above-ground biomass for each plot displayed for both measured time periods (1982 and 2016) represented as megagrams per hectare. Asterisk (*) indicates a greater than 10% change in biomass.

Fig. 10. Above-ground biomass by species in each of the six old stands in 1982 and 2016. Species codes are as follows; ABLA: subalpine fir, PICO: lodgepole pine, PIEN: Engelmann spruce, PIFL: limber pine.
CHANGES IN TREE MORTALITY FROM 1982 TO 2016

In a majority of the permanent plots throughout the 34-year monitoring period, for all tree species combined and for individual tree species, we observed an increase in annualized mortality rates through the census periods that ended in 2013 (Figs. 11 and 12). The most recently measured period (2014-2016) shows that while mortality rates are still relatively high when compared to the first mortality census (1983-1994), in most plots the annualized mortality rate has declined (Fig. 11). Four of the six older plots and three of the younger plots displayed strong decreases in mortality rates from 2014-2016 when water deficits were also decreasing (Fig. 13a).

BW2 was one of the few stands that declined in mortality from 1983-1994 to 1995-2007. This could be attributed to the relatively open canopy characteristic of the site. However, increased water deficits (Fig. 13a) did coincide with high limber pine mortality (Fig.12) for the 2007-2013 period. Of the six old stands, MRS4 was the only plot to increase in mortality rate during 2014-2016. Spruce death during this time, was nearly double lodgepole pine and fir (Fig. 12). Most recent mortality is the result of a wind blow down event during the winter of 2011-2012 (Wohl, 2013). MRS4 was one of the two plots that were affected. The other being BL6, had the highest mortality rate for the two most recent census periods. Though the effects of wind blow down were visible in BL6, most tree deaths were the result of subalpine fir decline (Table 3). This is evident during 2014 to 2016, where 90% of mortality was fir and 10% spruce. Subalpine fir decline was also apparent in both BW3 and MRS7 where fir was the only tree mortality in 2014-2016 (Fig.12, Table 3). However, decreases in mortality rates are still evident in BW3 and MRS7 during the 2014-16 time period.
Table 3. Percentage of tree deaths with evidence of mortality agents for all mortality periods.

<table>
<thead>
<tr>
<th>Biotic agents</th>
<th>% Tree Mortality</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Mountain pine beetle</em></td>
<td>1.4</td>
</tr>
<tr>
<td><em>Fir engraver beetle</em></td>
<td>0.0</td>
</tr>
<tr>
<td><em>Spruce bark beetle</em></td>
<td>1.4</td>
</tr>
<tr>
<td><em>Western balsam bark beetle</em></td>
<td>2.9</td>
</tr>
</tbody>
</table>

The pattern of mortality during all time periods for the four lodgepole pine-dominated young stands, is variable. With time, MRS1 and MRS10 have an accelerating trend of tree mortality until 2013. Following 2014, MRS1 tree mortality declined by a third of the previous year while there is no new mortality in MRS10. This decline during 2014-2016, is also exhibited in MRS8. Given that these stands are in the stem-exclusion phase, mortality rates are still high when compared to the older plots. The canopy openings may be allowing for less intensive self-thinning in all young site, excluding MRS9 where mortality rates are the highest during the 2014-2016 census period.

Fig.11. Mean annualized mortality for each plot from 1982 to 2016 as a percent of the live tree count at each census time period. Old stands (a) are separated from young post-fire stands (b). Mortality values are presented for four periods of observation: (1) 1982-1994, (2) 1995-2007, (3) 2008-2013 and (4) 2014-2016.
Annual Thornthwaite precipitation deficits show an increasing frequency of drought from 1982 to 2010 (Appendix C). The two highest annual deficits are reported in 2002 and 2006 (c 16 and -13mm). These trends are nearly the same as the trends in annual SPEI (Table 4) which exhibit an increasing frequency of drier periods (negative values) until 2013 (Fig. 13a). The mortality census period of 2014-2016 shows high SPEI (positive values), indicating greater wetness. The mean SPEI for 1982-1994 of -0.05 is higher than the following period (1995-2007) of -0.52. The mean for 2008-2013, is a value of 0.38. This mean is strongly influenced by the 2011 and 2013 years, which were exceedingly wet. Excluding those years, the mean is -0.27. The final census period of 2014-2016 has the highest SPEI mean of 1.09. The largest wet SPEI years were 1983, 2011 and 2013-2015 with values of 1.8, 1.56, 1.8, 1.6, and 1.5, respectively. The greatest SPEI dry years were 2000-2002, with values of -1.6, -1.5, and -2.0, respectively. These data correspond highly to the trends in annualized mortality (Fig.13c). To further associate trends in mortality to climate variability, the frequency of higher maximum temperatures during summer months is shown to increase through 2005 and remain high until 2011, after which they decline through to 2016 (Fig. 13b).

Table 4. Minimum, Maximum, and Mean values of SPEI for each mortality period

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Min</strong></td>
<td>-1.42</td>
<td>-2.00</td>
<td>-0.70</td>
<td>0.08</td>
</tr>
<tr>
<td><strong>Max</strong></td>
<td>1.79</td>
<td>1.40</td>
<td>1.80</td>
<td>1.60</td>
</tr>
<tr>
<td><strong>Mean</strong></td>
<td>-0.05</td>
<td>-0.52</td>
<td>0.38</td>
<td>1.09</td>
</tr>
</tbody>
</table>
Fig. 13. (a) Annual SPEI (C-1) for 1982-2015. Alternating shading of the background separates measured mortality periods. (b) The number of days where maximum temperature was greater than one standard deviation from the mean daily maximum June - September for 1982-2016. Black line represents the estimated line of the condition mean to identify the pattern within points. The shaded area represents the 95 percent confidence interval of the fitted line. (c) Mean annualized mortality computed for each year calculated as the mortality of each census period divided by the number of year within each period. Black line represents the line of the condition mean.
DISCUSSION

VARIABILITY OF ABOVE-GROUND BIOMASS WITHIN THE SUBALPINE FOREST ZONE

Our results indicate that the high degree of topographic variation as well as stand composition and age are reflected by large differences in stand-level above-ground biomass. For example, for the similarly aged xeric stand BW2 and the adjacent mesic stand BW3, AGB were 188 and 287 Mg h⁻¹, respectively (Table 5). For the two similarly aged plots MRS4 and MRS7, the more xeric plot (MRS7) had 47 Mg h⁻¹ less AGB. The bog forest at MRS5 despite being the oldest stand had the lowest AGB among the old plots and 21 Mg h⁻¹ less AGB than the old mesic site BL6 (Table 5). Overall, in pine-spruce-fir stands we found the mean AGB to be 211 Mg h⁻¹, in pure spruce-fir 175 Mg h⁻¹, and lodgepole pine 171 Mg h⁻¹. On average, the pure young post-fire lodgepole pine stands had lower AGBs than the old stands of spruce and fir with or without pines admixed. However, the AGB of 213 Mg h⁻¹ in MRS8 was greater than biomass amounts of some of the old spruce and fir dominated stands. Among the pure young lodgepole stands, AGB was quite variable in the stands at higher elevation, ranging from 143 to 213 Mg h⁻¹ for MRS8-10 (Table 5). The monotypic lodgepole pine stands in the permanent plots, displayed a large variation in AGB estimates, despite having established at the same time.

The AGB estimates for the pine-spruce-fir stands in the current study are somewhat higher; mean of 211 vs. 182 and 170 Mg h⁻¹, than those found for the same forest type by Bradford et al. (2008) and Kueppers and Harte (2005). Similarly, the mean of Prescott et al. (1989) fell below our calculated mean, as did the overall range of reported biomass values (Table 6).
For pure spruce-fir stands, Arthur and Fahey (1992) measured biomass in twenty spruce-fir dominated sites within Loch Vale watershed in north central Colorado and found a mean AGB of 124 Mg h\(^{-1}\) and a range of 24 to 148 Mg h\(^{-1}\), substantially less than the range of 165 to 186 Mg h\(^{-1}\) in the current study. For 18 old-growth spruce-fir stands (with two containing lodgepole pine) in Rocky Mountain National Park, Binkley et al. (2003) estimated a mean of 254 Mg h\(^{-1}\) and a range of 130 to 288 Mg h\(^{-1}\) (Table 6).

Overall, the spatial variability in AGB measured in the current study and supported by existing studies where sampling was limited to stands of homogeneous composition and topographic position (e.g. Binkley et al. 2003, Kueppers and Harte 2005) document large differences in AGB for stands of differing species composition, age, and topographic position. Consequently, efforts to scale up subalpine forest biomass estimates to larger areas (e.g. Bradford et al. 2008) should consider the heterogeneity of stand types and topographic positions across the subalpine forest landscape. The current and existing studies of spatial variability in biomass of subalpine forests in the Central Rocky Mountains imply that a single estimate of the forest carbon pool across a large complex landscape is unlikely to be accurate.

Table 5. Above-ground biomass (AGB) estimates for all permanent plots represented as Mg h\(^{-1}\)

<table>
<thead>
<tr>
<th>Plot</th>
<th>BW2</th>
<th>BW3</th>
<th>MRS4</th>
<th>MRS7</th>
<th>MRS5</th>
<th>BL6</th>
<th>MRS1</th>
<th>MRS8</th>
<th>MRS9</th>
<th>MRS10</th>
</tr>
</thead>
<tbody>
<tr>
<td>Topographic Position</td>
<td>xeric</td>
<td>mesic</td>
<td>xeric</td>
<td>xeric</td>
<td>hydric</td>
<td>mesic</td>
<td>xeric</td>
<td>xeric/mesic</td>
<td>xeric/mesic</td>
<td>xeric/mesic</td>
</tr>
<tr>
<td>Age</td>
<td>267</td>
<td>257</td>
<td>357</td>
<td>377</td>
<td>556</td>
<td>464</td>
<td>122</td>
<td>122</td>
<td>122</td>
<td>122</td>
</tr>
<tr>
<td>AGB</td>
<td>188</td>
<td>287</td>
<td>208</td>
<td>161</td>
<td>165</td>
<td>186</td>
<td>177</td>
<td>213</td>
<td>153</td>
<td>143</td>
</tr>
</tbody>
</table>
Table 6. Mean (and range) of above-ground biomass (AGB) estimates in subalpine rocky mountain studies represented as Mg h$^{-1}$.

<table>
<thead>
<tr>
<th>Location</th>
<th>Colorado Front Range*</th>
<th>Colorado Front Range*</th>
<th>Colorado and Wyoming†</th>
<th>Central Colorado‡</th>
<th>Northcentral Colorado§</th>
<th>Northcentral Colorado‡</th>
<th>Southwestern Alberta*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>Pine-Spruce-Fir</td>
<td>Spruce-Fir</td>
<td>Pine</td>
<td>Pine-Spruce-Fir</td>
<td>Spruce-Fir</td>
<td>Spruce-Fir</td>
<td>Pine-Fir</td>
</tr>
<tr>
<td>Age</td>
<td>314 (257-377)</td>
<td>510 (464-556)</td>
<td>122</td>
<td>158 (111-210)</td>
<td>325 (200-450)</td>
<td>250-500</td>
<td>90-350</td>
</tr>
<tr>
<td>AGB</td>
<td>211 (161-287)</td>
<td>175 (165-186)</td>
<td>88 (44-177)</td>
<td>182 (152-226)</td>
<td>170 (90-232)</td>
<td>254 (130-488)</td>
<td>124 (24-148)</td>
</tr>
</tbody>
</table>

Studies:
* Current
† Bradford et al. (2008)
‡ Kueppers & Harte (2005)
§ Binkley et al. (2003)
❖ Arthur & Fahey (1992)
● Prescott et al. (1989)

INFLUENCE OF STAND DYNAMICS ON ABOVE-GROUND BIOMASS

Over the 34-year census period, successional patterns inferred from size class frequency distribution were consistent with interpretations of tree age structures of the same stands (Veblen 1986a and Smith 2012). The uneven-aged, late-successional stands, presented negative exponential (“reverse J”) diameter distributions, indicating the presence of abundant small trees and successively fewer trees in the larger size classes; such a size structure is indicative of continuous recruitment into all size classes and of a stable or growing population size (Dyakov 2013, Meyer 1952). This trend was consistent for the shade-tolerant Engelmann spruce and subalpine fir in all stands. In contrast both limber pine and lodgepole pine had bell-shaped diameter distributions due to a dearth of individuals in small and largest size classes. For these shade-intolerant species, this finding is consistent with their successional status when growing in stands mixed with the shade-tolerant species (Peet 1981). In the young, post-fire lodgepole pine dominated stands, diameter distributions were variable. Even so, the general pattern suggests absence of new recruits in combination with high mortality, has caused an increase of trees in
larger size classes, consistent with the stem-exclusion phase. The presence of small numbers of subalpine fir and Engelmann spruce in these young post-fire stands implies that over a time span of several centuries the lodgepole pine may be replaced by these shade-tolerant species.

Early literature suggested that old forests near-steady state, maintain a constant level of biomass through the offsetting of mortality by recruitment and growth (Kimmins 1987). In contrast, young post-disturbance stands are expected to accrue biomass rapidly until successional changes reach stability. More recent literature indicates that old-growth forests that have attained a compositional equilibrium with continuously regenerating tree populations may continue to accrue more biomass (Keeton et al. 2010, Luyssaert, 2008). Overall, our findings indicate that biomass has continued to accrue in the young, post-fire stands as expected and also in nearly all the old seral stands and stands in compositional equilibrium.

Furthermore, variability within regions can depend not just on successional status or stand characteristics but on the stand-level topoclimatic conditions. The array of site characteristics displayed throughout the permanent plots, allows us to infer stand level topoclimatic influences on increment in AGB. In the hydric and mesic sites, we saw the highest increase in AGB. The indication being that availability in moisture enabled a high potential for growth. However, mesic site BL6 did not follow this pattern. Instead, the abrupt mortality in subalpine fir made this one of only two sites to not increase in biomass. The other being MRS4, concurrently experienced sudden mortality of multiple species. In both cases, rapid mortality was the product of disturbance.

POTENTIAL CLIMATIC INFLUENCES ON BIOMASS CHANGES FROM 1982 TO 2016.

While successional status can explain some of the change in diameter distributions from 1982 to 2016, there also appears to be a climatic signal in the observed patterns of tree mortality
which in turn affects total stand biomass. For example, moisture limitations have not impacted BW2, an open canopy stand, as intensely as BW3 the adjacent denser stand. With similar age structure and species composition, individuals in BW3 have more competition for water and therefore may be more susceptible to drought stress (Frelich and Reich 2010) and ultimately insect outbreak (Waring and Pitman 1985, Romme et al. 2006). In MRS5, the oversaturated soils allowed for a notably delayed response to moisture deficits, where higher mortality was only evident during the third mortality census (2008-2013).

A principal finding of this study is that mortality patterns across all plots exhibited sensitivity to short-term variability in drought. We observed increased magnitude and frequency of drought through the third mortality period (2008-2013), when mortality rates were at their highest. The brief period of high precipitation events toward the end of the third mortality period and throughout 2014-2016 coincides with a substantial decrease in mortality rates for all plots not impacted by disturbance (biotic factors or wind).

Ecological disturbances, such as, fire, wind blow-down, landslides, and insect/pathogen outbreak, are crucial features in subalpine forests and subsequently shape forest dynamics by influencing both stand structural characteristics and ecosystem processes. Over geologic time, disturbance regimes are expected to change with ecosystem changes. In Colorado forests in general, where trends towards increased frequencies of annual water deficits have been documented (Saunders 2008), we have seen synchronous increases in tree mortality caused by bark beetle outbreaks (Chapman et al. 2012, Hart et al. 2014). The warmest periods (1982-1994, 1995-2007, 2008-2013) have the highest insect related mortality, while the wettest period (2014-2016), showed the lowest mortality associated with insects (Table 3).
In the case of BL6, Western Balsam Bark Beetle generated mortality rates in subalpine fir that could not be compensated by growth or recruitment, prompting the inability to gain biomass. In MRS4, high mortality from wind blow down diminished AGB. These sites were the only two to be affected by significant disturbances and consequently were the only plots to not gain AGB over the period from 1982 to 2016. The lack of annual observations makes it difficult to interpret effects of climate on tree demography and biomass accumulation. However, our overall findings imply that these forests are highly responsive to variations in climate, which can impact the processes of stand development (mortality, natality, growth) as well as the productivity of biomass.
CONCLUSION

Re-measurement of 10 permanent plots in the subalpine forest of the Colorado Front Range identified shifts in tree population size structures consistent with predictions based on interpretations derived from the age structures of the tree populations at the time of plot installation. In mixed-species stands, there has been a slow trend towards replacement of the shade-intolerant lodgepole pine and limber pine by the shade-tolerant subalpine fir and Engelmann spruce. Young post-fire stands have experienced the highest increments in AGB but nearly all the old stands also show a trend towards continued biomass increase. Total biomass varied from 161 to 287 Mg h\(^{-1}\) among old stands, while young post-fire stands ranged from 143 to 213 Mg h\(^{-1}\). Stands of similar species composition and age exhibited large differences in AGB across short distances of steep environmental gradients in moisture availability. This suggests that spatial variability in biomass related to both topoclimatic site conditions and particularly to stand age is large and needs to be considered in future landscape scale assessment of carbon pools.

Although the lack in measurements of tree mortality on an annual basis complicates the association of changes in mortality patterns with climate trends, at a time-scale of 3 or more years there is a coincidence of changes in tree mortality patterns with climatic conditions. Elevated tree mortality is associated with higher levels of drought. Conversely, periods of just a few years of higher moisture availability are associated with declines in tree mortality. These findings, in combination, with previous research showing that tree seedling establishment and tree radial growth is limited by moisture availability, demonstrates the overall sensitivity of tree growth and survival to moisture limitation. This is an important finding in the context of the
common expectation for high elevation forests globally that rising temperatures may enhance tree growth and tree population sizes (Rossi et al. 2008, Harsch et al. 2009).

In subalpine forests of the Colorado Front Range, continued research is needed to further clarify the ecological processes limiting above-ground biomass. In understanding how successional and stand-level characteristics influence above-ground biomass, we can better interpret the effects climate will have on future carbon stocks in subalpine forests. Regardless, the demonstrated sensitivity of the stands monitored in these permanent plots to climate variations can have implications for predicted future warming. If recent mortality patterns persist, under continued or accelerated warming we should expect to see substantial decreases in live biomass in subalpine forests in the Colorado Front Range.
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Veblen, T.T., 1986b. Treefalls and the coexistence of conifers in subalpine forests of the central


APPENDIX A: Above-ground biomass equations

Appendix Table 1. Above-ground biomass equations for all species in the permanent plots. $R^2$ was reported by authors for the original regressions.

<table>
<thead>
<tr>
<th>Species</th>
<th>Scientific name</th>
<th>Equation</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Subalpine Fir</td>
<td>Abies lasiocarpa</td>
<td>$y_{\text{wood}} = \beta_{\text{wood1}} D^{\text{wood2}} H^{\text{wood3}} + e_{\text{wood}}$</td>
<td>0.99</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$y_{\text{bark}} = \beta_{\text{bark1}} D^{\text{bark2}} H^{\text{bark3}} + e_{\text{bark}}$</td>
<td>0.94</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$y_{\text{foliage}} = \beta_{\text{foliage1}} D^{\text{foliage2}} H^{\text{foliage3}} + e_{\text{foliage}}$</td>
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<td></td>
<td>$y_{\text{branches}} = \beta_{\text{branches1}} D^{\text{branches2}} H^{\text{branches3}} + e_{\text{branches}}$</td>
<td>0.65</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$y_{\text{total}} = \hat{y}<em>{\text{wood}} + \hat{y}</em>{\text{bark}} + \hat{y}<em>{\text{foliage}} + \hat{y}</em>{\text{branches}} + e_{\text{total}}$</td>
<td>0.97</td>
</tr>
<tr>
<td>Engelmann Spruce</td>
<td>Picea engelmannii</td>
<td>$y_{\text{wood}} = \beta_{\text{wood1}} D^{\text{wood2}} H^{\text{wood3}} + e_{\text{wood}}$</td>
<td>0.99</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$y_{\text{bark}} = \beta_{\text{bark1}} D^{\text{bark2}} H^{\text{bark3}} + e_{\text{bark}}$</td>
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<tr>
<td></td>
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<td>$y_{\text{foliage}} = \beta_{\text{foliage1}} D^{\text{foliage2}} H^{\text{foliage3}} + e_{\text{foliage}}$</td>
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<td>$y_{\text{branches}} = \beta_{\text{branches1}} D^{\text{branches2}} H^{\text{branches3}} + e_{\text{branches}}$</td>
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<td>$y_{\text{total}} = \hat{y}<em>{\text{wood}} + \hat{y}</em>{\text{bark}} + \hat{y}<em>{\text{foliage}} + \hat{y}</em>{\text{branches}} + e_{\text{total}}$</td>
<td>0.98</td>
</tr>
<tr>
<td>Lodgepole Pine</td>
<td>Pinus contorta</td>
<td>$y = (\alpha + \beta \ast D + c \ast (D^d)) \ast 0.453592$</td>
<td>0.98</td>
</tr>
<tr>
<td>Limber Pine</td>
<td>Pinus flexilis</td>
<td>$y = -3.4961 + 0.01916D^2H$</td>
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</tr>
<tr>
<td>Quaking Aspen</td>
<td>Populus tremuloides</td>
<td>$y = -3.4961 + 0.01916D^2H$</td>
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</table>

<table>
<thead>
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<th>Variables</th>
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<tr>
<td>$y$</td>
<td>total above-ground biomass in kg</td>
</tr>
<tr>
<td>$D$</td>
<td>Diameter at breast height (DBH) in cm</td>
</tr>
<tr>
<td>$H$</td>
<td>tree height in m</td>
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<tr>
<td>$\alpha$, $\beta$, $c$, $d$</td>
<td>Given parameters</td>
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APPENDIX B: Tree basal areas and densities per hectare

Appendix Table 2. Basal area (m$^2$ h$^{-1}$) of all live trees reported for the two full measurement years (1982 and 2016).

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Appendix Fig. 1. Change in basal area increment for each plot displayed for both measured time periods (1982 and 2016) represented as m$^2$ hectare$^{-1}$.
Appendix Table 3. Tree density (trees $h^{-1}$) of all live trees reported for the two full measurement years (1982 and 2016).

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</table>
APPENDIX C: Annual precipitation deficit

Appendix Fig. 2. Total annual precipitation deficit reported in millimeters of actual precipitation subtracted from the thornthwaite calculated potential evapotranspiration (PET). Y-axis has been inverted to allow for comparison with SPEI. Shaded background separates periods of measured mortality.