Montane pine species differ in water use efficiency under drought conditions across a small, headwater catchment

Alex Loomis
University of Colorado Boulder

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Montane pine species differ in water use efficiency under drought conditions across a small, headwater catchment

April 10, 2013

Alex K. Loomis

Department of Geography

Undergraduate Honors Thesis

Thesis Advisor:
Dr. Holly R. Barnard, Geography

Thesis Committee:
Dr. Holly R. Barnard, Geography
Dr. Nichole N. Barger, Ecological and Evolutionary Biology
Dr. William R. Travis, Geography, Honors Council Representative
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Abstract

As models of future climate project increasing frequency and severity of drought, understanding how trees, which provide valuable ecosystem services and store large amounts of carbon, respond to drought events, is of utmost important. This study examines how tree response to drought varies between species and across topography in a montane headwater catchment. Foliar $\delta^{13}C$ was compared between a wet and dry year to characterize changes in water use efficiency (WUE) in the area’s two dominant tree species: ponderosa and lodgepole pine. Lodgepole pine had a significant increase in $\delta^{13}C$ in the dry year, indicating that trees were forced to tolerate drought stress by increasing WUE. Ponderosa pine did not significantly change from the wet to dry year, indicating that it was likely able to avoid drought stress through various physiological mechanisms that allow it to obtain enough water even in drought conditions. Topographically-derived GIS surfaces for incoming solar radiation and topographic wetness index were used to model spatial variability in drought response. While these surfaces were generally not predictive of $\delta^{13}C$ in response to drought, improved models could better predict topographical influence on drought sensitivity. The stark contrast in the WUE response of ponderosa and lodgepole pine highlights the importance of understanding variation at the individual catchment scale to effectively model and predict regional and global tree drought response under changing future climate conditions.
Introduction

Water is the primary limiting factor on tree growth and mortality across the western United States (van Mantgem et al., 2009), and climate driven changes in growth and mortality can have substantial impacts on the composition of forests and the ecosystem services forests provide, including carbon sequestration (Boisvenue and Running, 2006). While the majority of assessments of vegetation’s response to global change have focused on averaged climatic conditions (Adams et al., 2009), the most impactful and dramatic changes in vegetation patterns are likely to result from extreme events, such as drought (Allen and Breshears, 1998). Studies have shown that even in humid forests, drought events have the potential to rapidly convert long-term carbon sinks into carbon source systems with a net loss in biomass (Phillips et al., 2009). A decrease in carbon sequestration would be expected in regional-scale drought events, and would lead to large annual reductions in carbon stored as above-ground biomass in trees due to a reduction in the amount of carbon fixed and stored annually as well as increased tree death and decomposition. This outcome would potentially result in a positive feedback between atmospheric carbon increases, more severe drought events, and increased tree biomass loss (Breshears and Allen, 2002). As global climate change is predicted to lead to more frequent, longer, and warmer droughts (IPCC, 2007a), the response of trees to water deficit driven by both local and regional droughts is of increasing importance (Allen et al., 2010).

Often overlooked in the analysis of changing climate’s impact on vegetation, is how this response might vary over finer, sub-regional scales, such as a single catchment. Despite the plethora of predictions of growth declines and tree mortality in response to changing climate (reviewed in Breshears et al., 2008; Adams et al., 2009), the varying physiological mechanisms
which drive decline during droughts are not completely clear (Sala et al., 2010). To more accurately predict potential tree response to drought, field studies incorporating a variety of climatic and physiological variables at a finer resolution are necessary (Hanson and Weltzin, 2000). While finer scale variation in forest response to drought may seem inconsequential compared to landscape and global level changes in vegetation, processes at these scales can drive changes in species distributions and diversity (Thuiller et al., 2002), which can ultimately impact vegetation response on a landscape and global scale (Thompson et al., 2009). Furthermore, many projections of the impacts of climate change on vegetation do not include the actual physiological mechanisms behind changes in vegetation, ignore the importance of spatial variability in environmental conditions, and thus fall short of effective modeling of vegetation response to climate and drought (Loehle and LeBlanc, 1996).

In Colorado, large drought events in the past have had catastrophic impacts on ecological systems including forest and human systems (Pielke et al., 2004). Many models of future changing climate project more frequent and more severe drought events not only worldwide (IPCC, 2007a) but specifically along the Colorado Front Range (Salas et al., 2005). As the availability of water is the primary limiting factor of tree growth in Colorado (van Mantgem et al., 2009), drought events may become the primary disturbance in Colorado Front Range forests and have much greater impacts on ecological systems which are essential to watershed processes (IPCC, 2007b), such as the greater South Platte River watershed with headwaters in the high elevation Rocky Mountains, which provides municipal water and other valuable ecosystem services to millions of people living in the region (Loomis et al., 2000). Understanding how tree response to drought varies on a single catchment-scale helps to better predict how drought events in the future will affect regional watershed processes and ecosystem services.
Stable Carbon Isotopes and Water Use Efficiency

An important tool for analyzing how trees respond to drought and other environmental conditions is the analysis of stable carbon isotopes. Carbon-12 ($^{12}$C) is the most abundant stable carbon isotope in the atmosphere, making up approximately 98.9% of the atmosphere, while Carbon-13 ($^{13}$C) makes up less than 1.1% of atmospheric CO$_2$ (Smith, 1972). Despite its relative rarity in the atmosphere, plants discriminate against heavier $^{13}$C through a process called fractionation (O’Leary, 1981). Two separate processes drive fractionation in plants. The first process is stomatal diffusion— as CO$_2$ diffuses through leaf stomatal openings, the additional mass of CO$_2$ composed of $^{13}$C causes it to diffuse into the stomatal cavity more slowly than CO$_2$ composed of lighter $^{12}$C (O’Leary, 1981; Park & Epstein, 1960). The second physiological mechanism behind plant carbon fractionation is through discrimination by the photosynthetic carboxylation enzyme RuBisCo (Ribulose biphosphate carboxylase). RuBisCo reacts more readily with $^{12}$C than $^{13}$C (Park & Epstein, 1960), and thus discriminates against 13C in the photosynthetic process (O’Leary, 1981).

Due to the photosynthetic mechanisms which drive carbon isotope fractionation in plants, Farquhar (1989) established that stable carbon isotope concentration ($\delta^{13}$C) can be used to infer photosynthetic water use efficiency (WUE) in C$_3$ plants, a topic that has since been the subject of extensive research and refinement (Farquhar et al., 1989; Ehleringer and Osmond, 1989; Pate, 2001). Water use efficiency is defined as a relationship between assimilation of carbon and a measure of water use, such as water transpired or stomatal conductance of water vapor (Farquhar and Richards, 1984; Seibt et. al, 2008). Generally, most recent studies focus on intrinsic WUE, which is defined by Seibt et al. (2008) as the ratio of assimilated carbon to stomatal conductance.
Foliage nitrogen content, which serves as a good estimation of foliage carboxylation capacity (Field and Mooney, 1986) can also be an important source of variation in δ^{13}C. Several studies have incorporated leaf nitrogen in δ^{13}C analysis and found that nitrogen content was positively correlated with δ^{13}C (Field et al., 1983; Toft et al., 1989; Sparks and Ehleringer, 1996; Bai et al., 2008), suggesting that carboxylation capacity can have the greatest impact on δ^{13}C in certain environmental conditions. Sparks and Ehleringer (1996) found that leaf nitrogen content was positively correlated with δ^{13}C even when water was added, which generally increases 13C discrimination.

δ^{13}C Response to Water Availability and Drought

Stomatal conductance varies in response to environmental conditions, and it is this response that creates the differences in δ^{13}C that can be used to measure water use efficiency. Stomata close as evaporative demand increases and/or moisture availability decreases (Taiz and Zeiger, 1991) and trees must use their limited internal CO₂. Under these CO₂ limited conditions, trees must efficiently use all carbon to avoid carbon starvation, and assimilate CO₂ with less discrimination against heavier 13C (Farquhar, 1989). Drought conditions often include increased evaporative demand, decreased moisture availability, or both (McDowell et al., 2008), and the influence of these conditions on δ^{13}C allow for relationships between moisture supply, evaporative demand, and δ^{13}C (as a proxy for WUE) to be used to measure response to drought.

Early studies into δ^{13}C and drought conditions were conducted with the goal of using isotopes in tree rings to help create an index of historical climate conditions and possible limitations to growth over the life history of a tree (e.g. Mazany et al., 1980, Francey and Farquhar, 1982), and related this directly to growing season water balance (Livingston and
Subsequent studies have emphasized the impacts of other site conditions on δ¹³C, which potentially devalues the efficacy of using tree-ring δ¹³C to construct paleo-climatic record (Saurer et al., 1995) but suggest that δ¹³C may be a useful indicator of tree response to finer-scale processes (Saurer et al., 1997). To investigate the influence of water availability on δ¹³C, studies have used a variety of measures to characterize water availability conditions. Ferrio and Voltas (2005) found that over a 24-year tree-ring record, δ¹³C increased significantly in years with less precipitation. Jansen et al., (2012) found that this response was controlled both by genetics and environmental conditions, highlighting the importance of genetically driven physiological processes on responses to water-availability. Sarris et al. (2013) used tree-ring δ¹³C in conjunction with stable oxygen isotope concentration (δ¹⁸O) to characterize drought response based on sources of water, considering root morphology as an important factor in a tree’s ability to respond to drought conditions. Studies have also used both foliage and tree-ring δ¹³C as an indicator of tree response to water availability (Panek and Waring, 1997).

Temporal variation in δ¹³C within individual trees has been used to estimate how tree response to drought may vary spatially and among species (Adams and Kolb, 2004). Leffler and Evans (1999) measured tree-ring δ¹³C response to stream flow in riparian trees (Populus fremontii) with high demand for water and found significant increases in δ¹³C in drier years. In a subsequent study, Leffler and Evans (2001) found that precipitation explained foliage δ¹³C between sites of varying climatic conditions, but that it had no significant impact in wood δ¹³C, suggesting that water availability explains some of the variation between populations, but other factors have important impact on δ¹³C. Panek and Waring (1997) found strong correlation between δ¹³C and various measures of stomatal conductance limitation including vapor pressure deficit, which suggests low atmospheric humidity was a major limitation on carbon uptake and
growth. A study on a ponderosa pine population (Gyenge, 2012), found that stand density and radiation had minimal effects on $\delta^{13}C$ during wet years, but became important in variation in $\delta^{13}C$ during dry years characterized by low soil moisture content and leaf water potentials. Adams and Kolb (2004) found significant decreases in $\delta^{13}C$ in several species across several sites between a wet year and a drought year, which they characterized using regional climatic and drought indices assuming that the relationship between $\delta^{13}C$, WUE, and water availability was strong enough that drought response could be investigated without finer-resolution climate data.

**Project Goal and Objectives**

In this study, my aim is to determine catchment scale variation in tree response to water availability and drought conditions across two dominant species. The specific questions I sought to investigate are: 1) How does foliar $\delta^{13}C$ as an indicator of WUE vary with respect to topography and species in wet versus dry years; 2) Does leaf nitrogen content explain spatial and temporal variation in foliage $\delta^{13}C$; and 3) Can topographically-derived measures of soil moisture and incoming solar radiation predict areas that are more or less responsive to drought?
Methods

Study Area

The study site for this project is Gordon Gulch (105.47 W, 40.01 N), a 3.75 km² catchment in the montane climatic zone, which lies within Arapahoe National Forest in the Front Range of the Colorado Rocky Mountains (Figure 1). The elevation ranges from 2446 to 2737 meters. Gordon Gulch is part of the greater Boulder Creek watershed, and is part of the NSF-Funded Boulder Creek Critical Zone Observatory. The drainage trends generally west to east, and has well-defined north- and south-facing slopes. The north-facing slope is more densely forested and dominated by lodgepole pine (*Pinus contorta* subsp *latifolia* Engelm ex Wats.). The south-facing slope is less densely forested; trees are predominantly large ponderosa pine (*Pinus ponderosa* subsp *scopulorum* Douglas ex Wats.) with open areas of grasses and small forbs in the understory. Soils in the study area are primarily stony sandy loam and depth to saprolite is typically 30-35 cm on the south-facing slope and 40-45 cm on the north-facing slope and this depth is generally uniform along the profile of each slope (Hinckley et al., 2012).

Gordon Gulch is divided into an upper and lower basin. The lower basin is narrower and has steeper slopes with a forested riparian area and has an average elevation of 2627 meters. The upper basin is broader, and includes some flat, open meadows and has an average elevation of 2680 meters. The stream is intermittent throughout the drainage, although the bottom of the lower basin is considered a perennial stream. The stream joins North Boulder Creek approximately 16 km below its upper-most headwaters near the continental divide.

Ten sample plots were selected out of 72 existing plots which had been previously measured for forest stand characteristics (including stand density, average diameter at breast
height, basal area, and species composition). Plots were chosen to represent the full extent of the study area and avoided areas of obvious recent logging or other disturbance. Four plots were located in Upper-Gordon Gulch and six in Lower-Gordon Gulch, and were evenly split between north- and south-facing slopes.

![Gordon Gulch- Foliage Isotope Sample Plots](image)

**Figure 1:** Map indicating location of ten plots sampled for foliage δ^{13}C

**Regional Climate and Micro-Meteorological Data**

Regional drought index data was obtained from the National Climatic Data Center (NOAA, 2013). Palmer Drought Severity Index (PDSI) which uses measured precipitation,
temperature, and modeled soil moisture and runoff to calculate a long-term drought trend was used to represent drought conditions over the 2011 and 2012 growing seasons, and the Palmer-Z index, which uses the same inputs to model short-term drought, was used to indicate month to month deviations from normal moisture conditions (Palmer, 1965). April 1st snowpack for the Boulder Creek drainage was obtained from the National Resource Conservation Service’s Weather and Climate Center (NRCS, 2013) and is based on five SNOTEL automated snow depth observation sites located from 2600-3200 meters in elevation across the watershed. A daily temperature record was obtained from the Denver Urban Drought and Flood Control Program’s nearby Sugarloaf Mountain Station from January 2011 to August 2012. Sugarloaf Mountain is located 3 km east of the study site. Daily average soil moisture from two arrays of 4 CS-107 soil moisture sensors (Campbell Scientific, Logan, UT), one each on the north- and south-facing slopes, placed at 25 cm depth, from January 2011 through September 2012 were provided by the NSF-funded Boulder Creek Critical Zone Observatory (CZO). Soil moisture sensors are part of the larger CZO infrastructure, and soil moisture data was acquired from the midslope sensor arrays that most-closely represent the location of plots sampled for this study. The CZO also provided precipitation, temperature, and incoming radiation data from two meteorological stations in Gordon Gulch beginning in June 2012, which was used to evaluate the more complete Sugarloaf NADP data collected nearby but not within the study area. Meteorological data was used to compare atmospheric conditions over the 2011 and 2012 growing seasons (May 1 thru October 30).

**Field Sampling**

Three trees were selected at each plot for foliage analysis. In an effort to minimize any confounding effects of competition for light and other resources, the most dominant trees that
were also representative of the stand were chosen within each plot. Although some plots contained species other than ponderosa and lodgepole pine (e.g. *Juniperus scopulorum, Pinus flexilis*), none of these species made up a substantial proportion of the canopy and were not selected for sampling. Foliage was collected from each of these three representative trees between October and December 2012. Foliage was collected from the mid to upper-canopy from branches exposed to direct sunlight. Green leaves from the 2011 and 2012 growing seasons were differentiated based on relative position on branches, bud scars and color, and removed from branches and stored separately. The species of each tree was recorded and the diameter of each sample tree was measured at breast height (1.4 m).

**Foliage δ¹³C and Nitrogen Concentration**

Foliage was oven dried for 50 hours at 35º C. Dried leaves were flash frozen with liquid nitrogen and ground by mortar and pestle. Ground foliage was packed into individual filter paper packets. Foliage components were extracted until only holocellulose was remaining in order to avoid analyzing more labile carbon sources which may vary in isotopic concentration and are not an accurate representation of isotopic concentration over time (Loader et al., 2003; Macfarlane et al., 1999) following the methods outlined in Leavit and Danzer (1993). Cellulose was extracted by solvents (Toluene and Ethanol), boiling, and bleaching (Sodium Chlorite under acidic conditions). Extracted holocellulose was analyzed for δ¹³C at the University of Colorado’s Institute of Artic and Alpine Research Stable Isotope Laboratory using a Thermo Scientific EA 1110 CHN- Elemental Analyzer (C.E. Elantech, Lakewood, NJ) interfaced to a SIRA continuous-flow mass spectrometer.
To calculate WUE efficiency, a measure of $^{13}$C abundance ($\delta^{13}$C) is calculated relative to a standard ratio of $^{13}$C/$^{12}$C (0.01124) established by Craig (1957), using the following equation:

$$\delta^{13}C(\%o) = \left( \frac{R(\text{sample}) - R(\text{standard})}{R(\text{standard})} \right) \times 1000$$

$\delta^{13}$C is expressed as per mil notation ($\%o$) and as plant material is always depleted relative to the standard, so values of $\delta^{13}$C in plants are always negative. This relative abundance can be used to calculate a discrimination value ($\Delta$) using the following equation:

$$\Delta = \frac{\delta_a - \delta^{13}C}{(1 + \delta^{13}C)/1000}$$

The discrimination value can in turn be used to calculate a formal WUE value (Farquhar et al., 1982), however many more recent studies use $\delta^{13}$C directly as a proxy for WUE efficiency (ex: Adams and Kolb, 2004; Warren et al., 2001; Panek and Waring, 1997) and this is the approach that will be taken in this study.

To measure foliage nitrogen content, bulk foliage was dried overnight at 60° C and ground by mortar and pestle to maximize homogeneity. Whole ground leaf tissue was analyzed for percentage of Nitrogen and Carbon content using a Thermo Scientific EA1112 CHN-Elemental Analyzer (C.E. Elantech, Lakewood, NJ).

**GIS Analysis**

GIS analysis was performed using 1-meter resolution Light Detection and Ranging (LiDar) surfaces from the Boulder Creek Critical Zone Observatory as source data. The last-stop LiDar surface was used as a digital elevation model (DEM) for the ground surface, and a first
stop LiDAR surface was used as a canopy top surface ArcMap 10.1 (ESRI, 2012) was used to model several raster surfaces for analysis. Slope and aspect surfaces were calculated using the Spatial Analyst toolbox and the last-stop LiDAR as the DEM input surface. A canopy height (meters) surface was calculated by subtracting the first-stop LiDAR DEM from the last-stop LiDAR DEM. A canopy cover (tree presence/absence) surface was created by using the canopy height surface to calculate a binary tree presence/absence layer for all cells. Tree presence (value of 1) was assigned to all cells with canopy height greater than 1.5m.

An incoming solar radiation surface was created for the top of the canopy using the Spatial Analyst incoming solar radiation tool, which uses a hemispherical viewshed algorithm that accounts for latitude and topography to model yearly radiation across a surface. Topographic wetness index (TWI), initially developed by Beven and Kirkby (1979) is an index which uses topography to calculate the ratio between hydrologic upslope contributing area and local slope to characterize topographical influence on hydrologic flow paths and soil moisture. A TWI surface was created using the TauDEM toolbox (Tarboton, 1997) using the last stop LiDAR surface. This toolbox calculates d-infinity derived catchment area to create a wetness index which measures slope over contributing area and is inversely related to the standard natural long of area over tangent of slope index (Tarboton, 1997). Mean values across 100 m² plots were calculated for each surface at each plot using the Spatial Analyst focal statistics tool.

**Statistical Analysis**

Foliage $\delta^{13}$C data of each species was analyzed using repeated measures MANOVA and MANCOVA with year as the repeated factor to account for two measurements of each tree, and plot, diameter at breast height, aspect, and elevation as factors/covariates. Also included in
repeated measures models were outputs from GIS analysis — topographic wetness index, slope, and incoming solar radiation. Pairwise comparisons of 2011 $\delta^{13}$C, 2012 $\delta^{13}$C, and change in $\delta^{13}$C between years was conducted using ANOVA and Tukey’s Honest Significant difference test. Nitrogen concentration is a good estimation of maximum carboxylation capacity (Field and Mooney, 1986), which can be a source of variation in $\delta^{13}$C (e.g. Bai et al., 2008), was also fit to the same repeated measures model to account for the possibility carboxylation capacity was a factor in foliage $\delta^{13}$C. All analysis was conducted in R (R Development Core Team, 2013).
Results

Regional Climate

The Palmer Drought Severity Index of regional climate across the South Platte River basin showed long-term drought conditions consistently in the non-drought to very moist range in the 2011 growing seasons and in the severe to extreme drought range through the growing season in 2012 (Figure 2). The Palmer-Z index of short term conditions mimicked this trend, although certain months (i.e. July 2011, September, 2012) deviated slightly (Figure 2).

Figure 2: Palmer Drought Indices for 2011 and 2012 Growing Season for Colorado Climate Division 4, Platte River Drainage. Palmer Drought Severity Index is a measure of long-term drought and wetness conditions, Palmer Z Index shows how monthly moisture conditions depart from normal, representing short-term drought and wetness. Both indices are on a -4 to 4 scale relative to normal conditions (0). Values less than -2.75 represent extreme drought, less than -2 represent severe drought, between -1 and 1.25 represents mid-range, and greater values represent moderate to extreme moisture.
Local Temperature

Air temperature at the Denver UDFCD (Urban Drought and Flood Control District) Sugarloaf station followed a similar trend in both 2011 and 2012. In comparing between the two years, mean and median temperature from April to October was within 1 degree Celsius, and followed a similar trend across that time period (Figure 3). Monthly average temperature was within 1° C for all months except for May and June, in which average temperature was 2° C warmer for 2012. Distribution of temperature readings (Figure 4) was also similar for both years, but there are slightly more extreme (> 30° C) readings for 2012.

Temperature data from both the north and south-facing slopes in Gordon Gulch is available from June 8th, 2012. From that date through October, daily average temperature for the south-facing slope followed the same trend as the Sugarloaf data for that period. The north-facing slope was consistently 1-3° C cooler than the south-facing slope.

Figure 3: 2011 and 2012 Temperature from Denver Urban Drainage and Flood Control District's Sugarloaf Met Station, approximately 3 km from study area and at similar elevation
Soil Moisture

Soil moisture varied between years and between the north- and south-facing slopes (Figure 5). The greatest difference between 2011 and 2012 soil moisture is the consistently higher moisture in 2011 from May through June on both slopes. A rapid increase in soil moisture occurs on both slopes in mid-April (Day of Year 110) in 2011; however, in 2012, the south-facing slope did not experience an increase in soil moisture early in the growing season. In contrast, the north-facing slope rapidly increased in soil moisture early-March (Day of year 70) 2012. As snow makes up the majority of precipitation in the study area (Wiliams et al., 2011), average snowpack levels are the primary driver of soil moisture, particularly early in the growing season (Hinckley et al., 2012). For the Boulder Creek watershed, April 1st snowpack was at 118% of the thirty-year average in 2011, and at 54% of average 2012 (NRCS, 2013).
Figure 5: March through October daily average volumetric soil moisture content from each slope in Lower Gordon Gulch

**Foliage δ¹³C and Nitrogen Concentration**

For lodgepole pine, foliage δ¹³C was significantly more enriched in 2012 than 2011 (P<0.01). For ponderosa pine, there was no significant difference in δ¹³C between 2011 and 2012 (P=0.53, Figure 6). In 2011, foliage δ¹³C was significantly less enriched in lodgepole pine than in ponderosa pine (P<0.01), but in 2012 there was no significant difference between the species (P=0.61). Within each species, there were no significant differences in δ¹³C between different plots, either within years or changes between years. In lodgepole pine, there were no significant differences in foliage δ¹³C for different elevations, sizes (diameter at breast height), aspect, topographic wetness index values, slope, incoming solar radiation, or between the upper and...
lower sections of the catchment. In both species, nitrogen had no significant impact on $\delta^{13}\text{C}$ and there were no significant differences in nitrogen between years.

In pairwise comparisons, there were no significant differences between any north-facing slope plots 2011 $\delta^{13}\text{C}$, 2012 $\delta^{13}\text{C}$, or change in $\delta^{13}\text{C}$ between years ($P>0.6$ for all comparisons). On south-facing slope plots, there were no significant differences between plots in either 2011 $\delta^{13}\text{C}$ or $\delta^{13}\text{C}$ ($P>0.45$ for all comparisons). However, there was a significant difference in the change in $\delta^{13}\text{C}$ between years between plots 1 and 3 ($P=0.048$). Plot 3 was the only south-facing plot which had an increase in $\delta^{13}\text{C}$ from 2011 to 2012 on average (Table 1), while plot 1 had a decrease in $\delta^{13}\text{C}$ from 2011 to 2012.

![Mean Foliage $\delta^{13}\text{C}$ by Species](image)

Figure 6: Mean foliage $\delta^{13}\text{C}$ for each species for each year. Error bars represent +/- 1 standard error.
GIS - Topographical Analysis

Mean values for topographically derived GIS surfaces did not provide any statistically significant predictions of $\delta^{13}$C in any models. However, there were overall differences in mean values for plots on each slope. Mean annual incoming solar radiation for north-facing plots was 1751 hours/year and 2018 hours/year for south-facing plots (Figure 7). Mean topographic wetness index was 0.063 for north-facing plots and 0.100 for south-facing plots (Figure 8), and mean slope was greater for south-facing slopes (19.3° compared to 16.7° for north-facing plots). Some plots did not follow these general trends however, and individual plot means are provided in Table 2. Canopy height (which provides a visualization of tree distribution and density across the catchment) and slope surfaces are included in Appendix A.
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<th>Canopy Cover (%)</th>
<th>Slope (degrees)</th>
<th>Topographic wetness index</th>
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Table 2: Mean results from forest characteristic surveys (stand density) and topographical derived GIS surfaces (all other values) for each plot.

Figure 7: Annual duration of direct solar radiation across study area.
Figure 8: Topographic wetness index across study area.
Discussion

How did climatic conditions vary between 2011 and 2012?

While regional drought conditions are not always indicative of the particular local environmental conditions that control tree growth, extreme PDSI values are likely to indicate drought conditions over the vast majority of the region (Gutzler and Robbins, 2011) and have been used to characterize physiological δ¹³C response to drought (Adams and Kolb, 2004). In this study, both short- and long-term regional drought indices suggest that 2011 was consistently moister than average, while 2012 was consistently drier than normal and experienced severe to extreme drought conditions. Based on the stark contrast in water availability across 2011 and 2012, comparing δ¹³C across these years serves as a measure of how drought events affect WUE and overall tolerance of trees to drought-induced stress. Similarity in 2011 and 2012 temperatures at the Sugarloaf Denver UDFCD Meteorological Station suggests that for this area, air temperature alone was unlikely to contribute to variation in plant physiological processes between the two years. While temperature alone can impact physiological processes in trees, the interaction of water availability and temperature has the potential to be a much greater influence on physiological process in trees (Teskey et al., 1987) including WUE and thus δ¹³C.

Soil moisture has been shown to be highly correlated with tree transpiration (Tromp-van Meerveld and McDonnell 2006), and with δ¹³C (Beerling, 1996), and offers the most proximate measure of moisture available to trees in this study. As expected, the south-facing slope had lower values for soil moisture throughout both years. Gordon Gulch develops a seasonal snowpack on north-facing slopes and an intermittent snowpack on the south-facing slopes during the winter, and on average 59% of the precipitation at the site falls as snow (Williams et al.,
In 2011, the rapid increase in soil moisture for both slopes in mid-April can likely be attributed to the major spring snowmelt event in the area, which is typically the largest annual hydrologic event and input of moisture of catchments across the Rocky Mountains (Bales et al., 2006). In 2012, the north-facing slope does show a signal that could be attributed to snowmelt; however it occurs much earlier (mid-March) than the steeper, more distinct 2011 signal. The south-facing slope shows no clear snowmelt signal in 2012, rather it declines steadily from March to extremely low values in July, when it increases quickly. The July increase can likely be attributed to a summer precipitation, the major source of later-summer moisture in the system (Bales et al., 2006). After the initial snowmelt signal in March, the north-facing slope soil moisture also follows this decline to extremely low values until an increase at the same point in July. These soil moisture patterns suggest that there was far more water available to trees in 2011 than in 2012, particularly early in the growing season (May-July).

Studies have shown that topographically driven micro-climate can have major effects on distribution of snowpack across a catchment, and this variation can impact soil moisture (Olyphant, 1984). Due to high incoming solar radiation, snowpack is transient on the south-facing slope of the study area and a clear snowmelt signal is unlikely on that slope, particularly in dry years, while a clear snowmelt signal is expected on north-facing slopes with seasonal snowpack. However, in a small catchment such as the study area, in which each slope is generally dominated by a single species, it can be assumed that precipitation inputs are relatively uniform across each slope (Hjert et al., 2004), and soil moisture is driven by gravitational potential moving moisture through the system (Quinn et al., 1991). Considering this assumption, it is unlikely that soil moisture spatially deviates far from the general, strong trend shown in the
soil moisture record of high moisture in 2011 and low moisture in 2012, particularly from May-July.

These climatic conditions provide an ideal way to examine how WUE varies across the study area under drought conditions. It is likely that low soil moisture in 2012 resulted in decreased water availability conditions to at least some of the trees in the study area compared to 2011. Stomatal closure, which increases with decreased water supply or increased demand, results in enriched foliar $\delta^{13}$C. While some studies have related drought driven increases in stomatal closure to $\delta^{13}$C (i.e. Panek and Waring, 1997; Leffler and Evans, 2001), studies that have shown how $\delta^{13}$C varies over a gradient of elevation allow the foliage $\delta^{13}$C data from this study to be put in climatic context of 2011 and 2012. Drought is not a specific condition, and even when comparing high- and low-moisture years, it is useful to consider the response of trees across environmental gradients. Korner et al. (1988) found that $\delta^{13}$C increased with increasing elevations, a finding that has been reinforced by several studies since (Morecroft et al., 1992; Diefendorf et al., 2010; Yan et al., 2012). Many studies suggest this trend can be explained by increased stomatal limitation with increasing elevation (Korner and Diemer, 1987; Friend et al., 1989; Morecroft and Woodward, 1996), a trend that would also be expected with decreased water supply, as was likely the case for trees in this study in 2012. However, Vitousek et al. (1990) found that on the moist east slopes of Mauna Loa, Hawaii, $\delta^{13}$C within one species increased with elevation, but on the drier northwest slopes, there was no such increase. They attribute this trend to physiological adaptations in the trees on the highly moisture limited slopes that limit assimilation of $\delta^{13}$C. Hultine and Marshall (2000), found that while $\delta^{13}$C did increase with increasing water demand and decreasing water supply across an elevation gradient, the rate of this trend varied between different species. This suggests that even under the drought
conditions of 2012 at Gordon Gulch, the differing water needs of different species and their ability to access moisture and keep their stomata open in drier conditions is essential to understanding response to drought.

**How does foliar δ\textsuperscript{13}C vary with respect to topography and species in wet versus dry years?**

The most striking source of variation in δ\textsuperscript{13}C between 2011 and 2012 was between the two study species. Ponderosa pine showed no significant difference in δ\textsuperscript{13}C between the wet and dry year, suggesting no change in WUE. Lodgepole pine however had a distinct, uniform increase in δ\textsuperscript{13}C from 2011 to 2012, suggesting that WUE changed, likely due to different environmental conditions during each year’s growing season. This pattern was consistent over all north-facing plots dominated by lodgepole pine and in 4 out of 5 predominately ponderosa pine south-facing plots. Based on δ\textsuperscript{13}C data, physiological response to water availability and drought conditions in this catchment is highly variable between different species.

Studies have used water use efficiency to characterize how drought response varies between and within species (Adams and Kolb, 2004; Valladares and Sanchez-Gomez, 2006). Characterizing these variations in responses is essential to contextualizing δ\textsuperscript{13}C and WUE, because drought-induced mortality varies between individuals within species and between different species (McDowell et al, 2008). In order to interpret δ\textsuperscript{13}C responses to various environmental conditions, it is important to understand that this response is driven by physiological mechanisms that may be different for different species. Furthermore, environmental conditions are the major driver of distribution of many species, and response to changing conditions including drought can be magnified at the extremes of a species’
distribution where individuals are already more likely to be stressed by normal environmental conditions (Allen and Breshears, 1988). This idea has led to studies focusing on ecotones, areas of transitions between different plant communities, and has included studies of $\delta^{13}$C in these areas (Adams and Kolb, 2004; McDowell et al., 2009). Based on this insight, it is clear that $\delta^{13}$C response to drought needs to be put into the context of the species being measured, the physiological mechanisms which drive their distribution and the position of study area relative to species distributions and the environmental factors which drive distribution.

Ponderosa pine is one of the most widely distributed and studied pine species of western North America. It grows in a wide variety of ecosystem types, but in Colorado it is often the dominant tree species on drier, mid-montane elevation slopes (Richardson, 2000). As it is so widely spread in water-limited regions, numerous studies have characterized its ability to tolerate drought, based on various physiological mechanisms (i.e. Domec et al., 2004; Maherali and Delucia, 2000; Panek and Goldstein, 2001). Studies have developed vulnerability curves to characterize vulnerability to both xylem cavitation (Maherali and Delucia, 2000) and to root embolism (Domec et al., 2004) in order to understand the physiological tolerance of ponderosa pine to drought conditions. Generally these drought avoidance mechanisms allow ponderosa pine to mitigate low water-availability and high water demand conditions—these mechanisms therefore allow ponderosa pine to keep stomata open during drier conditions than otherwise possible which would preclude an increase in $\delta^{13}$C and WUE under those conditions. Ponderosa pine in the study area is in what is characterized as xeric lower-montane woodland, which is near the upper elevation limit of ponderosa pine, but generally dominated by large ponderosa pine trees (Peet, 1981).
Domec and Gartner (2003) found that mature ponderosa pines had highly plastic growth response to environmental conditions in response to water availability, allowing trees to persist in drought conditions. This growth response is likely due to stomatal conductance, which Panek and Goldstein (2001) found to regulate carbon uptake in response to soil water, vapor pressure deficit (VPD), and temperature. While a change in stomatal conductance alone would likely result in a change in WUE in response to drought, other physiological mechanisms may be of greater importance in ponderosa pine and could explain the lack of variation in $\delta^{13}$C between the wet and dry years. Maherali and Delucia (2000) examined how transpiration demand influenced the vulnerability of ponderosa pine to xylem cavitation, and found that anatomical differences in trees were caused by evaporative demand and not soil drought. However, they found no intraspecific variation in xylem vulnerability to cavitation between populations from dry, desert regions and wetter montane systems, suggesting that flexible anatomical response to climate is the primary mechanism through which ponderosa pine persists in drought conditions. Domec et al. (2004) investigated root physiology, and found that root xylem embolism works in conjunction with stomatal response to limit water loss and maintains water levels during drought events. They also found that ponderosa pine appears to mitigate drought stress through hydraulic redistribution, the movement of water via roots from moist to drier portions of the soil, allowing trees to avoid some of the stress of drought. These studies support the notion outlined by Zhang et al., (1997), that in ponderosa pine, physiological mechanisms that allow trees to avoid the stresses of drought and keep stomata open under these moisture limited conditions, are more important for survival and growth than using water efficiently.

Based on the soil moisture information for the south-facing slope of Gordon Gulch, where ponderosa pine in the study area are located, ponderosa pine in the study area had far less
soil water available in 2012 than 2011, yet there was generally no $\delta^{13}C$ response. Warren et al. (2005) found that ponderosa pine were able to effectively store and utilize moisture from precipitation events late in the growing season. As even during the dry year (2012) there were rain events later in the growing seasons, this ability may have helped ponderosa pine mitigate the impact of drought stress. These physiological processes, which allow ponderosa pine to avoid drought stress rather than simply tolerate drought conditions, limit the need for the ponderosa pine in the study area to use water more efficiently under drought conditions, resulting in no increase in $\delta^{13}C$ in the drier growing season of 2012.

A single ponderosa pine-dominated plot on the south-facing slope (plot 3) did show an increase in $\delta^{13}C$ between 2011 and 2012 and was statistically significantly different from all four other ponderosa-dominated plots. While the measured plot conditions and tree characteristics were similar to the other four plots containing ponderosa pine, this plot showed an increase in WUE and may have been influenced by topographical, site-specific conditions that pushed it past the point of drought avoidance in the dry year in 2012 and led to drought stress that caused the change $\delta^{13}C$ as that plot had to tolerate drier conditions than the other plots.

Lodgepole pine is also widely distributed across western North America, but compared to ponderosa pine it generally grows in moister, higher elevation areas (Richardson, 2000). In Colorado, lodgepole pine often forms dense, monotypic stands across high elevation regions (Peet, 1981). Within the study site, the drastic difference between vegetation on the north- and south-facing slope suggests that species may be persisting at the limits of their distribution and the environmental conditions which drive distributions. Based on the characterization of vegetation patterns across Colorado by Peet (1981), the study area is near the lower elevation limit for lodgepole pine and is likely to be at the low-moisture limit, as the two slopes are so
drastically different, indicating the difference aspect-driven environmental conditions are enough change to allow lodgepole pine to dominate one slope and barely exist on the other.

The increase in δ\textsuperscript{13}C in lodgepole pine between the dry and wet years was consistent across all trees and all north-facing plots, where lodgepole pine dominates. Furthermore, the two lodgepole pines on south-facing, ponderosa dominated slopes, also increased in δ\textsuperscript{13}C while the ponderosa pine at those sites did not (Plots 7 and 9). This suggests that unlike ponderosa pine, lodgepole pine is not able to avoid the drought conditions experienced in 2012, and used water more efficiently in order to tolerate the water conditions. Unlike ponderosa pine, physiological studies of how lodgepole pine responds to climatic conditions are limited. Marshall and Zhang (1994) showed δ\textsuperscript{13}C changed with changing elevation, but studies have not characterized δ\textsuperscript{13}C in lodgepole pine in response to drought. Pataki et al. (2000) used sapflow data to characterize how lodgepole pine responds to drought in an area which also receives most of its moisture as spring snowmelt. That study found that sapflow decreased in response to soil drought, suggesting that lodgepole pine is sensitive to soil moisture. Sap flux is indicative of transpiration and is related to stomatal conductance (Taiz and Zeiger, 1991), and this supports the notion that the increase seen in δ\textsuperscript{13}C and WUE in lodgepole pine 2012 is a response to stomatal closure due to low water availability. Hu et al. (2010) found that lodgepole pine is particularly reliant on moisture from snowmelt, and as the snowpack moisture was so limited in 2012 compared with 2011 and the 30-year average conditions, this could be the primary driver of the δ\textsuperscript{13}C response. Within the study area, which is already near the limit of where lodgepole pine grows in the region (Peet, 1981), the impact of a dry year may be particularly strong, as the large change in δ\textsuperscript{13}C between the wet and dry years indicates.
Based on the change in δ^{13}C between 2011 and 2012, it seems that lodgepole pine was not able to avoid drought stress and instead showed an increase in WUE as a tolerance mechanism. Lodgepole pine root systems have been shown to be less extensive than ponderosa pine root systems of trees of similar ages growing in similar soil (Berndt and Gibbons, 1984) and are also particularly prone to windthrow (Richardson, 2000), suggesting that their roots are less extensive at depth. These differences in root structure may allow ponderosa pine to obtain enough moisture during drought conditions to avoid water stress, while the shallower, smaller lodgepole roots may be unable to obtain enough moisture from soil in dry, low snowpack years to avoid water stress, resulting in the δ^{13}C response.

While δ^{13}C response to drought conditions showed significantly differential response to drought in two widespread species, understanding of what drives this difference and how it might be important would be greatly enhance with better understanding of the physiology of lodgepole pine. While it is clear there was generally a WUE response in lodgepole pine and not ponderosa pine in the specific conditions of this study, without a better understanding of the physiological traits of lodgepole pine it is challenging to predict how this might apply in different climate conditions and in other areas. Vulnerability curves have quantified the water deficit conditions under which xylem cavitation occurs in ponderosa pine (Maherali and Delucia, 2000), but not in lodgepole pine. Research has shown that carbon assimilation of lodgepole pine will be significantly lower in under the warmer climatic conditions predicted in many models (Hu et al., 2010), but further research into the physiology of lodgepole pine on an individual tree scale would greatly enhance our ability to predict response to drought conditions on a catchment scale and to changing climate on a landscape scale.
Can topographically-derived measures of soil moisture and incoming solar radiation predict areas that are more or responsive to drought?

The topographically-derived GIS surfaces did not provide any statistically significant prediction of variation in $\delta^{13}C$ response to drought. Incoming solar radiation is highly correlated with photosynthetically active radiation (Meek et al., 1984), which influences water use of trees, as stomatal aperature increases with increasing radiation up to a saturation point (Taiz and Zeiger, 1991). However, while there was a large spread in modeled amount of solar radiation for each plot, this did not correlate with spatio-temporal patterns in $\delta^{13}C$ beyond the generalized effect of north- versus south-facing slopes. As the variation in radiation based on aspect is well established (Gates, 1980) and it is easy to determine aspect in a catchment such as the study area, predicting radiation patterns on that scale is not particularly useful.

Topographic wetness index (TWI) also did not provide any statistically significant prediction of $\delta^{13}C$ response to drought conditions. TWI does not account for the amount of moisture input to the system through precipitation and does not actually attempt to predict the amount of soil moisture (Dyer, 2009). Water may have been too limited to be present at the levels that TWI would provide a meaningful index for its abundance. It is also possible that flow paths that are not incorporated in the slope-contributing area ratio of TWI might dominate the hydrologic system of the study area. While TWI has been shown to be correlated with groundwater flow paths as well as soil moisture (Sorensen et al., 2006), it is based on surface topography and does not truly account for vertical infiltration and subsurface heterogeneity.

While these spatial indices were not predictive in any of the statistical models used, they may help explain the one pair of ponderosa pine plots that had statistically significantly different change in $\delta^{13}C$ between 2011 and 2012. Plot 3, the only site where ponderosa pine had an
increase in $\delta^{13}$C from 2011 to 2012, had the highest incoming solar radiation and lowest topographic wetness index of all south-facing plots. Plot 1, located closer to gulch-bottom than any other plots, had by far the lowest incoming solar radiation value and one of the higher TWI values. While these values were not statistically predictive, this could suggest that despite their shortcomings, these indices are indicative of the underlying environmental factors that may drive the different response in these plots.

As it is located nearer the bottom of the gulch than all other plots, plot 1’s low incoming solar radiation values are not surprising despite it being on the south-facing slope which has otherwise higher incoming solar radiation. Lower solar radiation could result in a cooler, moister site that may help explain the decrease in WUE at that site during the drought year. High incoming solar radiation values and low TWI predict high evaporative demand and lower water availability at plot 3, which could result in greater drought stress and explain the change in WUE that did not occur in other ponderosa pine. Plot 5 is the most similar in location to plot 3; it is located at a very similar elevation on the same slope, and the incoming solar radiation values for the two plots are nearly identical. However, plot 5 is located at the base of a large rock outcropping and has by far the highest mean TWI value, nearly twice that of any other plot, suggesting that it may have disproportionately high water availability compared to other plots. Plot 5 showed no change in $\delta^{13}$C from 2011 to 2012, and the only striking measured difference between Plot 3 and Plot 5 was TWI.

It is possible these spatial indices may be more predictive of tree response to various environmental conditions if the average values are calculated over a larger area than a 10 by 10 meter plot. While 100 m$^2$ is likely to cover the extent of any one individual tree, environmental conditions over a larger area may affect trees in the plot. Predictions of both soil moisture and
incoming solar radiation may be more indicative of the impact on any one tree or plot if the boundaries within average values for each plot were calculated are expanded. An average weighted by distance from a tree or plot could provide a better prediction. Solar radiation and moisture are not confined by arbitrary boundaries, so creating fuzzy boundaries to calculate these indices may more accurately represent the environmental conditions a tree or plot are subject to.

While some studies have shown the Tarboton TWI method is the most correlated with soil moisture and other hydrologic conditions (Sorensen et al., 2006), other methods for deriving relative wetness from topography may improve on this method, provide better models for spatial variation in soil moisture, and ultimately help in creating better predictions of how response to drought may vary across a catchment. Dyer (2009) modeled soil moisture using a water balance method which attempts to use GIS to predict the actual amount of soil moisture, rather than simply create an index such as TWI which is simply correlated with soil moisture. Dyer’s method uses elevation, soil, and climate data to model variation in evaporative demand and create a prediction of soil moisture based on water balance. This method offers a more comprehensive approach that may be better able to predict variation in soil moisture over a catchment, particularly as higher resolution soil data become available. Using this approach may lead to better predictions of spatial variation in drought response.
Conclusion

Tree response to drought is of critical importance in the face of predictions of increased drought event frequency and intensity. The use of foliage δ¹³C over a wet and dry year highlighted how drought response can vary between species. As these species are widespread throughout North America, understanding how their response to drought might vary is applicable over a wide geographic region. Ponderosa pine was able to avoid drought-induced stress, likely through a variety of physiological avoidance mechanisms through which trees are able to obtain enough water to keep stomata open in dry conditions. These avoidance mechanisms appear to be essential to ponderosa pine’s ability to persist during drought events, and the robustness of these mechanisms may determine its long-term response to increasingly frequent and severe drought conditions. Lodgepole pine increased its WUE under drought stress, suggesting its drought tolerance mechanisms are more important to how it might be impacted by drought in the future. Further research into the physiology of lodgepole pine would greatly enhance our ability to project its ability to persist through changing future climate conditions. While topographically-derived indices for solar radiation were not predictive of spatial variation in δ¹³C drought response, more comprehensive models may be better able to predict fine-scale variation in drought response. Incorporating models of how the water balance varies topographically into δ¹³C analysis of various species response to drought could provide insight into how changing climate conditions will affect forests and the valuable ecosystem services they provide.
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References


Appendix A: Additional GIS Surfaces

Upper Gordon Gulch - Canopy Height

Legend
★ Isotope Plots
Canopy Height (meters)
High: 20
Low: 0

Plot 9
Plot 10
Plot 7
Plot 8
Lower Gordon Gulch - Canopy Height

Legend
- Isotope Plots

Canopy Height (meters)
- High: 20
- Low: 0

Plot 1
Plot 2
Plot 3
Plot 4
Plot 5
Plot 6

0 0.125 0.25 0.5 0.75 Kilometers

N