



Tree species mixture under drought stress

Results of *Quercus gambelii* – *Pinus ponderosa* stands in the Southwestern US

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Master thesis • 60 credits

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MSc. Forest Ecology and sustainable Management

2024:13 • ISSN 1654 - 1898

Umeå 2024



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Credits: 60

Level: Advanced level, A2E

Course title: Masterarbete i Skogsvetenskap

Course code: EX0957

Programme/education: MSc. Forest Ecology and sustainable Management

Course coordinating dept: Forest Ecology and Management

Place of publication: Umeå

Year of publication: 2024

Cover picture: Jonas Laurens Kappen, 2023, Picture of the site Coulter Park

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Title of series: Examensarbeten / SLU, Institutioner för skogens ekologi och skötsel

Part number: 2024:13

ISSN: 1654-1896

Keywords: tree growth, drought stress, species mixture, Gambel Oak, Ponderosa Pine, Arizona, Southwest, US, diameter, competition, growth ratio

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Abstract

Drought as a stressor has a strong influence on the tree growth, leading to reduced growth and die-backs. Possible ways are researched to mitigate this impact on trees; mixed species forests are often discussed in this context. Existing research points out a possible positive effect on the growth under drought, based on reduced competition and facilitation. However, differences between the effect, depending on the combined species seem to exist. Pine and oak species are often found coexisting, especially as well in dry climates, which suggests the question if complementarity might play a role. Research of the two genera showed often positive but varying effects of mixture, $dbh_{1,3}$, I therefore investigate, if this applies as well for two common species of the US American Southwest: *Pinus ponderosa* and *Quercus gambelii*. Due to the regular droughts in the region, I expect a strong positive impact on the tree growth by mixture. Based on analysed increment cores I found a stronger, but also more varying growth of *Pinus ponderosa* compared to *Quercus gambelii*. The high correlation of growth patterns with the drought index SPEI, shows the dominating growth limitation by the dry climate in the region. The use of a generalized linear model gave more insight in the influence of species mixture as well as the diameter and competition on the growth. Though statistically not significant the results suggest a clear negative influence of increasing tree diameters but higher growth under drought for *Pinus ponderosa* with a higher share of *Quercus gambelii* in their neighbourhood, compared to trees growing in a monospecific mixture. The clear differences between the increment as well as its variability between the two species, is likely caused by the different adaptations to drought. I found possible explanations for the positive mixing effect for *Pinus ponderosa* in the decreased competition above and below ground, facilitation by *Quercus gambelii* through hydraulic redistribution of deep soil water as well as decreased evaporation due to a protecting microclimate under the canopy of *Quercus gambelii*. The results point out the possibilities of species mixtures in mitigating the increasingly difficult growth conditions due to dry climate. Especially for the two researched species a positive effect can be expected, which suggests the use of its potential in the forest management of the Southwestern US.

Keywords: tree growth, drought stress, species mixture, Gambel Oak, Ponderosa Pine, Arizona, Southwest, US, diameter, competition, growth ratio

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Abbreviations

AIC	Akaike Information Criterion
BC	Beaver Creek
CP	Coulter Park
dbh _{1.3}	Diameter on Breast height
DCI	Competition Index, based on Hegyi
NAM	North American Monsoon
SPEI	Standardized Precipitation Evapotranspiration Indice

1. Introduction

Due to the changing climate, ecosystems all around the world face elevated stress factors, including drought and higher temperatures (IPCC, 2022). For forest ecosystems drought is one of the major sources of stress, leading to reduced leaf- and stem-growth, increased occurrence of tree mortality and phenological changes (Allen et al., 2010; Dickson & Tomlinson, 1996; Fernández et al., 2014; Hinckley et al., 1979; Park Williams et al., 2013). A well reported case is the region of the southwestern US, including Arizona. The region is experiencing a fundamental change in growth conditions, caused by increasing levels of drought. Since the beginning of the century an ongoing, so called “Megadrought”, has led to higher temperatures and drought conditions (Seager et al., 2007; Seager & Vecchi, 2010; Williams et al., 2020). Surveys, as well as predictions, show that trees in the region are negatively affected by these new conditions (Breshears et al., 2005; Fettig et al., 2019; Szejner et al., 2020). However, not only specific drought events, but also whole weather systems seem to have changed. Recent studies show that the North American Monsoon (NAM), a weather system providing the Southwestern US with the highly needed precipitation in the summer months (Strange et al., 2023), is changing in its seasonal distribution towards a later start as well as an increasing intensity within the monsoon season (Cook & Seager, 2013). Rainfalls may change as well towards a lower total precipitation and higher vapour pressure deficits in the summer (Strange et al., 2023). Increasingly dry conditions are expected to affect forests at a higher rate: similar conditions have already shown their impact on trees growing in lower elevations that experience usually more arid conditions in the Southwestern US (Adams & Kolb, 2005; Fettig et al., 2019).

The mixture of tree species is a widely discussed topic in publications of the recent years (Bravo-Oviedo et al., 2018; Pardos et al., 2021; Pretzsch et al., 2017; Sebald et al., 2021; Steckel et al., 2020). Research has suggested that the presence of multiple species in forest ecosystems is often advantageous compared to single species forests (Bravo-Oviedo et al., 2018; Steckel et al., 2020). Mono-specific forests are often favoured in terms of simplifying processes in economic aspects as well as the preference of certain species (Evans, 1992). However, they are connected to high risks such as calamities and changing environmental conditions (Matyssek et al., 2010). Forests consisting of multiple species are proposed to play a key role in diversifying risk (Matyssek et al., 2010) and have been suggested to

increase harvest yields to levels above mono-cultures (Pretzsch et al., 2017). Yet, advantages in term of productivity are only one aspect; mixed species forests are also known to support sustainability, multifunctionality, regulating functions, social values, as well as many other ecosystem functions (Bravo-Oviedo et al., 2018).

An important approach in explaining differences in the growth increment of pure stands compared to mixed stands based on the number of occurring tree species, is the “net biodiversity effect”, as described by Loreau and Hector (2001). The authors see this difference in growth as the combined result of selection and complementarity between the species. Complementarity and therefore potential higher increments in mixture, can be caused by a reduction in competition or facilitation (Loreau & Hector, 2001; Pretzsch et al., 2017). Competition is caused by the limitation of growing space above and below ground, as well as resources such as light, nutrients and water (Matyssek et al., 2010). If resources are accessed in different times or physical locations, competition can be lower in heterospecific mixture, compared to a monospecific stand of only one species (Pretzsch et al., 2017). This could be the case, for example, by different rooting depths of two species (Pretzsch et al., 2017). Facilitation can be explained by the stress gradient hypothesis. This assumes that positive interactions should be common in plant communities in environments with a higher level of physical stress (e.g. drought), and that plant-plant interactions shift from competition to facilitation the more stressful an environment becomes (Bertness & Callaway, 1994; Michalet et al., 2006). Facilitation describes positive interactions between two or more species, where one is improving the situation of another; for example by increasing the availability of a critical resource or by improving the environmental conditions (Pretzsch et al., 2017). However, research shows, that this concept, as it is in our current understanding, might be limited. Under extreme levels of stress, facilitation seems to rather decrease, than increase (Michalet et al., 2006) depending on the stressing factor and the interacting species (Maestre et al., 2009). Holmgren and Scheffer (2010) even suggest that facilitative plant interactions might be common at moderate levels of stress as well. The classic stress gradient hypothesis therefore has to be applied carefully, however it still depicts an important theory in explaining the role of interactions in the existence of stressors. Positive effects of complementarity also apply for drought on the growth increment (Thurm et al., 2016), which is the focus of this thesis.

Existing research shows us that the effects of tree mixtures are based on highly complex relationships between the individual trees of forest ecosystems (Pretzsch, 2009). Both positive and negative species interactions have been shown to influence tree growth in mixed forests. On the one hand, based on the complementarity hypothesis, I can predict that niche complementarity or facilitation can promote ecosystem processes, when more than one species are present (Pretzsch et al., 2017). One such promoted process could be volume (diameter) growth, as

measured in this study. On the other hand, negative interactions between species are also possible; if mixture leads to increased competition, resources may not be used optimally, and productivity may not be enhanced in mixtures, or may even decline (Pretzsch, 2010). These alternative possibilities for species interactions should be considered in research focused on species mixture effects. Mixed forests are also expected to play an important role, given the changing climatic conditions (Pardos et al., 2021; Sebold et al., 2021). However, research also shows that these effects could be limited (Paquette et al., 2018). Especially regarding drought, many aspects such as specific species combinations, stand characteristics, and water availability seem to influence if tree species mixtures are beneficial (Pardos et al., 2021).

Pine and oak species occur in many parts of the world (Denk et al., 2017; Nobis et al., 2012), which is thus the focus of my thesis. In the last decades, studies on the mixture of pine and oak species have showed partially contradictory results. In earlier studies, their mixture was understood as a problem of competition for water between the two species, and therefore a threat to the productivity of *P. ponderosa*, especially since *Q. gambelii* trees were seen as less valuable (Tew, 1967). Nevertheless, later studies found positive effects, suggesting niche complementarity (Bello et al., 2019; Biondi et al., 1992) and facilitation (Abella & Springer, 2008; Biondi et al., 1992; Klemmedson, 1987, 1991) of mixtures between the two genera. Also, Pardos et al. (2021) showed that the mixtures of coniferous and broadleaved species have a higher positive effect on their drought reaction, than their pure counterparts. Steckel et al. (2020) showed that the mixture of Scots pine (*Pinus sylvestris*) and Penduculate oak (*Quercus robur*) as well as Sessile oak (*Quercus petraea*) is capable of reducing the influence of drought. Especially the two oak species were profiting from the mixture, rather than Scots pine, as Steckel et al. (2020) showed. Bello et al. (2019) found positive mixture effects on the growth under drought for Sessile oak, but not for Scots pine. However, there is a gap in knowledge: little research is available to evaluate these relationships between North American genera.

The species Gambel oak (*Quercus gambelii* Nutt., later on referred to as “*Q. gambelii*”) and Ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson, later on referred to as “*P. ponderosa*”) are two very common and drought tolerant species of the American Southwest (Conkle & Critchfield, 1988; Poulos, 2009). Both species form together a common plant association in the region, adjacent to pinyon-juniper woodlands where water is increasingly limited (Mary Stuever, 1997). These forests grow in a climate characterized by dry seasons (Poulos, 2009; Williams & Anderson, 1967) and frequent drought. Despite the fact, that *P. ponderosa* as well as *Q. gambelii* are drought tolerant species, both are physiologically rather different, also considering their phylogenetic status (Abrams, 1990; Maherali & DeLucia, 2000; Zhang et al., 1997).

Besides species mixture as the focus of this work, tree size and competition are also potentially important indicators to understand the context of droughts in forest ecosystems. Though many studies appear to show significant results, more research is clearly needed. As well as for tree size, respectively social situation in stands (Martín-Benito et al., 2008; Merlin et al., 2015; Zang et al., 2012), as for competition between trees (Aldea et al., 2017; Bello et al., 2019; Bottero et al., 2017) results, of how tree growth is affected seems only to be valid for the investigated species or possibly genus and are partly contrasting. Species and genus specific research is therefore needed. Tree size (e.g. diameter) and competition intensity are potentially important parameters in forest management and therefore also often investigated. Since both parameters are comparatively easy to measure, they also take an important role as a measure of the situation of a tree or group of trees, in many studies, as shown above. The mentioned aspects will be therefore also discussed in this study.

Dendrochronological tree ring measurements are a very suitable and commonly used method to research the growth of trees under various influences (Biondi et al., 1992; Schweingruber, 2012) but especially climatic influences, including drought (Martín-Benito et al., 2008; Merlin et al., 2015; Steckel et al., 2020; Strange et al., 2023; Zang et al., 2012). Limiting factors such as water availability, lead to a response in the tree ring patterns, resulting in narrow and wide rings. Based on a suitable site selection, ring width patterns of climate sensitive trees can be used to investigate climatic influences on tree growth (Speer, 2010). This study uses this method to analyse the trees of two unmanaged forests of mixed *Q. gambelii* – *P. ponderosa*, where they occur close to their elevational drought limit. The selected forest sites in the southwestern US are expected to be strongly influenced by drought and would therefore give crucial insights into whether species mixtures might be less sensitive to drought conditions. Such analysis may have important implications for silviculture in the region. Therefore I will investigate, based on dendrochronological measurements, the following questions and hypotheses:

- Q1: Which species, *Pinus ponderosa* or *Quercus gambelii*, has a higher growth increment; furthermore, for which species is the growth increment more sensitive to drought?
- H1: I expect a typically higher increment of *Pinus ponderosa* in comparison to *Quercus gambelii*. The increment of *Pinus ponderosa* is however more affected from drought than the increment of *Quercus gambelii*.
- Q2: Is the species mixture of *Pinus ponderosa* and *Quercus gambelii* affecting their increment under drought? Do both or especially one species show a positive or negative influence of mixture on their increment?
- H2: I expect that a mixture of *Pinus ponderosa* and *Quercus gambelii* can reduce the drought sensitivity of each species. Further, I expect that *Quercus gambelii* will benefit more from mixture than *Pinus ponderosa*.

2. Material and Methods

2.1 Study sites

For this study I conducted measurements in two sites with soils formed from volcanic origin, in the Coconino national forest between Flagstaff and Phoenix in the southwestern US (Baker Jr, 1981; Bills et al., 2007). Geologically, the region is situated at the Mogollon Rim, which forms the southwestern edge of the Colorado Plateau (Bills et al., 2007). Here the land falls down from Flagstaff with warm summers and cold winters towards lower elevations with hot summer summers and mild temperatures in the rest of the year as Williams and Anderson (1967) describe. The general climate is semiarid and continental (Williams & Anderson, 1967). The particular height changes at the Mogollon Rim are influencing temperatures and precipitation, with two distinct precipitation periods: snow and rain occurs between November and April, whereas summer monsoon rains occur between July and August (Williams & Anderson, 1967). Precipitation events in the region is triggered by the elevation increase of the Mogollon Rim (Adams & Comrie, 1997). Precipitation increases with increasing elevation in the region: the lower situated site Beaver Creek (hereafter referred to also as “BC”), has an elevation of 2055m above sea level, a 30 year mean temperature of 8.9°C and average precipitation of 585,3mm per year (Adams & Comrie, 1997; PRISM-Climate-Group, 2023). The higher site Coulter Park (hereafter referred to also as “CP”), has an elevation of 2190m above sea level, 30 year average mean temperature of 8.5°C and an average annual precipitation of 613.7mm (PRISM-Climate-Group, 2023).

As Williams and Anderson (1967) describe; Soils in the Beaver Creek area developed mostly from weathering of volcanic stones, especially basalt and cinders. Though often fertile, soils are rather rocky with a limited capacity of storing water for plant growth. The dominant soils are fine, smectitic, mesic Typic Argiustolls; stony-clay-loam with up to 10% slope, as well as silt-loam (Soil-Survey-Staff, 2023). Other soils in the area are fine, smectitic, mesic Calcic Argixerolls, in form of clay loam as well as stony rough land of basalt and cinders (Soil-Survey-Staff, 2023). Based on geological information of the region (Baker Jr, 1981; Bills et al., 2007) and examination on the sites, I expect similar soils and geological conditions at the site Coulter Park.

I chose the sites because of their relatively undisturbed character and their similar mixture of *P. ponderosa* and *Q. gambelii* trees. Mixed forests of the two species are a common plant association in Arizona as well as surrounding areas (Stuever & Hayden, 1997). From lower elevations and dryer climates towards the Mogollon rim with increasing precipitation, the Grassland-Desert Shrub vegetation changes first to Pinyon-Juniper woodlands, then to the association of *P. ponderosa* and *Q. gambelii* (Williams & Anderson, 1967). This change also applies to the chosen sites: while the site BC is located close to the transition zone towards Pinyon-Juniper woodlands, the site CP is positioned deeper into the *P. ponderosa* – *Q. gambelii* forest-areas. I found only a few additional tree species and in very small number, other than *P. ponderosa* and *Q. gambelii*. I therefore did not include them in the further analysis. Trees of the same species showed a similar age in both sites, based on estimations from increment core data (see Table1).

Table 1: measured minimum mean age of *P. ponderosa* and oaks at both sites and standard error. Age can be expected around 10 to 20 years higher than shown, due to incomplete measurements (missing tree rings).

Site	Species	Estimated mean age	Std
Beaver Creek	<i>P. ponderosa</i>	111	15
Beaver Creek	<i>Q. gambelii</i>	146	36
Coulter Park	<i>P. ponderosa</i>	104	25
Coulter Park	<i>Q. gambelii</i>	167	39

I assumed that no management operations were conducted in the last century, based on few strongly decayed stumps and information by local authorities (Moser, 2023). Both sites have a subsistent amount of deadwood in form of standing and laying trees. I found *P. ponderosa* to be mainly evenly distributed on the sites, while *Q. gambelii* occurred mostly in clumped groups. Based on the focal trees in the groups used for the study, both sites showed a similar diameter in breast height (dbh_{1.3}), tree height, as well as similar competition situations (see Figure 1 and Figure 2). Differences between the two species are also similar between the sites; in general *Q. gambelii* trees showed a lower height, smaller diameter and higher competition than the analysed *P. ponderosa* trees, likely caused by the typical growth behaviour of *Q. gambelii*. Competition is characterized as the Hegyi-Index (see also chapter 2.6) where higher values represent a higher competition.

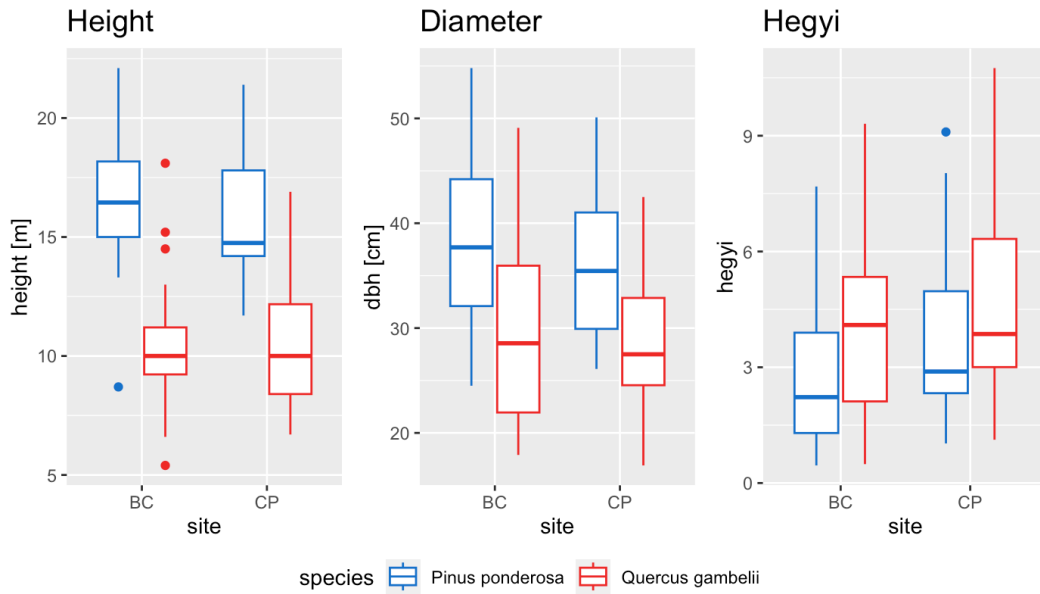


Figure 1: Height, diameter and hegyi index of focal trees in their groups of 7m radius, per species and site, “BC” = Beaver Creek, “CP” = Coulter Park.

2.2 Study design

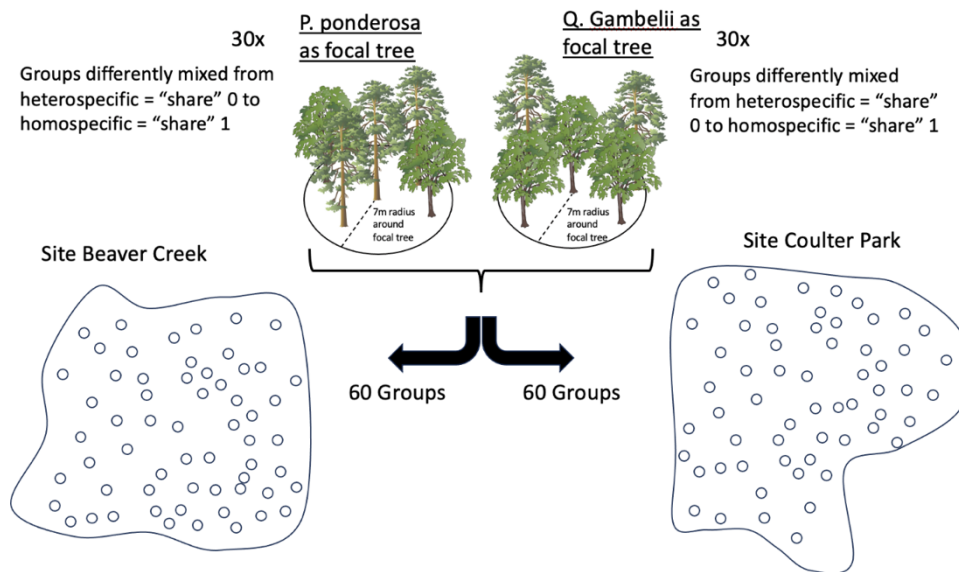


Figure 2: A schematic visualisation of the study design. Each 30 groups of the two researched species were chosen from focal trees surrounded by the other species (“heterospecific”, share 0) to an increasingly pure species situation within the groups (“monospecific”, share 1). I performed this selection similar on the two sites, Beaver Creek and Coulter Park. Shown is not the actual position of the groups. The spatial distribution of the groups is not even, but based on where I found suitable focal trees and species mixtures..

For the present study, I took measurements in the sites Coulter Park and Beaver Creek. To study the influence of species mixture, my goal was to find a possibly high and similar number of different mixture situation per species and site (compare schematic visualisation in Figure 2). To achieve this, I searched for tree groups with a focal tree of one of the two species and different mixture situations. To cover possibly all mixture proportions of the two species, I aimed to find mixtures in the groups ranging from up to 25%, between 25% and 75% and more than 75% of the same species as the focal trees (see Figure 3 and 4). This categorization allowed me, to cover a relatively wide and consistent variety of mixture situations. I defined tree groups as the combination of a focal tree and all trees of a minimum dbh_{1.3} of 1cm within a radius of 7m around the focal tree. In that way I selected 30 tree groups, with a focal tree of *P. ponderosa* and 30 groups with a focal tree of *Q. gambelii*, at each site (Coulter Park and Beaver Creek), resulting in a total of 120 tree groups. I chose either dominant or co-dominant healthy trees without signs of damages, burning, or fungal infections as focal trees. I chose groups mainly based on the mixture, not on their spatial distribution; therefore it can be seen as relatively random, dependent on the found species mixture.

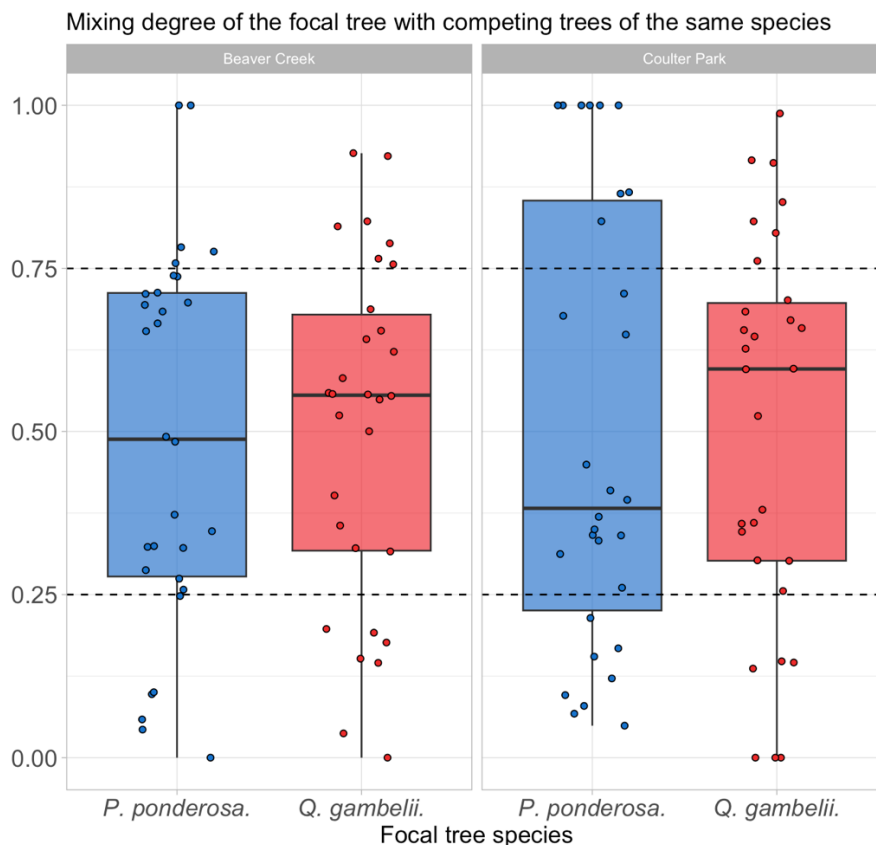


Figure 3: Species mixing degree of the focal tree, ranging from only trees of the other species (0.00) up to a mixture with 100% of the same species neighbours (1.00). The dashed line shows the three mixture classes that were searched for, when choosing the groups, to get the needed mixture ratios of every species. The figure shows that most mixture degrees were covered by the selected groups.



Figure 4: Two groups in Coulter Park, with *P. ponderosa* as a focal tree. Left side: low share of *Q. gambelii* (monospecific species mixture), right side: high share of *Q. gambelii* (rather heterospecific species mixture). The focal tree is marked with a blue tape in each group.

2.3 Measurements

Of the 120 focal trees, I measured tree height and height of the crown base with an electronic laser hypsometer (Nikon Forestry Pro II), diameter at breast height ($dbh_{1.3}$) with measurement tape (π -division, unknown manufacturer) and I took as well two increment cores from the north and east side of each tree (increment borer, Haglöf, Sweden). Therefore I took a total of 240 cores, from 120 focal trees. I measured the diameter in the same way of all other trees within the groups, as well as the tree height of one surrounding *P. ponderosa* and *Q. gambelii* tree in each group. Additionally I measured the distance from the surrounding trees to the focal tree with measurement tape (unknown manufacturer) as well as the angle with a compass (Suunto, Finland).

I scanned collected increment cores (Epson Perfection V850 Pro, Epson), measured after preparation their ring widths and cross-dated them with the programs CDendro and Coorecorder (Lars-Åke, 2023). Additional cross-dating, I conducted within the program R (R-Core-Team, 2022) and the packages treeclim (Zang & Biondi, 2015) and dplR (Bunn et al., 2015). As additional reference to ensure correct cross-dating, I used a tree ring reference for *P. ponderosa* in the area of Flagstaff, Arizona (Becky et al., 2021). I compared measured tree-ring-series of

two cores per tree to each other, the reference chronology as well as the chronologies of the other collected samples. The latest tree-ring of 2023 was in most trees only partly developed; therefore I did not include the year in the measurements. I downloaded weather data of the two sites from the website of the Prism Climate Group (PRISM-Climate-Group, 2023) for further analysis. To visualise data produced by the model, I used the R package sjPlot (Lüdecke, 2023).

2.4 Data analysis

The in this study analysed tree cores allow a view on the tree growth over long time period (see Figure 6). The analytic part of this study as well as a more detailed view on the connection of growth and drought (Figure 7, Table 3) focused however on a part of this growth history from 2000 until 2022. The rationale for this focus is that further back in time the neighbourhood structure of the plots is less certain. Therefore, I chose a time interval of growth for this study, where I expect competition and mixture situations to be relatively similar to what was observed at the time of sampling, in 2022. Another reason of starting detailed analysis in the year 2000, is the onset of the so called “megadrought (Seager et al., 2007; Seager & Vecchi, 2010; Strange et al., 2023; Szejner et al., 2020; Williams et al., 2020). For an analysis within this period I expect rather comparable conditions.

To evaluate the influence of drought on tree growth, it is important, to know when over the year, drought is usually relevant for the tree growth. I decided to use the Standardized Precipitation Evapotranspiration Indices “SPEI”, calculated over several months as a measure of drought. The SPEI is a drought index, developed from other indices, to combine their positive properties and is especially suitable to detect the influences of global warming and droughts (Vicente-Serrano et al., 2010). Based on the weather data I calculated a 3-, 6-, 9- and 12-month SPEI preceding for all months of the year, as well as the site aridity index. I calculated the SPEI values, as introduced by Vicente-Serrano et al. (2010) with the “SPEI” R-package of Vicente-Serrano (2023).

Since it is potentially the most relevant for the vegetation, I decided to use the SPEI₁₂ of the month July. This SPEI showed a high correlation with the measured growth curves (see Figure 5) in a comparison using the R package “treeclim” (Zang & Biondi, 2015). The figure shows the correlation of calculated SPEI values including increasingly longer time periods (by quarter years: 3, 6, 9, and 12 months) with the calculated mean growth chronologies for each species and site. In most cases both sites were equally well described by each SPEI. The levels of correlation decreased slightly and then increased for *P. ponderosa* until August, before a strong decrease. The SPEI correlations for *Q. gambelii* increased until June, before a strong decrease. In general, SPEI indices calculated over a long period, as SPEI₁₂

showed a higher correlation. For *P. ponderosa* the SPEI12 (August) and for *Q. gambelii* the SPEI9 (June) showed each a slightly higher correlation; however, I decided to use the mentioned SPEI12 for July as a compromise between both species. Due to the regions climate also precipitation in form of snow fall from December to February has to be considered as an important water source for tree growth (Williams & Anderson, 1967). The SPEI12 for July includes this time. Based on the high correlation between the SPEI12 for July and the growth chronologies, as well as the strong stand level signal (high EPS value) in the measured tree ring data, I expect that drought plays an important role as a growth limiting factor for both species at Beaver Creek and Coulter Park. The expressed population signal (EPS), similar to the r_{bar} , is used to express the common variability in a chronology (see also chapter 3.1). As Speer (2010) describes, the EPS indicates the dominance of individual tree signals versus coherent stand level signals, if found to be below a certain point. A level of 0.85 is commonly used here (Speer, 2010). For the calculation of the site aridity index, I used the formula described in the “world atlas of desertification” of the UN (1992):

$$site\ aridity = annual\ aridity\ index$$

$$annual\ aridity\ index = \frac{annual\ precipitation}{annual\ potential\ evapotranspiration}$$

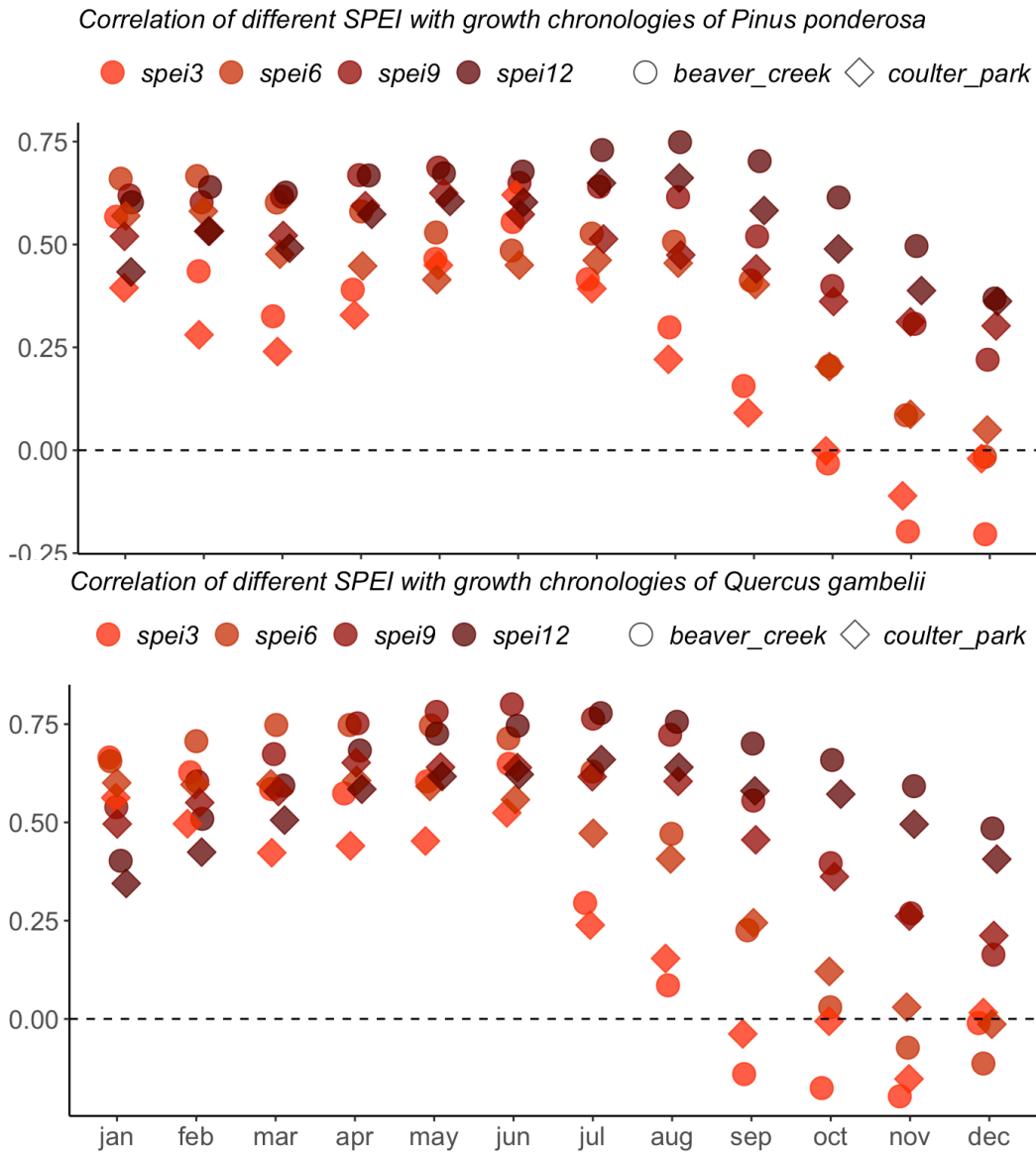


Figure 5: Correlations of the SPEI 3, 6, 9, and 12 for the months January to December. The colours are referring to the different SPEI, the shape is referring to the sites Beaver Creek and Coulter Park. The upper part of the figure is showing the correlation with *P. ponderosa*, the lower figure the correlation with *Q. gambelii*. Since only one SPEI type is needed to allow comparison in further analysis, I used the SPEI12 for July, which showed a high correlation for both species.

For the following calculations, I analysed the climate from the year 2000 onwards. Based on the aridity index for the lower situated site Beaver Creek (0.47) and higher situated site Coulter Park (0.50), both sites have a semi-arid climate, with a tendency towards a dry-subhumid climate. Results of the calculated SPEI12 for all years of the analysed period are shown in Figure 7. Differences in the SPEI12 between the sites are marginal, with a mean SPEI12 value for July of -0.279 (SD 0.954) at BC and -0.300 (SD 0.955) for CP. Though differences, both sites show

distinct, but minor differences in their climate, therefore both sites have to be considered rather as repetition, than two sites with different climatic conditions.

2.5 Growth chronologies

I performed the data analysis with the `dplR` package (Bunn et al., 2015) and the statistical software R (R-Core-Team, 2022). With the included functions, I could detrend the cross-dated chronologies, using a cubic smoothing spline function, with a 50% frequency cut-off and a length of 30 years. By detrending (or standardization) I could remove trends from the chronologies, that are not of climatic origin (as for example age related changes in growth), however information about the growth in form of variance is lost to some extent (Speer, 2010). A cubic smoothing spline function minimizes this loss due to its flexibility in fitting the data (Speer, 2010). To ensure the significance of the chronologies, I truncated them to a minimum subsample signal strength (SSS) greater than 0.85, for each site and species. Result of the detrending process are dimensionless and standardized ring width indices (RWI) for each year per tree. Those, I then used to build mean chronologies per site and species. To analyse growth also in absolute numbers, I calculated the basal area increment (BAI) from non-detrended data. I used the method as described by Biondi and Qeadan (2008):

$$BAI_t = \pi \times R_t^2 - \pi \times R_{t-1}^2$$

Based on the RWI I calculated EPS and RBAR values. GLK and first order autocorrelation I calculated with data, that was not detrended. To test on correlation between growth curves as well as correlation with the SPEI12 values, I used the Pearson correlation test. Furthermore I tested the condition of linearity with the Shapiro test.

2.6 Calculation of competition and mixture

To calculate the competition index of every focal tree (DCI, also called hegyi index in the following), based on the formula of Hegyi (1974), I used the competition and mixing indices, measured diameter and distance here as explained by Pretzsch (2010):

$$DCI_j = \sum_{i=0}^n \left(\frac{d_i}{d_j} \times \frac{1}{dist_{ij}} \right)$$

j is the focal tree, i is one of its 1 to n competitors ($dbh_{1.3} \geq 1\text{cm}$) within its group of a 7m radius around the focal tree. The higher the hegyi (DCI) index, the higher the competition of the neighbouring trees on the focal tree.

To obtain information regarding the species mixture situation of the focal trees, I used the hegyi index (DCI). The calculation based on the species-specific hegyi index (DCI), allows to compute a mixture index (species share), that represents a relevant mixture situation for the focal tree:

$$species\ share_j = \frac{DCI_{interspecific_j}}{DCI_{total_j}}$$

The species mixture index (species share) ranges from 0.00 to 1.00, indicating a range from fully heterospecific mixture (only the other species is surrounding a focal tree) to a monospecific mixture situation (only the same species) of a focal tree, respectively.

As stated before, I could calculate the competition index as well as the information of the mixture (species share), only for the present state of the two sites, since no measurements were available from the past. I assumed hegyi index and species share therefore to be constant over the analysed period between 2000 and 2022. Furthermore, due to the very slow growth of the trees (see Figure 6, Table 2) I expect that few changes in the competition situation as well as the mixture of the chosen tree groups happened in the chosen time period.

2.7 Calculation of the Dry:Mean ratio and definition of the model

Based on these assumptions of a static hegyi index and species share, I decided to use the mean ring width of four selected drought years between 2000 and 2022 and ratio of the mean ring width between 2000 and 2022 (Dry:Mean ratio) as the response variable for the following models. I derived this concept from the analysis used in studies by Adams and Kolb (2005) and Fekedulegn et al. (2003). The advantage of using this variable is that it can describe growth responses over a long period (e.g. the 20 year increment I focused on in this study), and such growth responses can be reduced to a single number. Furthermore, this ratio focuses especially on the growth under drought, since just selected, strong years are included. This allowed me to compare growth responses to drought with other known properties of the sites, for example hegyi index, species share and the $dbh_{1.3}$ of the trees. The ratio describes the intensity of the mean growth decline of one of the two species on each site in intense drought years. A lower Dry:Mean ratio (closer to 0) can be understood as a strong relative decline of growth in drought years, compared to a higher Dry:Mean ratio (closer to 1) describing a rather similar

growth in drought years compared to the average growth over the period. The ratio is calculated from the RWI and defined as follows, with j as each, one of the focal trees:

$$\text{Dry: Mean ratio}_j = \frac{\text{mean dry years}_{RWI j}}{\text{mean 2000 to 2022}_{RWI j}}$$

In the period of 2000 until 2022 I chose the four years with the strongest drought to calculate the ratio: 2002, 2004, 2006 and 2018 based on their SPEI between -0.9 and -2.1 (see also Figure 6). Though it had a very low SPEI, I did not include the year 2020 as a drought year in the analysis, since the drought caused a growth decline mainly in the following year.

With the following model I want to test if the species mixture can explain differences in the Dry:Mean ratio and therefore how much a tree is affected by drought, based on the changes in the species composition. To test this, I used a generalized linear model with a gamma-distribution. Along with the species mixture (species share) as focus of this work, I am using the explanatory variables competition (*hegyi*) and diameter (*dbh_{1.3}*), as they are likely to influence the growth under drought conditions as well. Since I also expect differences between the species and the sites, I included them in the model. I standardised all explaining variables. To find the most optimal, I compared different models based on the AIC (Akaike Information Criterion). The chosen model had the highest AIC, while being the simplest and most relevant. I checked the model on collinearity with Variance Inflation-Factors (VIF) and robustness by its residuals and the existence of outliers. The following model was used:

$$\text{Dry: Mean ratio} \sim \text{species} \times \text{share} + \text{site} + \text{hegyi} + \text{dbh}$$

Based on the high correlation between the drought Index SPEI and the tree ring widths of the chronologies, I will discuss drought as a possible growth limiting factor on the sites. I expect the influence of drought to lead to a strong decrease in growth. To describe the strength of the growth decrease, I use the calculated Dry:Mean ratio, where a smaller ratio can be read as a higher impact of drought on a tree. I will use the model shown above to search for possible differences in the Dry:Mean ratio, based on the species, the mixture of a tree as well as the site, competition and the diameter.

3. Results

3.1 Higher and more variable radial increment of *Pinus ponderosa* – Q1

According to the analysed tree rings, the two analysed species and sites showed relatively similar growth patterns, based on basal area increment. As Figure 6 shows, the chronologies for *Q. gambelii* were much longer (until 1842 at Beaver Creek and 1866 at Coulter Park) than for *P. ponderosa* (until 1912 at Beaver Creek and 1917 at Coulter Park). I considered only chronology parts with a minimum sample depth corresponding to a subsample signal strength (SSS) above 0.85 in this case. The observed growth of *Q. gambelii* has, in general, a lower and more stable BAI, when visually compared to pine, which has a higher BAI and much stronger variation. It is noticeable that the BAI between the sites also shows limited similarities. Coulter Park shows a strong peak around 1925 for both species. Beaver Creek shows a low between 1950 and 1985, with a following strong peak.

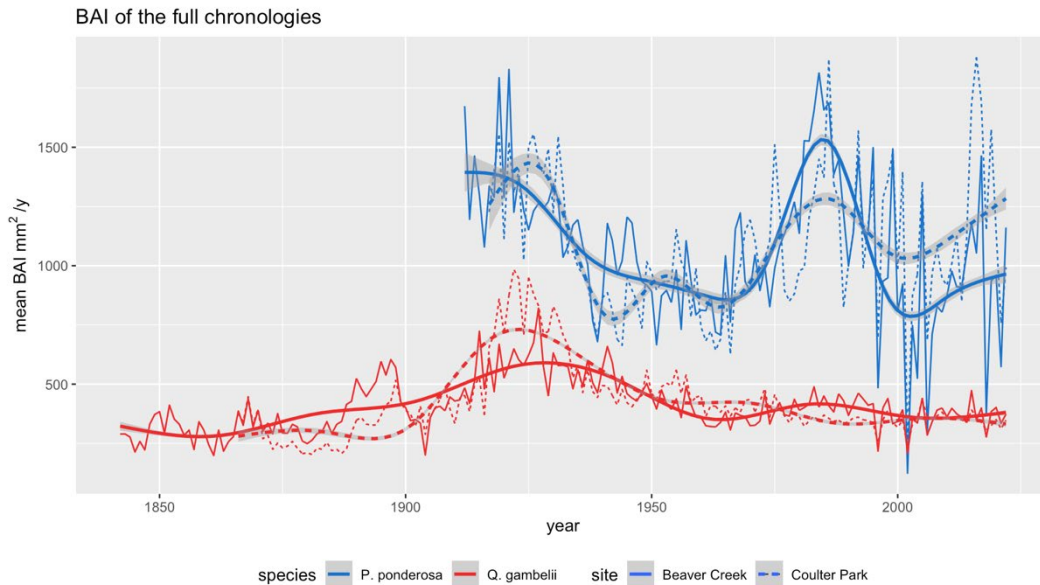


Figure 6: Mean basal area increment (BAI) per species and site. Included in the shown mean chronologies are only parts with a total minimum sample depth of 5 chronologies. The full line represents the site Beaver Creek, the dashed line Coulter Park. The species *P. ponderosa* is shown in blue, *Q. gambelii* in red.

Table 2 & Figure 6 describe the growth for the full measured chronologies. Table 2 includes corresponding basic statistic information regarding the quality and informational value of the chronologies. The mean ring width was similar within each species in comparison of the sites, but higher for *P. ponderosa* in the comparison. The mean basal area increment was considerably higher for *P. ponderosa* and on the site CP. First order autocorrelation, a value representing the similarity of growth from year to year was highest in *Q. gambelii* at CP followed by *Q. gambelii* in BC. As Figure 6 suggests, both chronologies showed a rather steady growth trend fewer less extremes and, therefore, rather constant growth from year to year, resulting in the high first order autocorrelation. Values for *P. ponderosa* in CP and BC followed a similar increment pattern, with high variability as seen in Figure 6. From 2000 the species increment is increasing likewise on both sites, however on a distinctively higher level in CP. The “gleichläufigkeit” (measure of the similarity between curves, short GLK) was highest in *P. ponderosa* at CP, followed by *P. ponderosa* at BC, showing a high similarity in the growth patterns of the species on both sites. *Q. gambelii* at BC, followed by CP had lower values, indicating possible higher differences in growth patterns of the analysed trees. Mean inter-series correlation (\bar{r}) describes the common correlation between the growth chronologies for their overlapping periods. It can be used as a measure for the significance of combined chronologies. The chronology for *P. ponderosa* at CP had a rather high \bar{r} , while in descending order *P. ponderosa* in

BC, *Q. gambelii* in BC and *Q. gambelii* in CP had much lower rbar values. The EPS, similar to the rbar, describes if differences in the growth are rather expressed on the level of single trees or on stand level. In the present study, chronologies of both species and sites, showed an EPS above the 0.85 threshold, which indicates the presence of a strong stand level signal.

Table 2: Basic statistical information of the Chronologies, based on the analysed growth chronologies. “SD” = standard deviation, “BAI” = basal area increment, “GLK” = Gleichmäßigkeit, “RBAR” = average correlation between series, “EPS” = expressed population signal. With ¹ marked results were calculated before de-trending With ² marked results were calculated based on the detrended chronologies. Included are chronologies with a total minimum sample depth of 5, for values of not detrended data and based on an SSS (subsample signal strength) higher than 0.85 for values of detrended data. The data is rounded to two decimals.

	<i>Q. gambelii</i> - CP	<i>Q. gambelii</i> - BC	<i>P. ponderosa</i> - CP	<i>P. ponderosa</i> - BC
Total period of chronology analysed	1866 - 2022	1842 - 2022	1917 - 2022	1912 - 2022
Mean ring width (mm) ¹	1.00	0.66	1.48	1.34
SD ring width (mm) ¹	0.56	0.39	0.91	0.84
Mean BAI ¹	439	420	1062	1046
SD BAI ¹	282	263	644	597
First order autocorrelation ¹	0.83	0.71	0.70	0.69
GLK ¹	0.59	0.63	0.69	0.66
RBAR ²	0.34	0.40	0.59	0.50
EPS ²	0.94	0.95	0.98	0.97

As visualized in Figure 7, I analysed the growth between 2000 and 2022. This period corresponds to the time frame of the growth data used in the model of this study and is therefore analysed in particular, regarding the influence of drought. The growth (here represented by standardised ring width data - RWI) of the tree species showed a relatively similar pattern on both sites. The correlation proofs this impression (see Table 3): both *P. ponderosa* curves had a strong positive correlation based on the Pearson test as well as the *Q. gambelii* curves. The curves between both species differed more, however were still moderately positive correlating, despite of a low positive correlation between *P. ponderosa* at CP and *Q. gambelii* at CP. The growth pattern seemed to follow the SPEI12 values as well; the growth of all our sites was strongly and significantly positive correlated with the SPEI12 values. The four chronologies and the curve of the SPEI12 showed striking lows in certain years: 2002, 2004, 2018 and 2020. For the month July, the visible correlation as well as the calculated results (Table 3) show a strong similarity between the trend of the growth chronologies as well as the SPEI12.

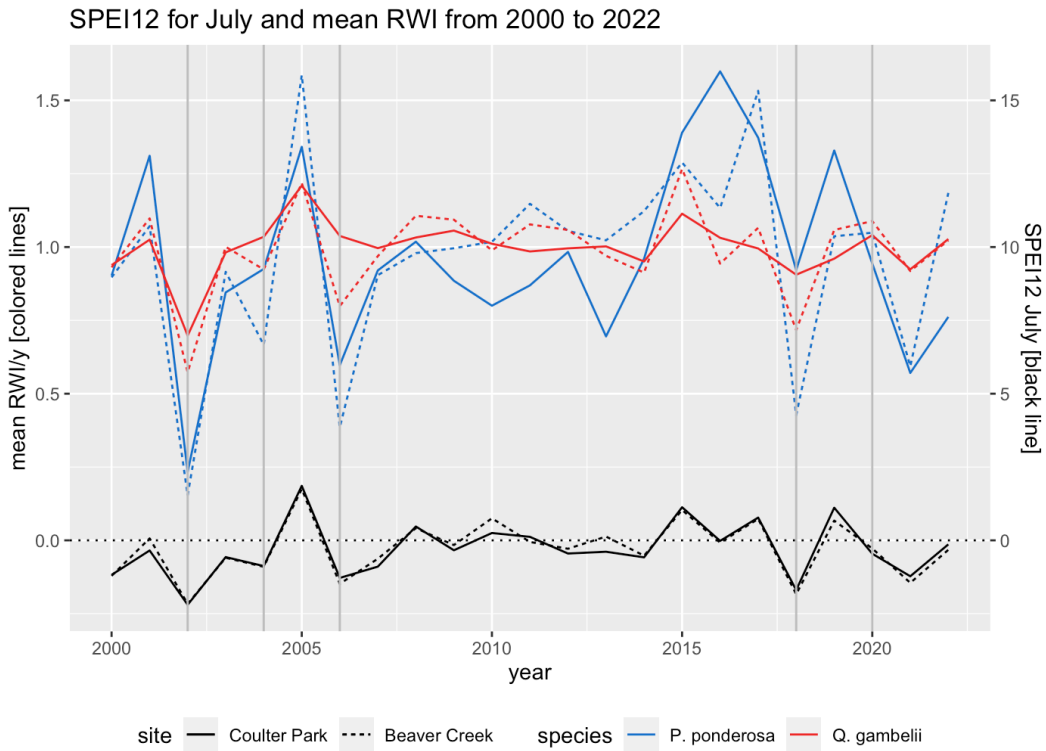


Figure 7: SPEI12 for the month October and mean RWI (ring width indice) from 2000 to 2022. The full line represents the site Beaver Creek, the dashed line Coulter Park. The species *P. ponderosa* is shown in blue, *Q. gambelii* in red. The SPEI 12 (July) of each site are shown as a black line. Included are chronologies with a total minimum sample depth based on an SSS (subsampling signal strength) higher than 0.85. Extreme drought years (corresponding to either a low mean RWI or SPEI12) are highlighted with a vertical grey line in the years 2002, 2006, 2004, 2018 and 2020.

Table 3: Correlation between the chronologies of each species and site as well as the SPEI 12 of the corresponding site. “CP” = Coulter Park, “BC” = Beaver Creek, “SPEI 12” = Standardized Precipitation Evapotranspiration Index of the month July. The *p*-values of the correlations are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. Included are chronologies with a total minimum sample depth based on an SSS (subsampling signal strength) greater than 0.85. The data is rounded to two decimals.

Site and species	<i>Q. gambelii</i> - CP	<i>Q. gambelii</i> - BC	<i>P. ponderosa</i> - CP	<i>P. ponderosa</i> - BC
<i>Q. gambelii</i> - CP	-	-	-	-
<i>Q. gambelii</i> - BC	0.81***	-	-	-
<i>P. ponderosa</i> - CP	0.60**	0.65***	-	-
<i>P. ponderosa</i> - BC	0.70***	0.85***	0.76***	-
SPEI 12	0.72***	0.86***	0.72***	0.88 ***

3.2 Lower drought influence on the radial growth of *Pinus ponderosa* in co-occurrence with *Quercus gambelii* – Q2

In order to answer if the species mixture of *P. ponderosa* and *Q. gambelii* affects their growth under drought, and if both or especially one species shows a positive or negative influence, I chose to use a generalised linear model. The model used the ratio of the mean growth in four selected dry years and the mean growth between 2000 and 2022 (Dry:Mean) to describe the influence of mixture on growth performance under drought. Along with the species mixture, the model also included the competition and diameter as possibly relevant predictors, as well as the given species and site of each focal tree.

The from the model estimated coefficients, showed a significant influence of the species and site on the Dry:Mean ratio of the focal trees (see Appendix A and Appendix B). The estimated change of tree growth under drought with changing mixture and tree size showed a clear influence in this study (Figure 9 and 11). For competition, this influence was less strong (Figure 10). However, though the modelled trends for mixture, tree size and competition were clear, they did not showed to be statistically significant (see Appendix A and Appendix B). Based on the collected data, I used the generalized linear model, to predict the influence of the explanatory variables. The results of these predictions are shown in the following.

The relation of the focal trees diameter in breast hight ($dbh_{1.3}$), to the Dry:Mean ratio is visualized in Figure 9 (here standardised between -2 representing small diameters and +3 representing wider diameters). For both species and sites, the Dry:Mean ratio decreased with an increasing $dbh_{1.3}$, representing a more reduced growth under drought with larger tree diameters. On the site beaver Creek generally a lower Dry:Mean ratio was found compared to Coulter Park. The species *Q. gambelii* had a less reduced growth under drought, compared to *P. ponderosa*.

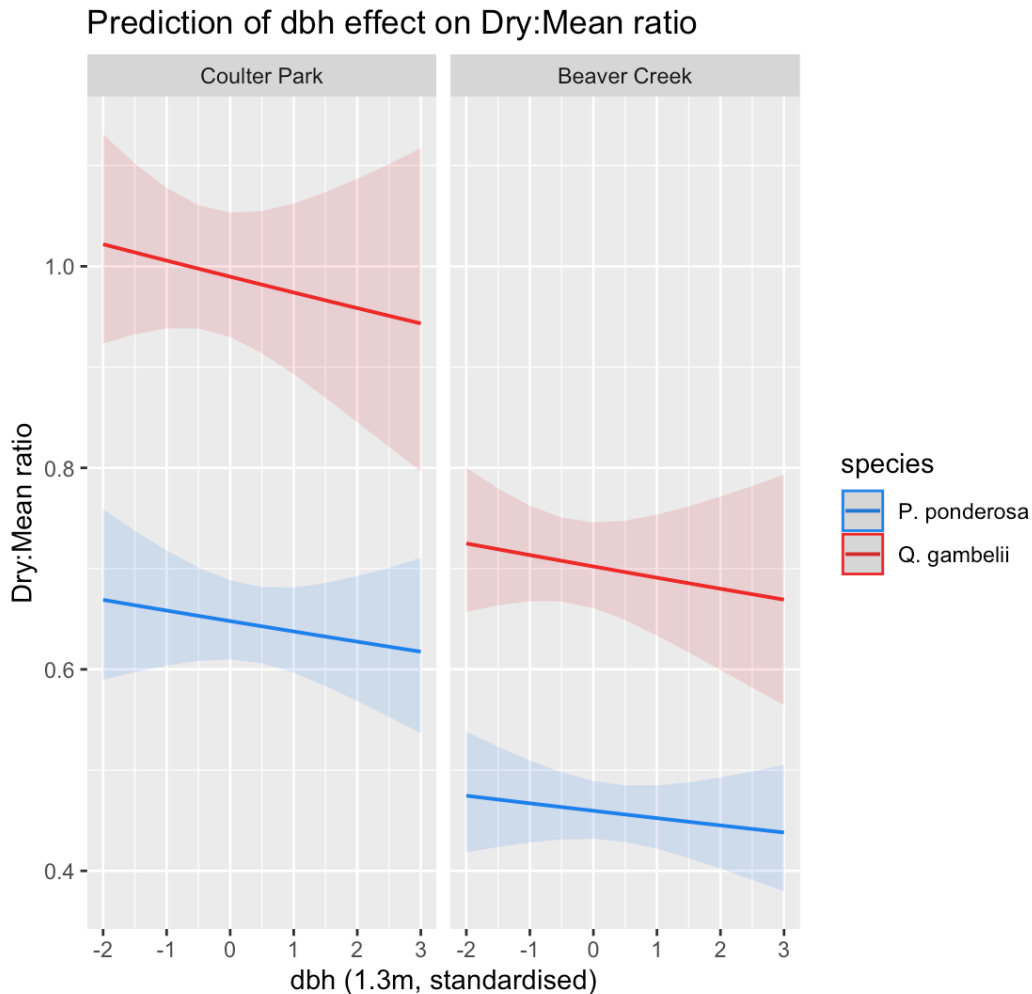


Figure 8: By the model predicted values for the relation of the diameter ($dbh_{1.3}$) of the focal tree with the Dry:Mean ratio. The species *Q. gambelii* is shown in red, *P. ponderosa* in blue. The predictions are shown based on the corresponding site; Coulter Park on the left, Beaver Creek on the right. The $dbh_{1.3}$ is shown standardised with 0 representing a mean diameter. Results for +1 and -1 give results for one standart deviation above, respectively below the mean measured diameter. Though a trend is visible, the effect was not significant.

The hegyi-index, as a measure of the competition experienced by the focal trees, was included as another explanatory variable in the model. Its predicted values showed a slightly negative connection with the Dry:Mean ratio. With increasing hegyi index (competition), the Dry:Mean ratio decreased very lightly, for both

species and sites, as Figure 10 visualizes. *Q. gambelii* had, in general, a less decreased Dry:Mean ratio in respect to growth, compared to *P. ponderosa*. The comparison of both sites showed a much lower Dry:Mean ratio and therefore increment for both species under drought on the site Beaver Creek.

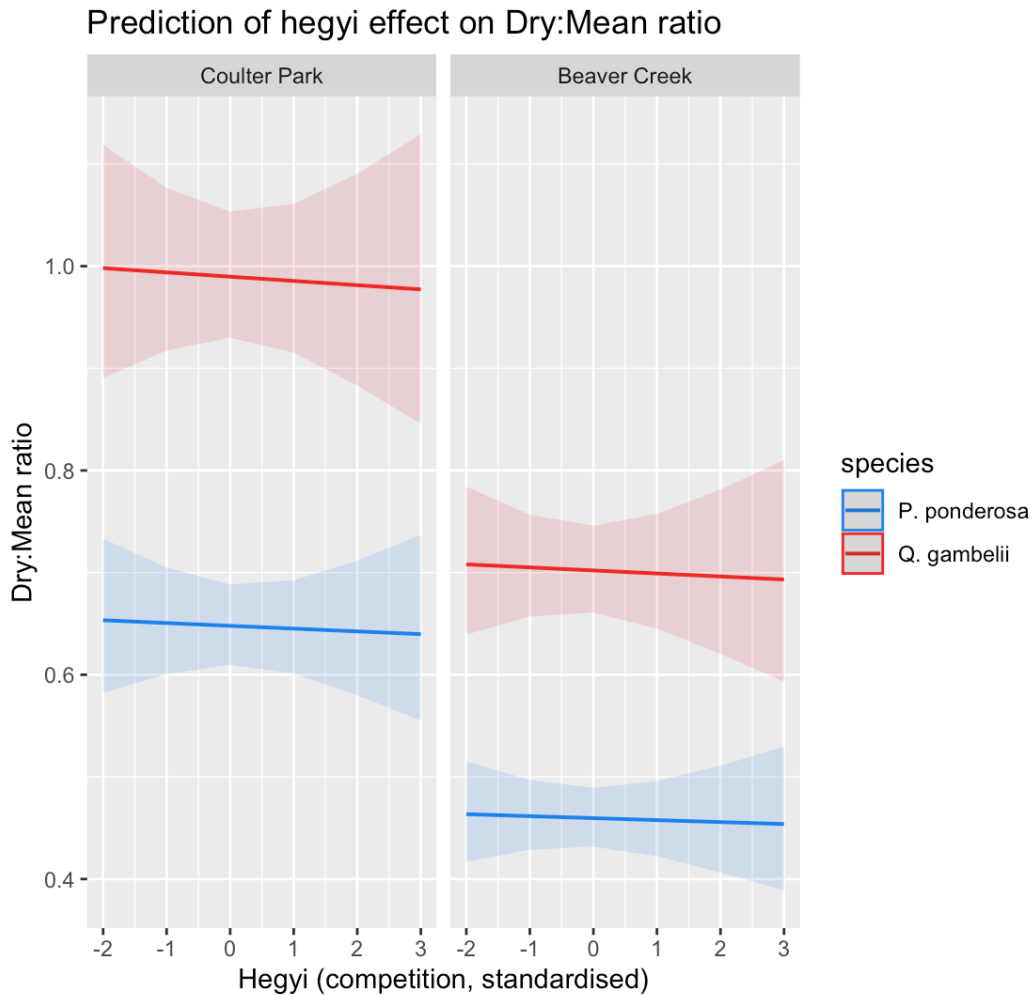


Figure 9: By the model predicted values for the influence of the competition (hegyi) experienced by the focal tree, on the Dry:Mean ratio. The species *Q. gambelii* is shown in red, *P. ponderosa* in blue. The predictions are shown based on the corresponding site; Coulter Park on the left, Beaver Creek on the right. . The competition is shown standardised with 0 representing a mean measured competition. Results for +1 and -1 give results for one standart deviation above, respectively below the mean measured competition. Though a trend is visible, the effect was not significant.

The predicted values for the relationship of the species mixture, surrounding the focal trees and the Dry:Mean ratio showed a clear trend for the species *P. ponderosa*, as seen in Figure 11. The species mixture (share) is here displayed in its standardized version, from -2 (heterospecific) representing a focal tree only surrounded by the other species, to an increasingly monospecific species mixture situation at +2 with a group of only one species. With a higher share of *P. ponderosa* surrounding *P. ponderosa* (higher positive value) a lower ratio of the Dry:Mean

values respectively increment under drought was connected. This trend was visible on both sites, with a generally lower level of the Dry:Mean ratio in Beaver Creek.

Q. gambelii trees showed no clear influence by changing proportions of *P. ponderosa* or *Q. gambelii* surrounding them. Also the influence of increasing dbh and hegyi reduced the growth under drought just lightly in Coulter Park, but much stronger in Beaver Creek. On both sites *Q. gambelii* had a generally less decreased growth under drought, compared to *P. ponderosa*.

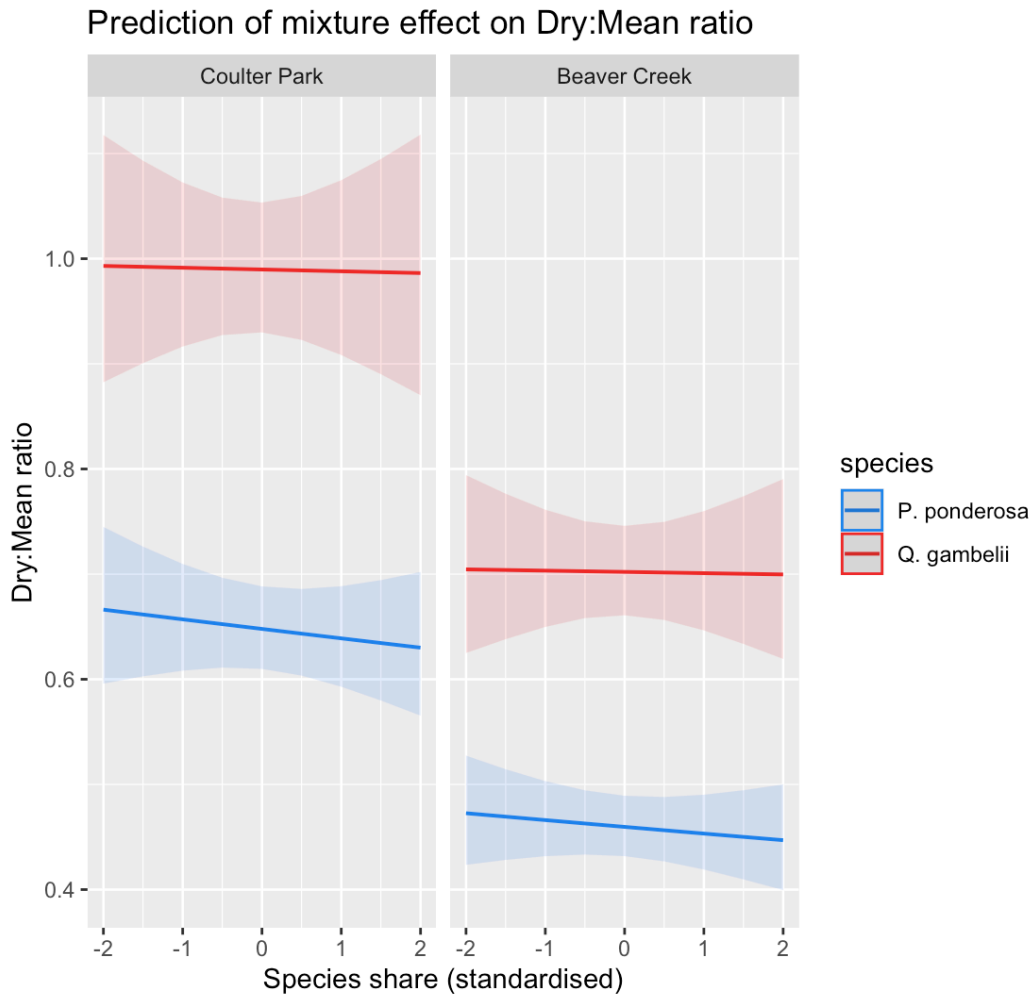


Figure 10: By the model predicted values for the influence of species mixture (share) surrounding the focal tree, on the Dry:Mean ratio. The species *Q. gambelii* is shown in red, *P. ponderosa* in blue. The predictions are shown based on the corresponding site; Coulter Park on the left, Beaver Creek on the right. The predictor “species mixture is shown standardised from -2 heterospecific to +2 monospecific, 0 represents an even mixture between the two species. Though a trend is visible, the effect was not significant.

4. Discussion

In this study I analysed tree ring chronologies of *P. ponderosa* and *Q. gambelii* trees, to describe their increment growth on semiarid sites of the southwestern US. In a second step, I investigated if drought plays a role as a growth limiting factor for the trees. This was the base for further investigation into the relationship of the growth decrease caused by drought conditions, as well as the potential dependence of responses on tree diameter, competitive situation, and degree of mixing between the two species.

4.1 Differences in increment between *Pinus ponderosa* and *Quercus gambelii* – Q1

I expect differences in the comparison of *P. ponderosa* and *Q. gambelii*. Existing growth measurements of the species in the region show clear differences in their diameter increment (Barger & Ffolliott, 1972; Biondi et al., 1992). Generally, a faster growth of *P. ponderosa* has been found (Abella & Station, 2008). Also in this study I could show these differences between the diameter increment (or basal area increment) of the two species. *Q. gambelii* had a rather small mean ring width and basal area increment, whereas *P. ponderosa* exhibited distinctively higher growth. These results of the mean ring width, basal area increment and first order autocorrelation support the observation, that *P. ponderosa* is a faster growing species with more variations in growth compared to *Q. gambelii* (Figure 6). Besides the actual growth increment, the variability of the growth between the years seems to be lower for *Q. gambelii*, as the first order autocorrelation (Table 2) and visual impression (Figure 6) suggests.

A possible explanation for these differences is the growth behaviour of both species, as *Q. gambelii* seems to be more drought resistant and adaptable. The species distribution reaches from its common association with *P. ponderosa* (Mary Stuever, 1997), to adjacent pinyon-juniper woodlands in lower and dryer altitudes (Burns et al., 1990; Williams & Anderson, 1967), forming not only trees, but also brush like growth forms. Existing research draws a similar picture, *Q. gambelii* seems more drought tolerant by its ability in avoiding water stress (Kolb & Stone,

2000). This will be further explained in section 4.4. Also, differences in the growth between the two species might be explained by various species-specific characteristics.

Comparing the growth of the species between both sites, it showed a similar pattern (Figure 6), though there was a higher BAI and mean ring width at CP. A possible explanation is the differences in the climate, with a slightly higher precipitation and position in the landscape towards higher altitudes. The high similarities of growth (BAI, ring width) and growth patterns within the species show their species-specific reaction to drought. The positive correlation between the sites is expressing similarities in the growth patterns of trees, independent of their actual location. This underlines the existence of a climatic growth limitation, in this case by drought.

4.2 Drought leads to distinct patterns of radial growth decrease – Q1

SPEI values are related to increasingly severe levels of drought (McKee et al., 1993; Tirivarombo et al., 2018). In the case of the in this study, both observed sites have a mean SPEI indicating a mild drought. However, during drought years, levels reach regularly moderate dry to severe dry states (-1 to -1.99, see Figure 7). Considering this as well as the general semi-arid climate, I assume a dominant climatic influence on the tree growth of both analysed sites. This hypothesis is emphasized by the high EPS levels of both species and sites (Table 2), indicating a strong stand level signal in growth, likely mediated by drought. Also the similarity of growth patterns between the sites and the species (Figure 7, Table 3) indicate similar influences as well as the high positive correlation between the measured growth of the species and sites with the SPEI12 values. Taking all this into account, I assume that drought is a limiting factor for tree growth, resulting in the measured tree ring patterns.

For the period from 2000 until 2022, I found 5 very distinct drought events. The growth of the species as well as between the sites showed a simultaneously drastic decrease in these years (Figure 6). The drought events in 2002, 2004, 2006, 2018 and 2020 are well reported in many studies (Fulé et al., 2022; Gaylord et al., 2007; Lisonbee et al., 2022; Reeves et al., 2020). For the year 2020 Lisonbee et al. (2022) discussed a strong drought, however the major impact can be seen in the year 2021. This is due to the low snow fall in the winter of 2020 to 2021 and early snow melt, resulting in a pronounced drought and decreased growth. As Kerhoulas et al. (2013) found, winter precipitation plays a more important role than precipitation during the summer months. Especially larger *P. ponderosa* trees, as on the researched sites, seem more dependent on those precipitations (Kerhoulas et al., 2013). This is a

possible explanation for the low in 2021. Since this drought impact was “shifted”, I excluded it from the analysis, to prevent possible errors.

As already mentioned before, these common and severe droughts are often described in the context of a “megadrought” in the southwestern-US. These pronounced drought events and the correlating growth confirms several aspects: It underlines the quality of the chosen SPEI12 for July as an indicator of drought, It shows that the tested area is experiencing a time of frequent and intense drought events and shows that drought depicts an important limiting factor for growth in the region.

4.3 The model and input data – Q2

In this study I analysed the growth of trees with different species mixture conditions in two *P. ponderosa* – *Q. gambelii* stands in the southwestern US. The goal of the work is to get a deeper insight in how species mixture is influencing the growth under drought conditions. I aimed to explain the growth of the trees under drought conditions, based on their species mixture, but also competition and diameter, by using a generalised linear model.

Before discussing the results of the used models, it is important to have a look on the data used for this study. To investigate the question of the species mixtures influence in my models, I used growth data from the year 2000 until 2022. Other model parameters as species mixture, competition situation and $dbh_{1.3}$ were only available for the year 2022. In this context, a self-suggesting question is, how representative can the data from 2022 be assumed in describing the mixture, competition situation and $dbh_{1.3}$ for the focal trees from 2000 onwards? With growth of the trees and natural succession I expect that all three parameters change over time. However, as shown in this study, the trees in the researched sites show a relatively slow growth of up to 1mm per year in the mean for *Q. gambelii* and 1,48mm for *P. ponderosa*. Within the period of 22 years, I expect therefore only minor changes in the situation of the focal trees.

To not overestimate the influence of small trees, I used the hegyi index as a measure for competition. It calculates competition based on diameter and distance, which results in lower competition values from small and more distant trees. Furthermore, I also calculated the species mixture situation based on the hegyi index, which allowed to take the tree size into account.

However, not only tree growth is a possible influence on the situation of the focal trees. Forest fires could change the competitive situation, mixture as well as the growth speed drastically in a very short time. *P. ponderosa* is known as a tree species with high fire resistance. The effect of fires on the growth of *P. ponderosa* is however rather unclear. For low-intensity fires, studies report positive and negative effects on the growth following a forest fire (Baird et al., 1999; Sutherland

et al., 1991). Keyser et al. (2010) found that mixed-intensity fires seem to have no strong influence in the growth of surviving *P. ponderosa* trees. *Q. gambelii* trees show a low fire resistance in comparison (Brown & Smith, 2000). Their strategy seems to be rather targeted towards regeneration; after fires, trees show strong sprouting and regrowth, often in shrub like growth form (Harrington, 1985; Kunzler & Harper, 1980). On both researched sites I found traces of past fires. I found many charred *P. ponderosa* trees in Beaver Creek, some in the form of strongly charred standing deadwood, but mostly lightly charred living trees. *Q. gambelii* trees were seldom charred, however their spatial distribution showed the possibility of fire induced patterns: mostly in groups, often as thickets with many trees of rather small diameters. I found this distribution pattern as well at Coulter Park, however with fewer very small trees and tree groups rather than thickets and no charred trees. A possible explanation for these traces could be a low-intensity fire in the far past of both stands. I found in none of the analysed tree cores fire scars or traces of burnings. A possible influence of fires on the trees growth is likely, however I assume this influence to be rather low, based on missing traces of fires in the analysed cores and the unclear influence, pointed out by existing studies.

Taking this and the influence by growth and natural succession into account, the parameters used in the model are likely to have changed over time. I assume the changes however small enough, to use the present values as a constant for the whole period of the model.

4.4 Site as well as species have a significant influence on how much growth is affected by drought – Q2

In the following, I will discuss the explanatory variables of the model and their results step by step. Species and site showed significant influences in the predicted growth under drought. Generally, *Q. gambelii* was less affected in its growth by drought; at both sites, the species showed a significant smaller growth decrease compared to *P. ponderosa*. At Coulter Park, growth was only marginally decreased, at Beaver Creek the growth decrease was more pronounced, however still less in comparison of the two species. Similarly, *P. ponderosa* showed a stronger growth decrease on the site Beaver Creek compared to Coulter Park.

These results were consistent for the influence of dbh, hegyi as well as species mixture. I expected significant differences between the species. As one was coniferous and the other was deciduous, both were different by anatomy respectively physiology and therefore likely varying in their growth performance and reactions to drought. The faster growing species *P. ponderosa* seems to be adapted to drought by its high hydraulic conductivity (Maherali & DeLucia, 2000) and sensitive stomata control (Zhang et al., 1997). *Q. gambelii* on the other hand is

a in comparison slower growing species, however it is a deciduous species with drought adaptations as other oaks; xeromorphic leaves and deep roots (Abrams, 1990). Its deep rooting behaviour is expected to allow growth on summer dry sites, using mostly deep soil moisture generated by winter precipitation, rather than profiting from summer precipitation (Phillips & Ehleringer, 1995; Poulos, 2009).

I expected differences between the sites, considering the small, but evident differences in their altitude and climate, as well as the visual impression and position of the sites. Compared to the other site, I noticed several Juniper trees and bushes in Beaver Creek; a species typical for the more drought affected Pinyon-Juniper woodlands. This plant association grows in close proximity to the analysed site. The site Coulter Park was located much further in the forests, dominated by *Q. gambelii* and *P. ponderosa* (around 53 kilometres, respectively 22 miles). Furthermore, slight differences between soils are likely to occur on both sites, including nutrients and the ability to store water. Also the measured trees showed limited differences in height, diameter and competitive situation between the two sites. The consistently higher ratios between the growth in drought years and the mean growth (Dry:Mean) at Beaver Creek, and therefore a stronger growth decrease, is likely caused by the dryer climate of the site. With less precipitation and higher temperatures in the average, I expect a more pronounced drought stress in the extreme events, that I used to calculate the growth ratio. A more intense drought may lead to a stronger decrease of the growth, compared to the mean. However also differences in the soils, height, diameter and competitive situation in the measured trees likely attributes to the resulting ratios.

4.5 Stronger growth decline of larger trees – Q2

The diameter of a tree, and based on their allometric relationship (Pretzsch, 2009, 2019; Shipley & Meziane, 2002), as well as the tree height and its root growth, are positively correlated. These characteristics are connected to the competitive situation regarding the neighbouring trees, and deciding therefore about the access to resources for growth, as nutrients, sunlight and water (Matyssek et al., 2010). I expect therefore that these characteristics also play an important role in the drought response. However, differences between species seem to matter: Martín-Benito et al. (2008) found less influence of drought on *Pinus nigra* trees that were not dominant. Also smaller *Pinus sylvestris* trees seem to be less affected, compared to larger ones (Merlin et al., 2015; Zhang et al., 1997). This picture stays, on the other hand, rather unclear for oaks: such a trend could neither be found for *Quercus petraea* in the study by Merlin et al. (2015), nor in the study of Zhang et al. (1997) for *Quercus robur*.

The results of this work are in line with this described relation of tree diameter, respectively height and drought impact as found in the studies for other pine species. Surprisingly a very similar relationship was found, not only for *P. ponderosa*, but also *Q. gambelii* in both sites; with increasing diameter, the estimated ratios showed lower growth under drought.

One explanation for this phenomenon could be the physical disadvantages: hydraulic resistance within vessels increases with tree size as Ryan and Yoder (1997) explain, causing increased water stress in the leaves. This forces the tree to close its stomata earlier under drought conditions, which lowers in turn the photosynthetic activity (Ryan & Yoder, 1997). This would imply, that smaller trees might be able to keep their growth up, for a longer time under drought, causing a lesser drought decrease. Other in the literature discussed aspects of influences by tree size are growth hormones (Martín-Benito et al., 2008) and different growth conditions due to shading and favourable conditions for microclimates by overstory trees (Wullschleger et al., 2001) as well as a connected lower summer temperature and a resulting lower vapour-pressure deficit (Aussenac, 2000; Dalton & Messina, 1995).

Though the influence of tree size seems species dependent, the results of this study support, that larger trees are more vulnerable to growth declines by drought. Considering the results for other oak species, this effect might apply however more certain for *P. ponderosa*, than *Quercus gambelii*. For the latter, more research is clearly needed.

4.6 Increased competition might be problematic in droughts – Q2

Competition depicts an important aspect in explaining the growth behaviour of single trees (Radtke et al., 2003). To include this aspect in the research of drought influences on growth, I chose the hegyi-index, as an expression of the competitive situation of a focal tree. Matyssek et al. (2010) is defining the competition between trees, by the limitation of commonly available resources, like water, space, nutrients and light. As soon as fewer resources are available than is needed for optimal tree growth, competition between individual trees sets in (Pretzsch, 2010).

Water, as key resource potentially limited by competitors, is however often limited as well by climatic conditions (Allen et al., 2010; Park Williams et al., 2013). Since water is also limited on the researched sites, it is therefore an important question, how changes in competition might influence the growth under these conditions. As Linares et al. (2010) and Gleason et al. (2017) describe, trees suffering under stress by competition were rather predisposed to growth decline

under the influence of drought. Lower stand densities of *P. ponderosa* lead on the other hand to a lesser growth decrease under drought (Bottero et al., 2017).

This amplifying effect of competition on drought stress, supports the results found in this study. An increase in the competition (Hegyí) impaired the growth for both species to a light extent in the predictions of the model, though not statistically significant.

The mechanisms behind the amplifying effect are however complex (Gleason et al., 2017). The number of transpiring trees is a likely to influence the water availability, as a higher tree density may lead to a higher water depletion of soils by evapotranspiration, and therefore intensify competition for water, as suggested by (Primicia et al., 2015; Schuster & Oberhuber, 2013) Yet, this concept might be limited in its validity (Sohn et al., 2016). Competition seems also to change the physiology and by that the drought reaction of *P. ponderosa* trees (Martinez-Meier et al., 2015). Furthermore species specific interactions should be considered as they can decrease competition, due to their positive interactions (Loreau & Hector, 2001; Pretzsch et al., 2017). In the mixture of *P. ponderosa* and oak, crowns show complementarity in their distribution, as well as roots, which leads to water uptake in different soil depths (Bello et al., 2019; Biondi et al., 1992; del Castillo et al., 2016).

Based on the findings of this study and discussion in the literature, I conclude that increasing competition and tree density seems to intensify the limitation of growth by drought stress. To which extent this applies for the *P. ponderosa* and *Q. gambelii* trees on the studied sites, is however unclear due to the low influence I found.

4.7 *Pinus ponderosa* is benefited from species mixture – Q2

The main question of this study asks, if the mixture of *P. ponderosa* and *Q. gambelii* can mitigate growth decreases caused by drought. This was never investigated before to my knowledge, however, the results of existing studies regarding other species combinations give important indications. Especially mixtures of other pine and oak species are here interesting, as their close relatedness might give applicable results. Bello et al. (2019) found in their study a positive effect for *Quercus petraea*, if grown in a mixed stand with *Pinus sylvestris*. As the study shows, were pine trees less constrained by water compared to pure stands. Steckel et al. (2020) found this positive effect on growth under drought, not only for oak, but also for the pine species. According to the author, was the mixture of *Pinus sylvestris*, *Quercus robur* and *Quercus petraea* being able to reduce the influence of drought on the growth for *Pinus sylvestris* as well as for both *Quercus* species. Based on these

results, I expected especially for *Q. gambelii* to be positively affected in its growth under drought.

The results of this study, did however not prove this hypothesis. Based on the model, especially *P. ponderosa* is benefited by the mixture in the researched stands. The growth of its trees in an increasingly heterospecific mixture with *Q. gambelii* decreased less in drought years. For *Q. gambelii*, no clear effect is visible. Therefore, these results are rather similar to the results of Steckel et al. (2020), however the positive mixture effect for oak, as in their study, and in the results of Bello et al. (2019) could not be confirmed. Though this study only confirmed a positive mixture effect for *P. ponderosa*, the question still arises, as to why the growth decline in drought years was smaller for mixed trees.

Complementarity is here a main approach in explaining this increased increment, in a situation with species mixture compared to a monospecific environment. Complementarity can be either archived by a reduction of competition or by facilitation (Loreau & Hector, 2001; Pretzsch et al., 2017). As discussed before, reduced competition is a well-known phenomenon between pine and oak species. The tendency of different oak species to access deeper soils for water uptake in mixed stands with pines, showed positive effects for their growth under drought (Bello et al., 2019; del Castillo et al., 2016). On the other hand seem pines to access soil water from upper soils, with no positive effects of mixture (Bello et al., 2019; del Castillo et al., 2016). These results however do not explain the growth, I found in this study.

Besides reduced competition, also facilitation might play a role, as the stress gradients hypothesis expects positive interactions to be more common in environments with prevailing stressors (Bertness & Callaway, 1994; Michalet et al., 2006) and especially for stress tolerant species like *P. ponderosa* and *Q. gambelii* (Maestre et al., 2009), as discussed in the beginning of this work. The deeper rooting behaviour of oaks must be taken into account here, as hydraulic redistribution or -lift, is mentioned for some oak species (David et al., 2013; Kurz-Besson et al., 2006). It describes a redistribution of deeper soil water by tree roots in dryer upper soil layers (Horton & Hart, 1998; Richards & Caldwell, 1987). Less growth decreases of *P. ponderosa* in heavy droughts, could be therefore explained by a redistribution of water by surrounding *Q. gambelii* trees. By the deep rooting of *Q. gambelii*, especially in mixture with *P. ponderosa*, access to deep soil moisture might be still possible, while soils closer to the surface are already depleted. Yet, this process needs more research, since also opposite results were found (del Castillo et al., 2016).

Apart from facilitation regarding the direct access to water, also an increase of organic biomass from *Q. gambelii* litter, might has an indirect influence on the water availability of *P. ponderosa*. Oak litter seems on the one hand, to increase the nutrient status of surrounding soils (Klemmedson, 1991; Parker & Muller, 1982),

but could play on the other hand an important role by increasing the moisture sustaining capacity of the organic soil and litter (Ilek et al., 2021). Such an increased storage of water might especially benefit *P. ponderosa* trees, with their tendency of rooting in upper soil layers.

Besides the discussed possible increased water storage capacity of the organic layer, also microclimatic conditions might have an impact on soils, in depths of the rather shallow rooting *P. ponderosa* trees. As discussed before with respect to tree size, microclimatic conditions with a low vapour-pressure deficit and decreased evapotranspiration, can be created under the canopy of trees due to shade, lower summer temperatures and wind speed (Aussenac, 2000; Dalton & Messina, 1995; Parker & Muller, 1982; Wullschleger et al., 2001). The distribution of *Q. gambelii* trees on the two sites, mostly in clumped groups, often also surrounding *P. ponderosa* trees, may give the favourable conditions for creating such protective microclimates. The shelter by the canopy of trees leads to a distinct difference in soil evaporation between open and closed conditions under semiarid climate (Breshears et al., 1998). Due to this conditions, especially upper soil layers might be less effected by drying due to evaporation, compared to the rather open conditions in the neighbourhood of *P. ponderosa*. These findings are also in line with those findings by Evenson et al. (1980), that *Q. gambelii* understories lead to darker situations on the ground than *P. ponderosa* understories.

Taking this favourable microclimate by the *Q. gambelii* trees, as well as complementarity and facilitation between both species into account, the positive mixture effect for *P. ponderosa* found in this study can be explained. The positive mixture effect for *Q. gambelii* hypothesized in this study could not be confirmed by the predictions of the model. These divergent results might have occurred due to the limitations of the used data as well as the simplifications of the model. The analysed dataset only analysed two sites. A higher amount of site replications might have given me a better chance to see an effect. Furthermore, the model I used in this study covered data of a time span from 2000 until 2022. Since no repeated measurement data of species and competition were available over the time, I used the present status and assumed it to be constant over the whole period. I expected changes in both factors over the time to be rather marginal. Higher changes than expected could however cause the discrepancies in the results.

However; despite this limitations, the results of this study show clear trends of the influence and importance of tree species mixture. The promotion of mixed *P. ponderosa* and *Q. gambelii* stands depicts an important measure with a high potential in mitigating the increasingly growth limiting influences of droughts in the southwestern US.

5. Conclusion

In this study, I analysed the growth of *P. ponderosa* and *Q. gambelii* trees in mixed species and pure growth situations in the Southwestern US, based on tree ring measurements. An analysis of the whole measured tree chronologies revealed a higher growth increment variability of *P. ponderosa* than of *Q. gambelii*. Both species were significantly limited in their growth by drought. This influence caused a very distinct growth pattern, however with growth decreases to a different extent for both species, emphasizing the impact of drought in the Southwestern US. Using the tree ring increment data from the period of 2000 until 2022, I calculated the ratio of the growth in the four strongest drought years and the mean growth, as an indicator of the influence of varying diameter, competition and mixture situation.

For the growth of *P. ponderosa* and *Q. gambelii* under drought I was able to show: 1) the extent of growth decreases were different between both species, with a generally more pronounced impact on *P. ponderosa*, resulting in stronger growth decreases 2) based on the evidence from the modelled predictions, that larger tree diameters are expected to increase the influence of drought on *P. ponderosa* and *Q. gambelii* trees. Competition showed only a very limited influence. Within the mixture of the two species, an increasing share of *Q. gambelii* shows to be beneficial for *P. ponderosa*, in coping with drought. Though trends were clear, I did not find statistical significance for the connection of diameter, competition and species mixture with the tree growth under drought. These results confirm existing findings regarding the strong influence of drought in the Southwestern US on two important and very common species of the region. Also the possible negative influence of large tree size in the context of this droughts plays a role. The results of this study point out that species mixture is important for the growth under drought. The combination of the two species has a supportive effect, especially for *P. ponderosa*.

Based on this findings, the promotion of the species mixture depicts a suitable solution for reducing the increasing impact of droughts, in the practical forest management. Future studies, using a larger dataset are however needed, to strengthen the findings of this work, by analysing potential benefits of mixing the two species. Results could not only play an important role in mitigating the influences of drought on forests in Southwestern US, but also give useful indications for silviculture worldwide. Forestry with the goal of timber production

plays these days only a minor role in the southwestern US. Yet, further results regarding species mixture and tree size could have a high potential to be used in practical silviculture, by ensuring increments under increasingly difficult growth conditions.

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Popular science summary

For many years already, climate change is a often discussed topic – we all know about the scenarios described by scientists: rising sea levels, more extreme weather and often dryer climate and rising temperatures. On hot days we can virtually feel what that means; we are sweating and seek for a cool drink. However, not only we are feeling this changes. Also our environment and as one important part of it, forests and trees are experiencing this heat and drought stress. Around the world scientists are describing similar phenomena: more often and to a much larger extent trees are showing less growth and die in severe cases. Especially in already dry places as the Southwestern US, this problem is effecting the trees. Ways have to be found to deal with this increasingly difficult conditions. Besides already existing adaptations of the trees to their dry environment, an often discussed aspect is the potential of mitigation by the mixture of tree species. The combined occurrence of Pines and Oaks can be found in many parts of the world, often in dry places. This rises an important question: is it possible to improve the growth of the two species under drought, by mixing pine and oak trees and therefore mitigate the impact of droughts? I researched this question for the species *Pinus ponderosa* and *Quercus gambelii*, two species often exposed to droughts in the Southwestern US. I answer this question by analysing the width of tree rings (tree ring chronologies) and therefore growth of trees in different mixture situations. I could show that both species grow very different. Compared to *Quercus gambelii*, *Pinus ponderosa* trees grew faster and with a much higher variation. This variation was the result of repeated drought years that strongly limited the tree growth. With the help of a statistical model I found, not only the mixture, but also the diameter of trees plays a role. Smaller trees and trees of the species *Pinus ponderosa* that where surrounded by *Quercus gambelii* trees could keep up their growth under difficult drought conditions, while larger trees and *Pinus ponderosa* surrounded by trees of the same species where growing much less. For *Quercus gambelii*, the neighbourhood of other species did not make a difference. This results where clear however not statistically significant. But how does that help the forests? On the one hand this results give a clue to other scientists; the mixture of *Pinus ponderosa* and *Quercus gambelii* seems to have a positive effect on their growth under drought, but more research has to be done to verify my results and learn about the interactions between the trees. On the other hand foresters can use this results, to promote younger and

mixed forests, which have a high potential to reduce the strong drought stress *P. ponderosa* are experiencing in the Southwestern US.

Acknowledgements

I want to thank my supervisors Michael Gundale, Hans Pretzsch and Gerhard Schmied, that supported me a lot as supervisors for my thesis. Michael Gundale as my main supervisor and important contact here in Umeå. Gerhard Schmied especially for the great time and teamwork in collecting the data for my thesis and the underlying project as well as the supervision in writing this thesis. Hans Pretzsch as well as Miren del Rio initiated the base project, organising the practical work for Gerhard Schmied and me in Arizona. Furthermore I want to thank Keith Warren Moser, as the local contact in Flagstaff who made it possible that the measurements could be done as well as his knowledge and deep understanding of the forests in the region. Enno Uhl, who took as well part in the underlying project. Magdalena Fassel gave me access to the laboratory and all the needed equipment at SLU, which made it possible for me to do the practical work. Last but not least I want to thank my family and friends that supported me a lot in many ways during the year of writing my thesis. Thank you so much everyone!

This thesis was supported by the Eva Mayr-Stihl Foundation (grant number 200102) under the project title “Trockenstress von Kiefer und Eiche in Mischung im Vergleich zum Reinbestand”.

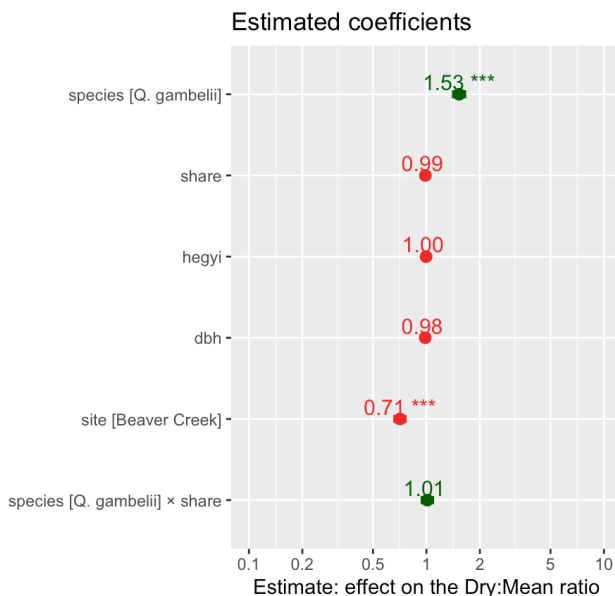
Appendix

*Appendix A: Estimated coefficients of the model. Included are as well the confidence intervals (CI) and the p-Values (p). Two predictors showed a significant influence on the dry:mean ratio (marked with ***): the influence of the species as well the influence of the site.*

Estimated coefficients

Predictors	Dry:Mean ratio		
	Estimates	CI	p
dbh	0.98	0.94 – 1.03	0.507
hegyi	1.00	0.95 – 1.04	0.853
share	0.99	0.94 – 1.03	0.546
P. ponderosa	Reference		
Q. gambelii	1.53 ***	1.42 – 1.65	<0.001
Coulter Park	Reference		
Beaver Creek	0.71 ***	0.66 – 0.76	<0.001
speciesQ. gambelii:share	1.01	0.94 – 1.08	0.730
Observations	120		
R ² Nagelkerke	0.705		

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$



*Appendix B: Estimated coefficients of the model. Table 4 in graphically visualised version. Included are as well the confidence intervals (CI) and the p-Values (p). Two predictors showed a significant influence on the dry:mean ratio (marked with ***): the influence of the species as well the influence of the site. Estimates colour coded; green ones showed a positive relationship, estimates in red a negative relationship.*

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