Two Invasive Species in the Sandhills of Nebraska: Their Response to Drought and Their Water Use Efficiency

GEO 511 – Master's Thesis
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Abstract

Several studies have shown that a wide range of tree species have invaded grasslands in different regions of the world. The invasion of *Juniperus virginiana* L. and *Pinus ponderosa* Dougl. ex Laws. into the semiarid Sandhills of Nebraska is one example for this ongoing process. By the means of dendrochronology we investigated their growth and their response to drought at different stand densities and locations to understand their capacity to adapt. One sample area is located in the Sandhills and two approximately 300 km to the east of the Sandhills in eastern Nebraska. In addition we analysed the water use efficiency (WUE) of *P. ponderosa*. Our results show that tree-ring widths highly correlate with precipitation in the Sandhills whereas outside the Sandhills the correlation was weaker. The WUE was higher in the Sandhills indicating a good adaptation of the trees to the limiting environmental conditions in the Sandhills. The climate seems not to limit growth heavily due to the ability of the species to be acclimated and adapted to this environment.

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If nothing else is mentioned, images were taken by the author.
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1 Introduction

1.1 The Sandhills

The Sandhills are a paleo-sand sea which current shape was formed during the last 8000 years. The dunes were shaped by strong north-westerly winds and nowadays align in a north-westerly to south-easterly direction. They cover approximately a quarter of the state of Nebraska in the USA. Their elevation increases from 500 m in the east to 1000 m in the west. The dunes are on average 120 m high, 30 km long and have a gradient of about 25 percent (Bleed & Flowerday 1998; Warren 2013). The original vegetation in Nebraska, and therefore also in the Sandhills, was mostly prairie. Only when European settlers arrived and extirpated grizzly bears, most elks and bison, crop cultivation and livestock farming started, transforming the prairie into grazing land for the cattle. Some areas, such as the Sandhills, had only been slightly cultivated and the native prairie grasses are still remaining (Gardner 2009; Kaul et al. 2011). Nowadays the Sandhills are a mixed grass prairie which covers around 50,000 km^2. They are the largest stable sand dunes in the Western Hemisphere due to the roots and rhizomes of the prairie grasses which have a stabilizing effect and prevent movement (Bleed & Flowerday 1998; Johnsgard 1995; Kaul et al. 2011; Warren 2013). Fine, water-retentive sand forms the area. As a result it is not as fertile and therefore not as suitable for agriculture as other parts of Nebraska. The European settlers did not pay much attention to this area. Since the 19th century, the area has only been used for low-intensity cattle ranching. Therefore, a flora rich in species can be found nowadays, supported by the slight use of the area for agriculture, the moderate rainfall and the underlying water of the High Plains Aquifer. This groundwater reservoir was formed due to the high permeability of the sand dunes and the underlying sand and gravel. In interdunal valleys, where the groundwater reaches the surface, lakes can be found. These create unique ecosystems and enhance the diversity of the flora and fauna in the region. The perennial presence of water in shallow depth, offers good conditions for the sensitive prairie vegetation. Most of the rivers in Nebraska drain eastwards. Among them, eastern and western woody species spread and interact and make the area unique in their variety of species. Due to the special conditions and the location of the Sandhills, the western coniferous forest, the eastern deciduous forest, the northern arboreal forest, the short-grass prairie and the tall-grass prairie can be found in a very small region (Bleed 1998b; Kaul et al. 2011; Wilhite & Hubbard 1998).

1.1.2 Climate

The climate in the Sandhills is semiarid continental with typically hot and dry summers and cold winters (Bleed & Flowerday 1998). A precipitation gradient from the east of the Sandhills with an average annual precipitation of 580 mm to the west with just 430 mm exists. The reasons for this include the continental position and the Rocky Mountains, which prevent the moisture from the Pacific Ocean to come into the region. Approximately 75 percent of the precipitation occurs from April to September which defines the growing season. Maximum precipitation is measured in May and June. Precipitation in July and August is affected by convection which causes heavy storms and varying amounts of rain over short distances. Precipitation from October to early March occurs mostly in the form of snow. The water, released by thawing processes, initiates the growing season, after a dormancy period during winter (Kaul et al. 2011; Wilhite & Hubbard 1998). Not only the precipitation, but also the temperature shows a gradient from the east, with mean annual temperatures of 9.5°C, to the west with 8.8°C (Wilhite & Hubbard 1998).

1.1.3 Soil

The soils in the Sandhills are in the beginning of their development. Only in active river valleys, developed soils are detectable. Where the soil is developed, slightly darkened topsoil is present. Little or no subsoil development, no accumulation, and no clay enriched B-layer can be identified, presumably because the material was not long enough in the soil (Lewis & Kuzila 1998).

1.1.4 Groundwater

The groundwater in the Sandhills, mentioned above, as a source for biodiverse ecosystems, is complex and not yet fully understood. The primary source of the Nebraskan High Plains Aquifer has to be rain in early spring and fall and snowmelt, as little surface and ground water flows into the Sandhills. Due to the relatively small amount of rain, the availability of water seems to be marginal, despite a huge aquifer (700-800 million acre-feet) developing. It can be assumed that the groundwater can be recharged because vegetation is dominated by C_4 plants which emerge late in the season and because of the permeable soils which prevent surface runoff and increase infiltration. The subsurface is also permeable and water can go easily into the groundwater layers. The groundwater depth ranges from 0-90 m in the north and from 30-60 m in the south of the Sandhills, depending on the local dune topography. Perhaps, this mostly shallow groundwater reservoir is responsible for the success of plants to establish in the infertile, sandy area (Bleed 1998a).

1.1.5 Trees

The most common trees in the Sandhills are cottonwood (*Populus* L.), green ash (*Fraxinus pennsylvanica* Marsh.), boxelder (*Acer negundo* L.), hackberry (*Celtis* L.), eastern redcedar (*Juniperus virginiana* L.), american plum (*Prunus americana* Marshall), chokecherry (*Prunus virginiana* L.) and american elm (*Ulmus americana* L.). About 2 percent of the Sandhills' area is woody vegetation, both cultivated and native. Native trees are mostly found along rivers or in the surroundings of lakes. Originally, just a few trees existed in the dry area of the Sandhills, where rivers are absent, but lately the invasion of different species in these regions has intensified. It is not yet clear how trees survive in these areas, but it is assumed that they build deep roots to reach soil layers with high water content where they can take up water during dry seasons (Kaul 1998; Miller 1998).

1.2 History of the Nebraska National Forest

The Nebraska National Forest (NNF) is an experimental forest planted in the Sandhills of Nebraska. After surveys in the Sandhills, the botany and horticulture Professor Dr. Charles E. Bessey from the University of Nebraska in Lincoln was convinced that the area had been previously forested and could be replanted. He and some colleagues, amongst others the superintendent for the U.S. Bureau of Forestry, William L. Hall, made experiments in the Sandhills to see if trees can survive in this dry area with sandy soil. They planted different species and investigated their growth. After two years of successful experimentation, they came to the conclusion that the plantation of a forest reserve is possible and desirable (Gardner 2009; Miller 1998). In 1902 they presented the idea for a forest reserve in the Sandhills to the former president Theodore Roosevelt. As a conservationist, Roosevelt allowed the plantation of the Sandhills (Miller 1998; Olson & Naugle 1997).

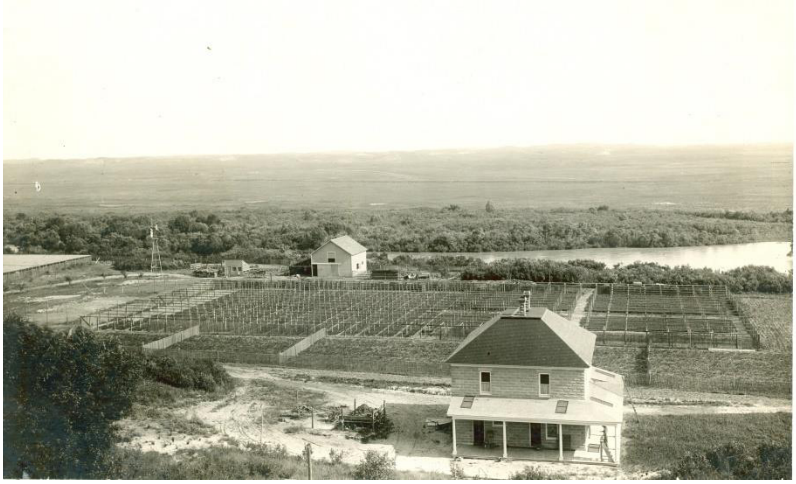


Fig. 1.1: The Bessey Nursery around 1905 (Bessey Nursery 2017)

To support the development of the national forest, a seedling nursery, today known as Bessey Nursery, was established in 1902 to produce seedlings for the planned forest. Today the nursery is still operating and produces 2.5 to 3 million seedlings each year, mostly for national forests (Miller 1998; USDA 2017a).

In 1902, after collecting seeds and seedlings from across the state, they successfully started to plant 14.2 ha of jack pine (*Pinus banksiana* Lamb.) wildlings. The newly planted 6.1 hectares of yellow pine (*Pinus jeffreyi* Balf.) wildlings as well as the 13.8 hectares of broadcasted eastern redcedar (*Juniperus virginiana* L.), blue spruce (*Picea pungens* Englm.), jack pine (*Pinus banksiana* Lamb.) and jeffrey pine (*Pinus jeffreyi* Balf.) seedlings unfortunately weren't as successful as the jack pine project. After these first experiences, some years of further experimentation followed. The project suffered a setback in 1910 when a prairie fire burnt several hectares. Some other fires, caused by lightning burnt a few hectares. To reduce the risk of fires, horses and cattle were brought to graze the area. In 1919 the first clearing of the forest took place. Trees were cut for use as Christmas trees (USDA 2017a).

It was intended to use the forest for wood production to satisfy the demand of wood products due to the increasing population, to produce resources for the future and to substitute wood that was lost in fires or uncontrolled harvesting (USDA 2017a). The forest was also used as an experimental forest, for instance to investigate which species and which density are most appropriate for windbreaks and to prevent soil erosion (Olson & Naugle 1997). Further there was the idea that planting trees would change the climate in the region and bring more rain. People believed that cultivation and closely planted trees would attract rainfall (Gardner 2009; Olson & Naugle 1997).

Due to all the efforts to plant trees, before the plantation of the Sandhills, Nebraska introduced an Arbor day on April 10th in 1872 and the Timber Culture Act. This act reduced taxes on land that was afforested, to encourage people to plant and care for trees. Because of these measures Nebraska was nicknamed 'Tree-Planter's State' (Gardner 2009).

Although the forest was never really successful in wood production, it still is important for wildlife, aesthetic and recreational reasons. It also became a prototype for a federal response against the Dust Bowl and the Great Depression. The idea behind it was to stop soil erosion and to protect the fields by building a shelterbelt system (Gardner 2009).

Fig. 1.2: Planting the Nebraska National Forest (Bessey Nursery 2017)

1.3 Dendrochronology

Dendrochronology, composed of the three greek words *dendron* (tree), *chronos* (time) and *logos* (science of) describes the science which uses tree rings to investigate temporal and spatial patterns of processes in the physical and cultural sciences (Fritts 1976). Schweingruber (1996) defines dendrochronology as a method to measure and date the annual growth rate of woody species. Resultant, past environmental conditions can be reconstructed and archaeological and historical woods can be dated. In general, dendrochronology covers all sciences that use wood for dating (Fritts 1966; Schweingruber 1996).

Tree species building one ring composed of early wood and late wood each year can be used for dating. At the bark, the cambium produces two kinds of cells. Xylem is produced for wood cells and phloem for bark cells. A tree ring consists of xylem and can be divided in early wood and late wood. Early wood is built in the beginning of the growing season. The cells function is to transport water and nutrients between the roots, leafs and needles. Early wood cells have thin walls and a large vessel volume for a rapid and efficient transport. Late wood cells are then built towards the end of the growing season. These cells are built mostly for stabilization and thus have thick walls and a small vessel volume (Fritts 1966). Species building tree rings are mostly found in regions with pronounced seasons in temperate zones. In cold winters, most trees stop growing until spring when increasing temperatures allow tree growth (Schweingruber 1996). On the one hand, the formation of a tree ring is influenced by the environment. The first scientist who officially identified tree rings and set them in a relation to environmental factors such as climate was Leonardo da Vinci: “Rings in the branches of sawed trees show the number of years and, according to their thickness, the years which were more or less dry. Thus, they reflect the individual worlds to which they belong, in the north [Italy] they are much thicker than in the south.” (Schweingruber 1996, p.62). He already recognized that one limiting factor of tree-ring growth is drought. Referred to the National Oceanic and Atmospheric Administration (NOAA), drought is defined as “… a deficiency in precipitation over an extended period, usually a season or more, resulting in a water shortage causing adverse impacts on vegetation, animals, and/or people.” (NOAA 2008, p.1). Others factors, such as precipitation, light, temperature, nutrient supply, soil characteristics, air pollution and also human intervention determine the growth of tree rings. The environmental conditions during the tree’s growing season are recorded in the tree-ring width. On the other hand, species specific characteristics, tree’s heredity, development, age or the longevity influence the formation of tree rings (Fritts 1966; Schweingruber 1996). To sum up, tree-ring growth is a function of the age related growth trend, due to ongoing ageing processes, the climate, disturbance factors within a stand, disturbances from outside the forest, such as insects and random processes which are not allocable (Cook et al. 1990). All the mentioned factors influence not only tree-ring growth but also dating and all further investigations in a positive and negative way. For instance a dry year in all samples, also called pointer year, simplifies the dating whereas the comparison of two different species can be hindered by their species specific responses to external factors. In summary, dendrochronology is used to date trees, to investigate tree growth, to look at reactions of trees in relation to changing environmental conditions or to analyse impacts of limiting factors on tree growth (Fritts 1976; Schweingruber 1983; Schweingruber 1996).

1.3.1 Crossdating

The fundamental principle of dendrochronology is crossdating. It allows identifying the exact year in which a tree ring was formed. Due to characteristic patterns in different tree-ring series, a reconstruction of the whole series can be done and their dating can be controlled. The following Figure 1.3 shows how single series can be compound to a chronology.

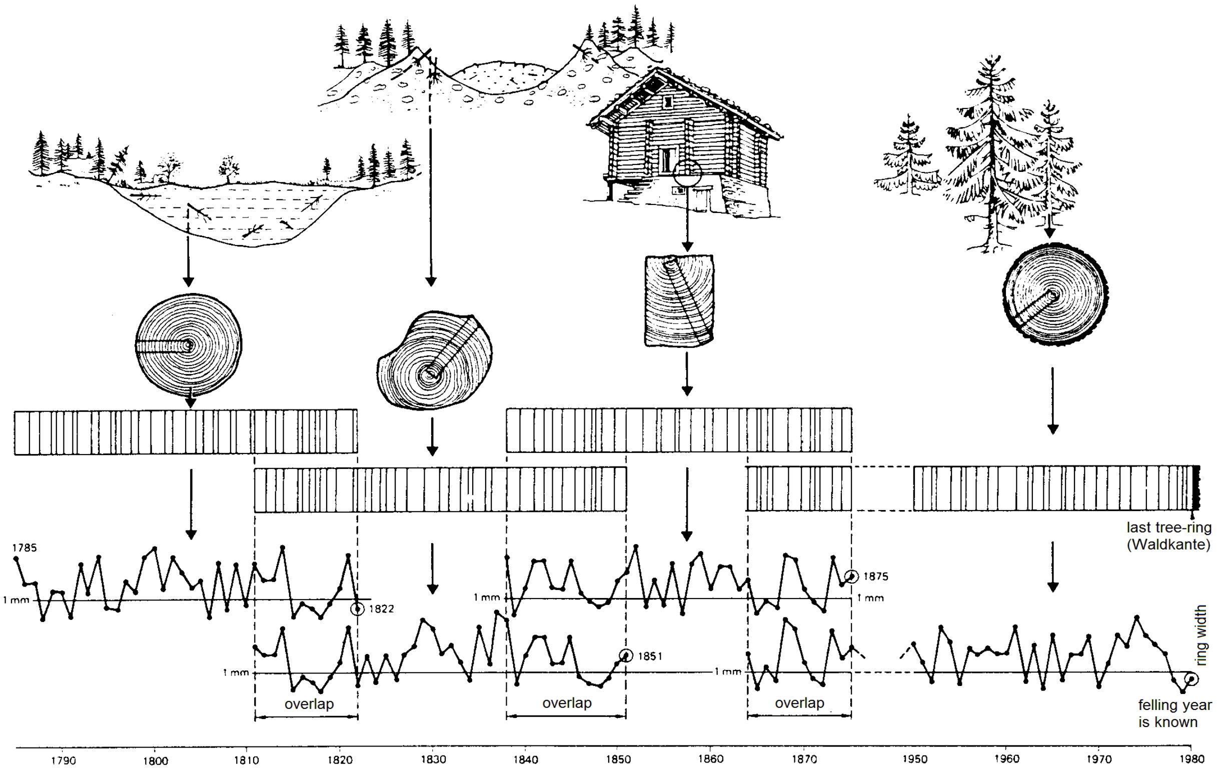


Fig. 1.3: Principle of crossdating (Schweingruber 1988)

Difficulties in crossdating are predominantly caused by intra-annual density fluctuation or by irregular growth due to injuries or inclination which triggers the formation of compression or tension wood. These factors, and the ones mentioned previously, disturb the pattern of the tree-ring growth and therefore complicate crossdating. To deal with these problems more than one core of a tree, a higher array of trees or a disk can be taken. Then, the internal variability of the tree growth can be investigated more easily and site specific growth patterns can be identified. Nevertheless, intra-annual density fluctuations give additional information. They are usually formed when variations, mostly droughts, in climate occur. They help correlating the growth pattern with the climate and can be used as pointer years for an exact dating (Cherubini et al. 2003; De Micco et al. 2016; Fritts 1966; Schweingruber 1996). Once the tree rings are counted and crossdated properly, a precise attribution to the calendar year and therefore an absolute dating can be done. The longest chronologies nowadays go back to late glacial times. Such chronologies allow the dating of old wood where the exact date of harvesting is unknown (Gebhardt et al. 2007).

1.4 Climate Change Effects in Semiarid Grasslands

In the North American grasslands, which the Sandhills are part of, predictions show that climate change will be expressed by a combination of increasing temperatures and modified precipitation patterns. Rainfall will mostly occur in spring and no longer predominantly during summer months. Together with higher temperatures, the intensity of summer droughts will be strengthening (Easterling et al. 2000; MacCracken et al. 2003; Polley et al. 2013; Woodhouse et al. 2001). Intensified and perhaps prolonged dry periods with a shift in soil water availability modify competition between species. In addition to the competition between already existing species, climate, vegetation and management changes allow additional species to grow in the grasslands. This might intensify competition even more and may lead to the suppression of various native species (Archer et al. 2000; Briggs et al. 2005; Huxman et al. 2005; Manabe & Wetherald 1986; Mitchell 2000; Wetherald & Manabe 1995).

Several studies have shown that a wide range of tree species have invaded grasslands in different regions of the world. When grassland ecosystems are transformed, biochemical cycles, species composition, competition, biodiversity, soil stability, accumulation of litter, soil resources and ecosystem services for animals and humans are highly influenced (Archer 1995; Archer et al. 2000; Briggs et al. 2002; Briggs et al. 2005; Brooks et al. 2004; Brown & Carter 1998; Engle & Moseley 1996; O’Connor et al. 2014). The invasion of *J. virginiana* and *P. ponderosa* into the Great Plains and especially into the semiarid Sandhills of Nebraska are one example for this ongoing process. Prairies of millions of hectares are converted to evergreen forests. Such changes have ecological and social consequences, social because these prairies are used for extensive livestock production, Nebraska’s most important economic sector, and ecological because prairies are important actors in the global carbon and nitrogen cycle (Archer et al. 2000; Bleed & Flowerday 1998; Knapp et al. 2000; Lauenroth et al. 1999; McKinley & Blair 2008; Polley et al. 2013). The main factors for a successful invasion of woody species into grasslands are land use changes such as the introduction of grazing cattle, land use management, overgrazing, climate change, nitrogen deposition, import of exotic species and the suppression of fires (Bond et al. 2004; Bragg & Hulbert 1976; Briggs et al. 2005; Daly et al. 2000). The reduction of fires is directly linked to socioeconomic factors. Humans control fires and introduce grazing. The cattle, which are usually grazing until autumn, leave only little vegetation and therefore there is not much flammable material left. Thus, fires are not fed sufficiently and cannot reach the heat and intensity needed to kill trees. Grazing management, combined with permanent supply of seeds to plant new trees for shelterbelts and soil erosion protection, result in a feedback allowing the trees to establish and to spread out (Briggs et al. 2002; Steinauer et al. 1987).

This chain reaction is often found in the Sandhills, where the Nebraska National Forest played a pioneering role to determine the most appropriate species and density for shelterbelts (Briggs et al. 2002). If the factors mentioned above collude, the influences may be reinforced (Archer et al. 2000; Briggs et al. 2002). Independent of the intensity of invasion, serious ecological consequences for the affected areas are reported, ranging from the loss of some species to the complete oppression of the understory (Briggs et al. 2002).

Juniperus virginiana, which is a native species, for instance, can invade into uplands as well as into lowlands. The trees have low habitat requirements what makes them very efficient and successful for invasion. *Juniperus virginiana* shows the typical evergreen characteristics: a rapid growth rate, a high reproductive output and the capability of widespread dispersal. In the case of *J. virginiana* dispersal happens with the help of birds disseminating the seeds (Auders et al. 2012; Briggs et al. 2002; Burns & Honkala 1990). Briggs et al. 2002 investigated the conversion of tallgrass prairie to forest with remote sensing in eastern prairies. They came to the conclusion that *J. virginiana* is able to expand over prairies and convert them into closed-canopy forests within approximately 40 years. Apart from the understory being lost in the dense *J. virginiana* forest, they found no other tree species in such stands. As a result the newly established forest is poor in biodiversity. The lack of understory and other species and the advanced age of the trees (young trees are not fire resistant) reduces the possibility of supressing the invasion by fire and other management strategies to prevent the dispersion of *J. virginiana* (Briggs et al. 2002; Engle & Moseley 1996; Kaul et al. 2011).

Even though *Pinus ponderosa* seems to be less invasive than *J. virginiana*, the trees are able to deal with droughts, extreme temperatures and surface fire. *Pinus ponderosa* increases the density in areas where it already exists in. The spatial distribution of *P. ponderosa* is more limited than *J. virginiana*'s due to the reproduction by seeds with wings which are usually not transported over large areas and due to fire suppression (Burns & Honkala 1990; Richard & Stephan 2008).

1.5 Ring Widths and Climate

Trees in regions with pronounced seasons, store information about climate and competition in annually released tree rings. The variables are expressed in tree-ring width, ring structure, ring density and the stable isotope ratio of carbon, hydrogen and oxygen (Carrer & Urbinati 2004; Fritts 1976; Roden & Ehleringer 2007; Saurer, Siegenthaler, et al. 1995; Schweingruber 1996). In semiarid regions, where precipitation is the dominant factor of tree-ring growth, climate signals are well stored in ring widths (Fritts 1966). If moisture is limited, rings are narrower. Not only the climate of the growing season, but also of the previous years' influences tree growth (Fritts 1966; Sander 1970). To evaluate the influence of different climatic factors, correlations between them and tree-ring widths are calculated (Fritts 1965). Despite the various information offered by tree rings, it comes with some imperfections. The tree's response to climate, expressed in ring width is influenced by various biological and abiotic factors such as age, stand density or competition, complicating the analysis of tree rings (Fritts 1976).

Further, so called false rings or intra-annual density fluctuations, formed by environmental stress such as high competition, wind, fire, physical damage, insect attacks and drought, make analysis difficult (Cherubini et al. 2003; De Micco et al. 2016; Edmondson 2010).

1.6 Stable Isotopes

Apart from ring widths, stable isotopic ratios of carbon and oxygen provide important information on species' response to different environments. Especially in the context of global climate change and invasions of non-native species, it is essential to have an idea of species' behaviour and adaptation under different conditions. Since stable oxygen and carbon isotopes and their combination can be linked to stomatal conductance and photosynthetic capacity, more detailed predictions of future behaviour can be made (Saurer et al. 1997; Scheidegger et al. 2000).

Different studies have shown that the values of $\delta^{13}C$ are influenced by the relative humidity of the atmosphere, temperature (Stuiver & Braziunas 1987), water availability (Leffler & Evans 1999), soil moisture (Leavitt 1993), nutrition, air pollutants (Beyers et al. 1992; Niemelä et al. 1997; Saurer, Maurer, et al. 1995) and atmospheric CO_2 (Saurer et al. 1995). Due to the large number of influences, causes and effects are hard to assign. But studies as conducted by Hemming et al. (1998), Leavitt & Long (1988) and Saurer et al. (1995) showed a correlation between the climate at the sample site and $\delta^{13}C$ signals. In addition to $\delta^{13}C$, information about the water use efficiency (WUE) of trees can be calculated and set in the context of prevailing climate (Roden & Ehleringer 2007). This is important for future forest and water resource management in regard to climate change, as measurements have shown that atmospheric CO_2 is increasing and tends to raise plants' water use efficiency (Caterina et al. 2014; Eamus 1991).

Stable isotopic ratios of oxygen indicate air humidity and annual variability in water sources used by trees and allows association with climate (Roden & Ehleringer 2007; Saurer et al. 1997). Deep lying water, which was presumably stored longer in the soil than water from the upper soil layers, has lower $\delta^{18}O$ values compared to water from the upper soil. The used water source of plants varies from year to year, depending on climatic conditions, offering the options to link $\delta^{18}O$ to climate (Roden & Ehleringer 2007). By comparing $\delta^{13}C$ and $\delta^{18}O$ values, from one plot to other sample areas, environmental influences on trees are identifiable and help to understand trees' response to particular sites (Scheidegger et al. 2000).

2 Research Questions & Hypotheses

In the first part of the present master thesis the focus lies on the response to drought of *P. ponderosa* and *J. virginiana* and it is intended to investigate the water use efficiency of *P. ponderosa* at sparse and dense stands. In a second part, a comparison between these data and other stands of *P. ponderosa* and *J. virginiana* in the east of the state of Nebraska, near Lincoln will be performed. The sample sites in the east of Nebraska show different soils and receive more rain than the area in the Sandhills.

With the cores of the two species, sampled at different plots in the three study areas, the following research questions will be answered:

1. How do the different tree species (*P. ponderosa* and *J. virginiana*) respond to droughts?
2. How do the reactions of the trees differ depending on the stand density?
3. From where does *P. ponderosa* take the necessary water? How efficient can the water be used? Is there any connection to the root depth?
4. How do the three sites (Nebraska National Forest, Horning Farm and Prairie Pine) differ from another?

The following hypotheses underlie the thesis:

A. Both tree species are tolerant to habitat requirements, but due to species specific responses to environmental conditions it can be assumed that the responses of *P. ponderosa* to droughts are less pronounced than the ones of *J. virginiana*.

B. It is hypothesized that the reactions to drought are less strong in sparse plots than in dense plots, due to the fact that the competition for water resources in dense stands might be much higher than in sparse stands.

C. Presumably *P. ponderosa* takes water from deep layers and can use the water very efficiently, because of its root structure, which consists of a massive taproot with a radius of small roots. A high interdependence between root structure and water use efficiency can be presumed.

D. It can be assumed that the three sites (Nebraska National Forest, Horning Farm and Prairie Pine) show different reactions in tree rings, because the soil and the climate at these sites are different.

3 Tree Species

3.1 *Pinus ponderosa* Dougl. ex Laws.

Pinus ponderosa and its varieties are one of the most common pine species in western North America. They extend from southwestern Canada (British Columbia) to Mexico, from the US' pacific coast to the east of Dakota, Nebraska and Texas. *Pinus ponderosa* is usually found at an altitude of 1300 to 2600 m a.s.l., but may also occur from sea level up to 3300 m a.s.l.. The best growing conditions can be found in the sierra of California (Auders et al. 2012; Burns & Honkala 1990; Richard & Stephan 2008).

Pinus ponderosa stems are straight and cylindrical without large branches in the lower part. The trees commonly reach a height of 25-40 m with a diameter at breast height of 0.7-1.3 m. Larger trees with a height up to 70 m and a diameter at breast height of 2.6 m exist (Burns & Honkala 1990; Richard & Stephan 2008). The needles are ordered in bundles of usually 2-3 needles. They are 15-25 cm long and 12-1.8 mm wide and slightly bendable (Auders et al. 2012; Kaul et al. 2011; Richard & Stephan 2008). The pollen cones are of red-brown colour and are 1.5-4.5 cm long. The seed cones occur sole or in pairs. In the beginning they are green, while ripening their colour changes to brown. They are up to 12 cm long. The seeds are 6-8 mm long and are endowed with wings of 15-25 mm. Their size depends on the cone's size. The wings are thin and woody and hold a hooked prickle (Auders et al. 2012). The bark of young trees is dark brown and changes its colour and texture with increasing age. Thickness increases to 10 cm and shows a furrowed surface. The older the tree, the brighter the bark gets. Its colour changes from dark brown to orange-brown. The wood is straight grained and clear tree-ring boarders are visible. The heartwood shows a dark yellow to orange brown colour whereas the sapwood is white to light yellow (Auders et al. 2012; Richard & Stephan 2008). *Pinus ponderosa'*s strong root system shows a taproot of around 2 m depth, but at locations with underlying rock with large fissures or in sandy soils without clay, roots can reach a depth of 11 to 12 m. In dense stands, the root system is not more extended than the crown whereas in sparse stands the roots may spread further than the crown diameter up to a distance of 46 m (Burns & Honkala 1990; Richard & Stephan 2008).

Pinus ponderosa does not reproduce by vegetative methods. For reproduction, the trees produce cones, filled with seeds. The amount of produced seeds varies and no clear pattern of its production has been found. Seeds are usually only allotted over short distances. Sometimes birds, mice, chipmunks or squirrels eat them and enable a distribution over a larger area (Burns & Honkala 1990). The most preferred habitats consist of dry, profound and well drained sand soils. *Pinus ponderosa* is able to deal with intense droughts and also tolerates extreme temperatures. It is one of only few conifers that are able to deal with such rough conditions. Due to their thick bark they also occur in areas where forest fires are present. A limiting factor of growth is shade. Due to *P. ponderosa*'s intolerance of shade the stands are usually even-aged (Burns & Honkala 1990; Richard & Stephan 2008). In the state of

Nebraska, *P. ponderosa* is found on dry and rocky slopes, in canyons and is moving into the Sandhills, mostly because prairie fires are fewer due to increased control (Kaul et al. 2011).

Because of its stem with no large branches in the lower part, *P. ponderosa* is the most important conifer in the west of the USA. There are many applications the wood is used for. The forests are usually used for livestock grazing and recreation due to a high aesthetical value. Animals, such as squirrels, birds, elks or deers use the forests as food source and habitat (Richard & Stephan 2008).

Fig. 3.1: a: *P. ponderosa* tree, b: *P. ponderosa* seed and seedwing (2.5 cm long), c: *P. ponderosa* cone (8 cm high), d: *P. ponderosa* core (15 cm length)

3.2 *Juniperus virginiana* L.

Juniperus virginiana is mostly found in eastern North America (Zamora & Caravaca Gallardo 2013). It is distributed at an altitude from sea level up to 1400 m a.s.l. (Auders et al. 2012). The evergreen conifer is fast-growing and usually reaches a height of 15-20 m, sometimes 25-27 m. The stem may reach a diameter of 30-60 cm. For *J. virginiana* two types of leaves are typical. The adult leaves are small, dark green and scale-like, 3 mm long and 1 mm wide. The others are blue to green and more needle like. The trees bear berry like seed cones. They are 2-7 mm in diameter and turn from green to dark blue (Auders et al. 2012; Kaul et al. 2011; Zamora & Caravaca Gallardo 2013). The wood is straight grained with small structures, closed pores and with lots of knotholes. The heartwood shows a reddish or purple-brown colour. The sapwood is light yellow (Zamora & Caravaca Gallardo 2013). Depending on the soil properties, *J. virginiana* forms fibrous and widely spread roots on shallow soils and additionally a taproot in profound soils, respectively. Fissures in the soil influence the root's development (Burns & Honkala 1990).

Juniperus virginiana does reproduce by grafting or from cutting, but it does not procreate by sprout or sucker. Usually reproduction takes place by the seeds. They are often eaten by animals, predominantly birds, which distribute them over large areas. Therefore numerous trees can be found along fences or under power lines. *Juniperus virginiana* is widely distributed over eastern North America showing the species' ability to adapt. Preferentially it grows in open places and on deep, moist, well-drained sites (Auders et al. 2012; Burns & Honkala 1990). In the state of Nebraska, it is found as a shrub or tree in pastures, prairies, shelterbelts, hedges and is scattered over the Sandhills (Kaul et al. 2011). The trees' roots may reach a depth of 7.5 m, depending on local conditions (Eggenmeyer et al. 2006). In natural stands, soil's pH ranges from pH 4.7-7.8. *Juniperus virginiana* is not tolerant to higher soil pH. If the species establishes, soil pH becomes neutral, due to the foliage having high calcium content. The species is very shade intolerant, but drought-resistant. Due to the thin bark and roots near the surface, *J. virginiana* is not resistant to fires, at least when the trees are young (Briggs et al. 2002; Burns & Honkala 1990).

The wood of *J. virginiana* is usually not commercially used, but is well known for its colour, durability and workability. It is used for fence posts, due to its resistance to rotting, or as lining for wardrobes, because of its fragrant and beautiful wood. Further, oil can be distilled from the wood and the leaves (Auders et al. 2012; Zamora & Caravaca Gallardo 2013). *Juniperus virginiana* forests provide shelter for wildlife and good nesting conditions because it is an evergreen. Additionally, the fruits are rich in carbohydrates, fat, fibre and calcium. They are eaten by a wide range of animals such as birds, turkeys, rabbits, foxes, raccoons, opossums and coyotes. Further, *J. virginiana* is one of the most effective soil erosion protectors. It is often planted in shelter belts in the Great Plains, because it is resistant to high and low temperatures (Burns & Honkala 1990).

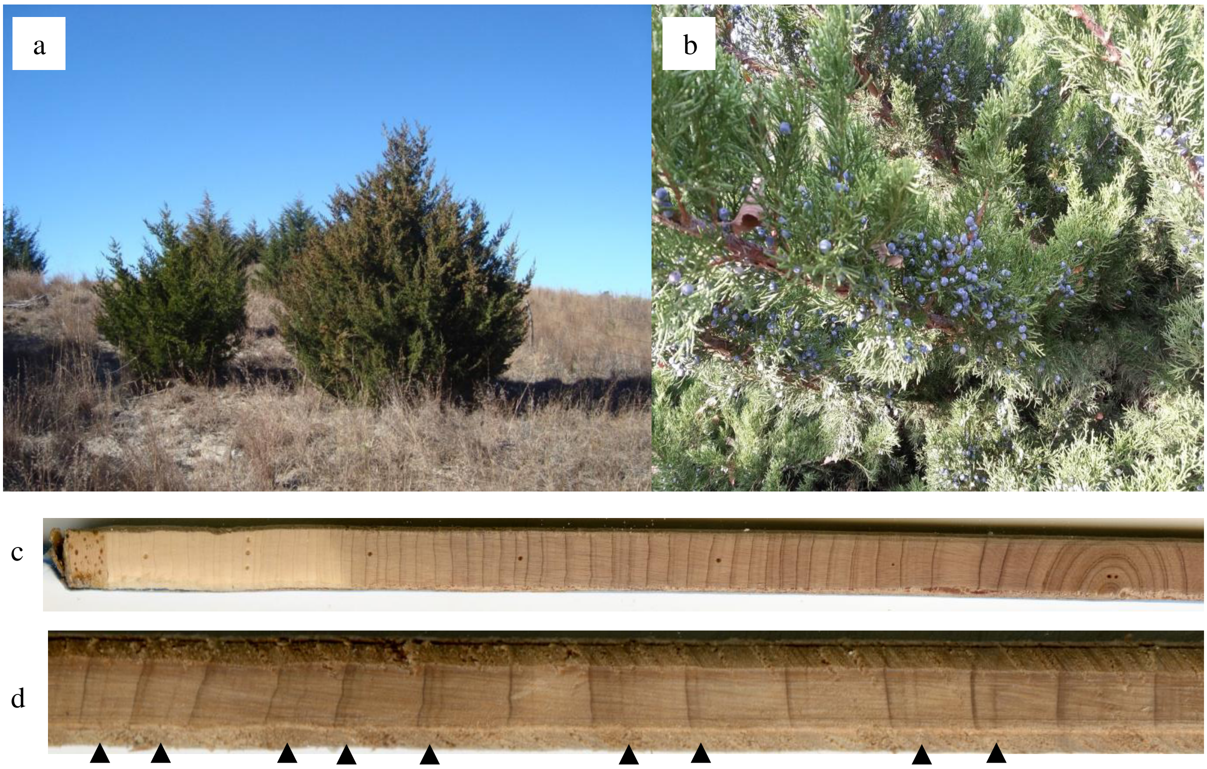


Fig. 3.2: a: *J. virginiana* tree, b: *J. virginiana* berry-like cones, c: *J. virginiana* cone (12 cm length), d: intra-annual density fluctuation (marked with arrows), a characteristic feature in *J. virginiana* cores

4 Sample Sites

All samples were taken in the US state of Nebraska. One sample series was taken in the Sandhills in Central Nebraska, the other two parts in eastern Nebraska. In the following section, these three study areas are described more precisely. The map below shows the three sample regions.

Fig. 4.1: Sample sites: Nebraska National Forest (NNF), Horning Farm (HRN) and Prairie Pine (PPN) (Esri 2017)

4.1 Nebraska National Forest (NNF)

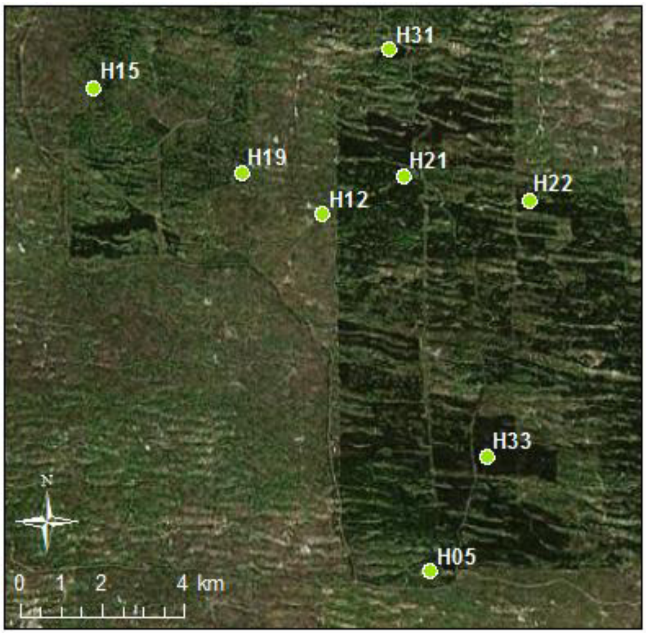


Fig. 4.2: Sample plots NNF (Esri 2017)

One part of the samples was taken in the NNF which is located in the Sandhills of the US state of Nebraska, near Halsey in Blaine and Thomas County, Nebraska (825 m altitude, lat. 41°51’45’’N, long. 100°22’06’’W). The area of the NNF shows a semiarid continental climate. The mean annual temperature is 8.4°C. The mean minimum temperature in January is ~ -13°C and the mean maximum temperature in July is ~32°C. The average annual precipitation is around 570 mm. Most precipitation, around 75 percent, falls in the growing season from April to September. The soils are Valentine fine sand (mixed, mesic, Typis Ustipsamments) (Lewis & Kuzila 1998; Sherfey et al. 1965; USDA 2017b). In the NNF samples of *P. ponderosa* and *J. virginiana* were taken at three different stand densities (number of individuals per unit ground area), sparse, mid and dense. Figure 4.2 shows the spatial distribution of the sample plots in the NNF. Table 4.1 gives a detailed overview of *P. ponderosa* at the different plots and shows the plot characteristics.

Table 4.1: Samples NNF *P. ponderosa*

species	*P. ponderosa*					
density	sparse		mid		dense	
n° plot	H05	H15	H12	H19	H21	H22
n° samples	30	30	30	30	30	30
collection date	07.11.2013	07.11.2013	07.11.2013	08.07.2014	08.07.2014	06.08.2014
approx. age [a]	40	75	70	80	80	80
trees per 10 m^2	< 5	< 5	5-10	> 10	> 10	> 10

The understory at the sparse sites of *P. ponderosa* consists of perennial grassland and is dominated by sand bluestem (*Andropogon hallii* Hack.), switchgrass (*P. virgatum*), little bluestem (*S. scoparium*), sand dropseed (*Sporobolus cryptandrus* (Torr.) A. Gray), white sagebrush (*Artemesia ludoviciana* Nutt.) and Kentucky bluegrass (*Poa pratensis* L.). At the mid sites, the understory shows a lower grass density. It is composed of indiangrass (*Sorghastrum nutans* L.), poison ivy (*Toxicodendron radicans* L.), little bluestem (*S. scoparium*) and patchy occurrence of prairie rose (*Rosa arkansana* Porter.). At dense sites, the occurrence of an understory is even lower. Only Kentucky bluegrass (*Poa pratensis* L.), little barley (*Hordeum pusillum* Nutt.), annual blue grass (*Poa annua* L.) and some other cool season grasses can be found.

Fig. 4.3: sparse site H05

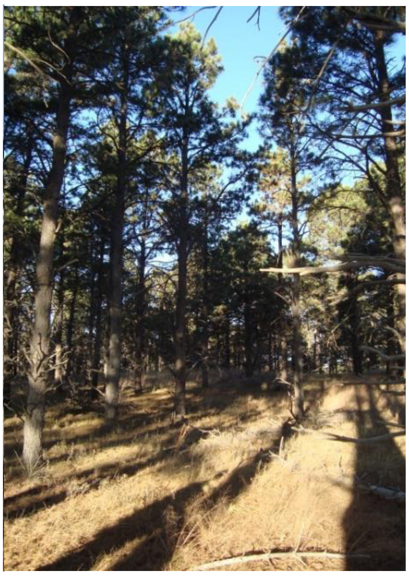


Fig. 4.4: mid site H12

Fig. 4.5: dense site H21

Below the same information for the plots of *J. virginiana* at the NNF is shown.

Table 4.2: Samples NNF *J. virginiana*

species	*J. virginiana*				
density	sparse	mid	dense		
n° plot	H15	H19	H21	H31	H33
n° samples	4	8	8	30	30
collection date	07.11.2013	08.07.2014	08.07.2014	05.08.2014	06.08.2014
approx. age [a]	25	30	45	75	65
trees per 10 m^2	< 5	5-10	> 10	> 10	> 10

The understory at the sparse sites of *J. virginiana* showed a perennial grassland with the following species; switchgrass (*Panicum virgatum* L.), little bluestem (*S. scoparium*), indiangrass (*S. nutans* L.), horse weed (*Conyza canadensis* (L.) Cronq.), some annual buckwheat (*Eriogonum annuum* Nutt.), cactuses (*Opuntia fragilis* (Nutt.) Haw. and *Opuntia macrorhiza* Engelm.). At mid stands, the understory is composed of the same species but there is less volume of grass due to sunlight limitation caused by the closer canopy. At dense sites, grasses are absent, just different species of mosses are detectable.

Fig. 4.6: sparse site H15

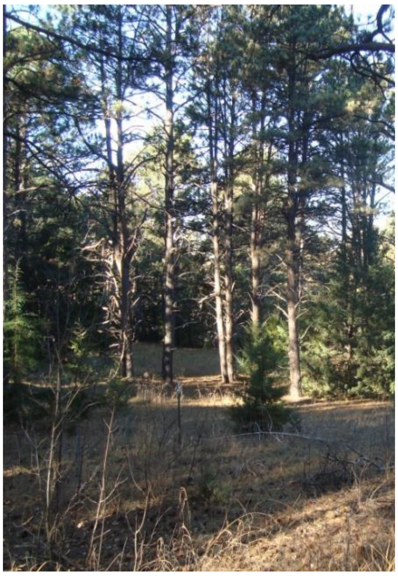


Fig. 4.7: mid site H19

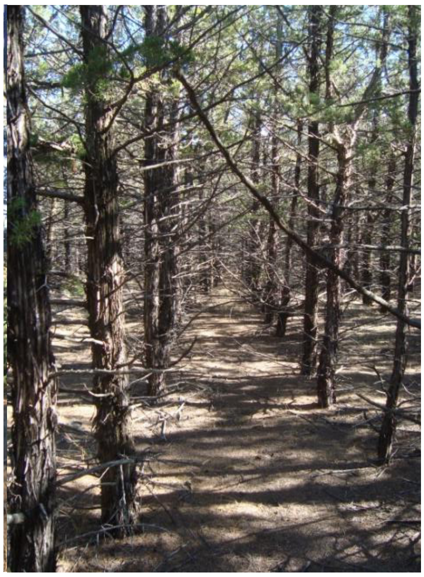


Fig. 4.8: dense site H31

4.2 Horning Farm (HRN)

Another part of the samples was taken at Horning Farm, a research area which belongs to the University of Nebraska, around 3 km from Plattsmouth in Cass County, Nebraska (354 m altitude, lat. 40°58'51.3"N, long. 95°52'30.6"W). The average annual temperature is 10.4°C. The mean minimum temperature in January is ~-21°C and the mean maximum temperature in July is ~35°C. The average annual precipitation is around 850 mm. The soils in this area are Marshall silty loam (fine-silty, mixed, superactive, mesic Typic Hapludolls) (USDA 2017b).

At HRN *P. ponderosa* and *J. virginiana* were sampled. At one plot (P01) samples of *P. ponderosa* were taken, and at the other two plots (P02 and P03) *J. virginiana* was sampled. Figure 4.9 shows the spatial distribution of the different sample plots at HRN. Table 4.3 gives a detailed overview of the different plots and shows the plot characteristics.

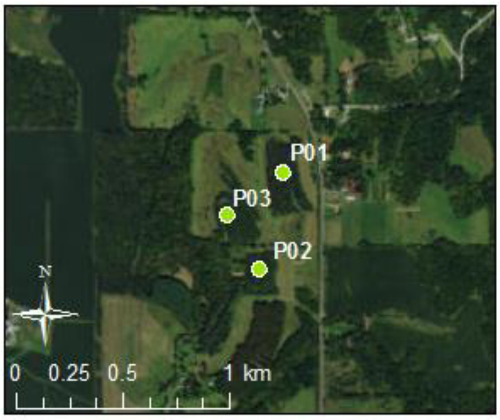


Fig. 4.9: Sample plots HRN (Esri 2017)

Table 4.3: Samples HRN

species	*P. ponderosa*	*J. virginiana*	
density	dense	dense	
n° plot	P01	P02	P03
n° samples	29	30	30
collection date	20.07.2015	20.07.2015	20.07.2015
approx. age [a]	40	40	40
trees per 10 m^2	> 10	> 10	> 10

At the *P. ponderosa* dense stand, the understory is dominated by smooth brome (*Bromus inermis* Leyss.). Between them amur honeysuckle (*Lonicera maackii* (Rupr.) Herder.), coralberry (*Symphoricarpos orbiculatus* Moench.) stinging nettle (*Urtica dioica* L.), american pokeweed (*Phytolacca americana* L.) and young black walnut trees (*Juglans nigra* L.) can be found.

The understory of the *J. virginiana* at stand P02 consists mostly of amur honeysuckle (*L. maackii*), whereas at P03 it consists predominantly of mosses. In addition, some small pokeweed (*P. americana*) and some stinging nettle (*U. dioica*) are present at both stands.

Fig. 4.10: dense site P01

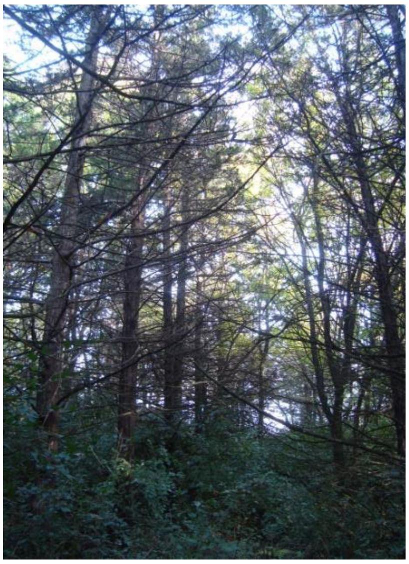


Fig. 4.11: dense site P02

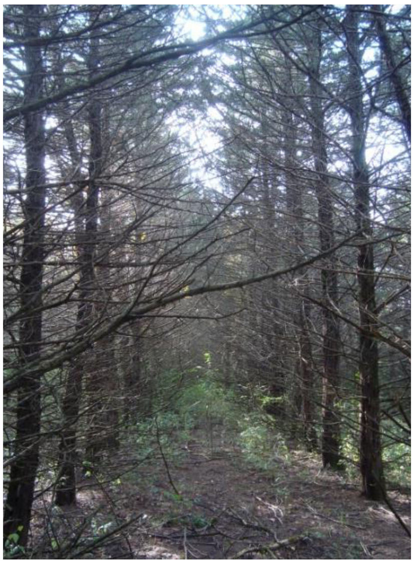


Fig. 4.12: dense site P03

4.3 Prairie Pine (PPN)

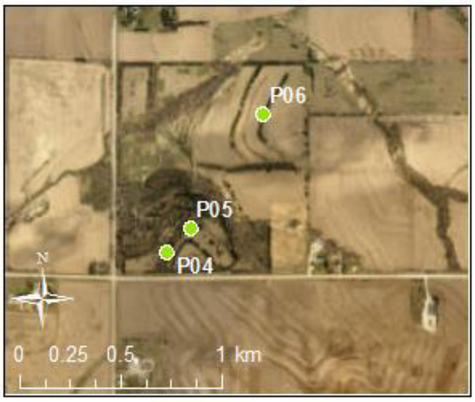


Fig. 4.13: Sample plots PPN (Esri 2017)

A third part of the samples was taken at Prairie Pine, another research area owned by the University of Nebraska, around 3 km from Lincoln in Lancaster County, Nebraska (375 m altitude, lat. 40°50'37"N long. 96°33'51"W). The average annual temperature is 10.7°C. The mean minimum temperature in January is ~-21°C and the mean maximum temperature in July is ~38°C. The average annual precipitation is around 730 mm. The predominant soils are Aksarben silty loam (fine, smectitic, mesic Typic Argiudolls) (USDA 2017b). Figure 4.13 shows the spatial distribution of the different sample plots at PPN. Table 4.4 gives a detailed overview of *P. ponderosa* at the different plots and shows the plot characteristics.

Table 4.4: Samples PPN *P. ponderosa*

species	*P. ponderosa*		
density	sparse		
n° plot	P04	P05	P06
n° samples	22	26	30
collection date	26.10.2015	26.10.2015	26.10.2015
approx. age [a]	40	40	45
trees per 10 m^2	< 5	< 5	< 5

The understories of P04, P05 and P06 are similar. They are dominated by smooth brome (*B. inermis*) with an infrequent occurrence of cool season grasses and small forbs.

Fig. 4.14: sparse site P04

Fig. 4.15: sparse site P05

Fig. 4.16: sparse site P06

5 Material & Methods

This chapter gives an overview of the methods used in this thesis. In the first part, the methods for the tree sampling, core preparation, tree-ring width measurements and crossdating are introduced. In the second part, the standardisation and the methods to calculate the correlations between tree-ring width and climate are presented. Afterwards, the sample preparation for the stable isotope analysis and the stable isotope analysis itself are explained.

5.1 Sampling

Two cores from each tree were sampled with an increment borer with a diameter of 5 mm. The cores were taken at breast height, at about 130 cm perpendicular to the growing axis of the tree, focussing towards the centre of the tree to reach the pith. The sampling height was chosen because it provides the most reliable chronology (Fritts 1966). After drilling the hole, the borer was turned back once to separate the core from the tree. Then the core was taken out of the borer by an extractor with barbs. One core was taken from the part of the tree facing south, the other from the north facing part. By comparing the two cores the internal variability of the tree growth is identifiable. The extraction of a core results in an injury to tree. The borer harms the tree mechanically due to the drilling, physiologically because of the trees response, and pathologically by reason of bacteria and fungi which may enter the hole (Schweingruber 1983). After the samples were taken, they were labelled, dried, put in test tubes and closed airtight.

5.2 Core Preparation

To enhance the visibility of the tree rings, the cores were sanded or cut. The samples from the NNF have already been sanded at the University of Nebraska in Lincoln, while the samples from HRN and PPN were cut at the WSL in Birmensdorf. In both processes, sanding and cutting, the flat surface for measuring afterwards should be oriented in a right angle to the fibre direction, otherwise the ring widths are forged (Schweingruber 1983). The dried cores from the NNF were sanded with a sequence of sandpaper grit, progressively getting finer, down to 220-grit. The cores from HRN and PPN were cut with a blade. Therefore they were fixed into the holder of a microtome and cut layer after layer of approximately 10 µm until the core had a plane surface over its whole extent (Gärtner et al. 2015).

5.3 Ring-Width Measurement and Crossdating

After the core preparation, the rings were counted by making a dot at every decade. These dots are an aid to guide for the further analysis under the microscope and the counting gives a broad overview of the age of the sampled trees. After the tree rings were measured under the microscope to the nearest

0.01 mm with a linear table called LINTAB (Frank Rinn, Heidelberg, Germany). The data was then presented in TSAPWin (Time Series Analysis and Presentation, Frank Rinn, Heidelberg, Germany). After visually crossdating each tree's northern and southern core, each site was visually crossdated in TSAPWin as well (Stokes & Smiley 1968). The different tree species were crossdated separately. Missing rings were inserted manually with a value of 0 to complete the chronology. The visually crossdated data was imported to the program CONFECHA for statistical analysis to check crossdating accuracy (Grissino-Mayer 2001). Additionally, the *Gleichläufigkeit* (Glk), a parameter for the sum of the same gradient in the whole chronology in percent and the cross dating index (CDI), the combination of the Glk with the t-value of the chronology, were considered (Rinn 2003).

5.4 Meteorological Data

Monthly precipitation and air temperature data was compiled for each sample site separately. For the NNF, a combination of data from two different stations was used. One, HALSEY 2 W, is at the NNF itself (825 m altitude, lat. 41°54'00"N, long. 100°19'00"W), whereas the other one, HALSEY, is around 10 km east of the town of Halsey (842 m altitude, lat. 41°54'00"N, long. 100°09'00"W). The data before November 1989 is from the observer station HALSEY 2 W. The data after this date comes from the more distant station HALSEY.

The data for HRN is also a combination of two stations. Despite both being approximately 12 km away from the sample site, they accurately represent the climate of the sample site. Station GLENWOOD 3 SW (299 m altitude, lat. 41°00'34"N, long. 95°46'25"W) covers the period from 1900 to 2008 whereas station GLENWOOD (323 m altitude, lat. 41°03'06"N, long. 95°44'57"W) provides data from 2008 to 2016.

Climate data for PPN is composed of measurements form three different stations, which are on average 12 km away from the sample site PPN. From 1921 to 1954 the data is provided by station LINCOLN AGRNMY FARM (366 m altitude, lat. 40°51'00"N, long. 96°37'00"W), from 1955 to 1972 from LINCOLN UNIV PWR PLT (354 m altitude, lat. 40°49'23"N, long. 96°42'09W) and from 1973 to 2016 from LINCOLN AP (365 m altitude, lat. 40°51'02"N, long. 96°44'51"W).

In addition, the Palmer Drought Index (PDI) from NOAA (NOAA 2017) was taken into account while calculating correlations between climate data and tree-ring widths. For the NNF, the north central station (lat. 42°18'N, long. 100°18'W), for HRN and PPN the southeast station (lat. 40°12'N, long. 96°53'W), was selected to represent the precipitation the most appropriate for the sample regions. The PDI is a tool to classify droughts on a regional level. By comparing the actual dryness or wetness to the average values in a region, the index allows to compare extreme values to normal ones. Not only precipitation, but also factors such as runoff, soil recharge, deep percolation, soil moisture conditions and evapotranspiration are taken into account to cover most of the factors which define the severity of a drought. Values of -2 indicate moderate droughts, -3 severe droughts, -4 extreme droughts and positive values stand for wet conditions (Alley 1984; Palmer 1965; Wilhite & Hubbard 1998).

5.5 Data Analysis

Former analyses have shown that trees show age trends. In the first years their rings are continuously broader compared to the rings in later years (Biondi & Qeadan 2008; Fritts 1966; Schweingruber 1983; Schweingruber 1996). Therefore all raw ring-width measurements were standardised with the program ARSTAN (Cook & Holmes 1986), using a 30-year smoothing spline and a variance stabilisation. After standardisation, correlations of the tree-ring widths with temperature, precipitation and the PDI for each sample plot were calculated in R, applying the *rcor.test* from the *ltm* package. To take the temperatures and precipitation of the previous year into account, this data was included in the analysis. The statistical significances of these factors were tested at a monthly basis and seasonal combination. In addition, to identify climate variables which influenced the tree growth the most, a Stepwise Linear Regression Modelling (SLRM), based on the Akaike Information Criterion (AIC), using a forward-backward approach (Cook & Pederson 2011), was applied. Temperature at a monthly basis and precipitation grouped by months, representing the seasons, were used for this analysis.

5.6 Stable Isotopes

5.6.1 Preparation

First, the most suitable cores for the stable isotope analysis had to be selected. Criteria therefore includes no missing rings in the years that have to be investigated, broad rings to have sufficient test material, rings ideally without reaction wood, and the ring width pattern which fits into the site chronology. From each tree only one core was used for stable isotope analysis. The rings of the selected cores were split with a scalpel, exactly at the tree ring's boundary. The tree ring then was cut into small pieces in preparation for milling. Then, each sample was milled in a centrifugal mill (ZM 1000, Retsch, Germany). With a brush the milled sample was taken out, collected on a weighing paper and filled into the microreaction tube. To avoid contamination, the mill was cleaned with a vacuum cleaner and ethanol after every sample. Afterwards, the samples were prepared for the extraction of the cellulose, which is the part of the wood that accumulates the needed stable isotopes the best. Therefore approximately 10 mg of the powdered wood samples were weighed out in Teflon pockets. The bags were closed with a heat sealer and a binary code was cut into the margin. The sign V represents a 0, whereas I stands for 1. The binary code replaces labels written on the bag. This step had to be done because the chemicals of the following extraction method remove any markings. The Teflon bags were then put in an Erlenmeyer flask with a volume of 250 ml.

5.6.2 Extraction (modified from Green 1963)

In a first step, fats, resins, oils, tannins and hemicelluloses had to be removed from the samples. Therefore the samples were washed in a 5% NaOH (sodium hydroxide) solution for 2 hours at 60°C in the water bath. The solution consisted of 1 litre of distilled H_2O and 50 g of NaOH pellets. After the first treatment the samples were washed a second time, again for 2 hours at 60°C in a newly prepared NaOH solution. After a total of 4 hours in the solution the samples were washed three times with boiling distilled water (Green 1963; Leavitt & Danzer 1993).

In a second step lignin was eliminated. The samples were washed with a 7% $NaClO_2$ (sodium chlorite) solution at 60°C. For 1 litre solution, 87.5 g (~80%) $NaClO_2$ and 3-4 ml acetic acid (CH_3COOH) were mixed. Additional acid was added until the pH reached a value between 4 and 5. Every 10 hours the solution was renewed. Altogether the solution was changes three times, so that the samples were in the solution for at least 30 hours. After the extraction the samples were washed three times with boiling distilled water and squeezed as much as possible to shorten the drying time. The pockets were dried in the drying oven at 60° for at least four hours (Green 1963; Leavitt & Danzer 1993).

5.6.3 Element Analysis

After the extraction, the samples were prepared for the elemental analysis-isotope ratio mass spectrometry (IRMS-EA). For this purpose, 0.9 mg to 1mg of cellulose had to be weighted into tin cups. These then were burned in the element analyser *Euro EA* (Hekatech GmbH). The flue gas was oxidised or reduced and separated chromatographically before the stable isotope ratios $\delta^{13}C$ (‰) and $\delta^{18}O$ (‰) were determined by isotope mass spectrometry with *IRMS Delta V Advantage* (Thermo Scientific). To ensure high accuracy some quality control measurements were made. The results were compared against the IAEA primary reference material VPDB, AIR (air) (Matthews & Hayes 1978).

5.6.4 Stable Isotope Data Analysis

After the stable isotope extraction, different analyses with the data were performed. In a first step the carbon values were atmospherically corrected, because $\delta^{13}C$ of atmospheric CO_2 has decreased due to fossil fuel burning in the last century (Keeling et al. 1989). Afterwards the WUE was calculated and the conceptual model of Scheidegger et al. (2000) was applied to link stable isotopes with stomatal conductance and photosynthetic capacity to understand the relations between climate and stable isotopes. In addition, PDI values were taken into account for a comparison between climate and stable isotopes. Correlations between climate and $\delta^{13}C$ and climate and $\delta^{18}O$ were calculated.

Calculation of WUE from C isotopes ratios was performed as described in Farquhar et al. 1982:
The $\delta^{13}C$ was used for the calculation of the WUE where:

$$\delta^{13}C_{plant} = \delta^{13}C_{atm} - a - (b - a) * (c_i / c_a), \tag{1}$$

with the two fractionation factors *a* (4.4‰) and *b* (27‰). The factor *a* represents the diffusion of CO_2 trough the stomata and factor *b* the Rubisco enzyme during photosynthesis.

Using the formula:

$$WUE = A / g_1 = (c_a - c_i) / 1.6 \tag{2}$$

where A represents the rate of CO_2 assimilation, g_1 the stomatal conductance, the factor c_i the intercellular CO_2 concentration and c_a the CO_2 concentration in the atmosphere. Values for c_a are from the NOAA from Mauna Loa station. The value 1.6 is the ratio of diffusivities of CO_2 and water in the atmosphere.
In a next step, the carbon isotope discrimination Δ is calculated. It stands for the difference between the carbon isotopic ratio of atmospheric CO_2 ($\delta^{13}C_{air}$) and the plant organic matter ($\delta^{13}C_{plant}$):

$$\Delta = (\delta^{13}C_{air} - \delta^{13}C_{plant}) / (1 + \delta^{13}C_{plant} / 1000). \tag{3}$$

The c_i / c_a ratio from below can be calculated as follows:

$$c_i / c_a = (\delta^{13}C_{plant} - \delta^{13}C_{air} + a) / (b - a), \tag{4}$$

where c_i can be calculated by the combination of equation 3 and 4:

$$c_i = c_a [(\Delta - a) / (b - a)]. \tag{5}$$

Combining the equations 2 and 5, the WUE can be calculated:

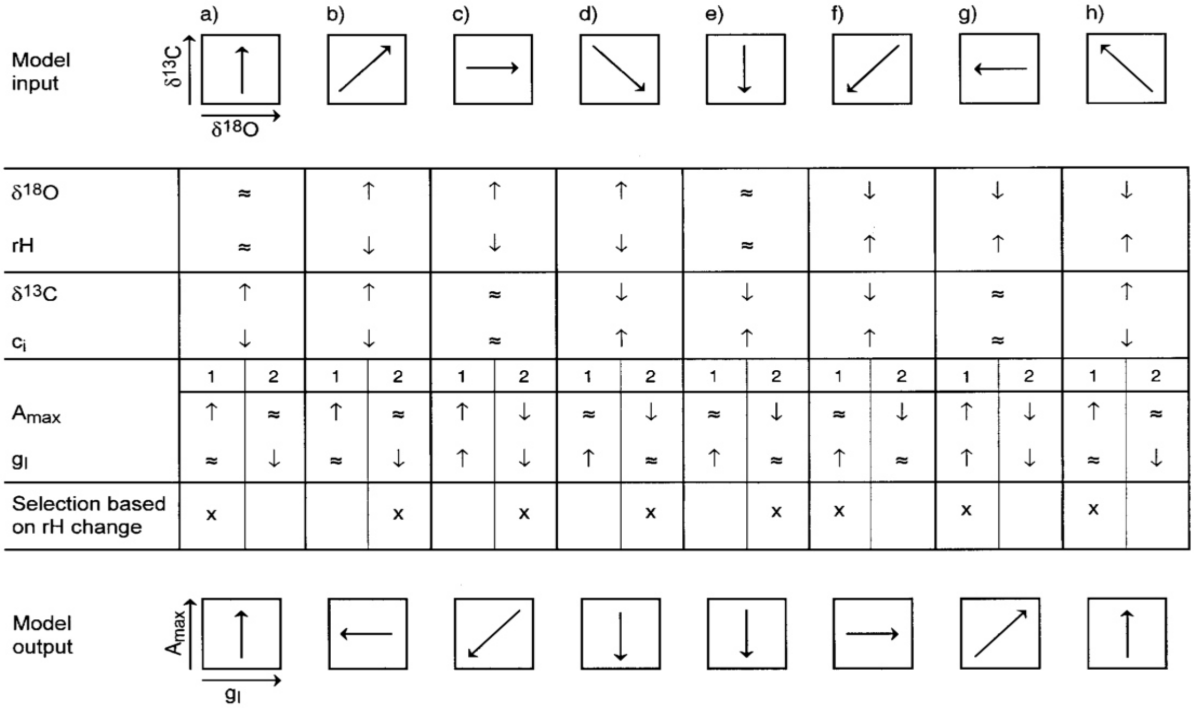
$$WUE = (c_a - c_i) / 1.6 = (c_a - c_a * (\Delta - a) / (b - a)) / 1.6 = c_a * (1 - (\Delta - a) / (b - a)) / 1.6$$
$$= c_a * ((b - a - \Delta + a) / (b - a)) / 1.6 = c_a * (b - \Delta) / (b - a) / 1.6 \tag{6}$$

(Altieri et al. 2015; Farquhar et al. 1982)

To link stable oxygen and carbon isotopes with stomatal conductance and photosynthetic capacity, Scheidegger et al. (2000) developed a conceptual model by estimating the intercellular CO_2 concentration (c_i) from $\delta^{13}C$ and the air humidity from $\delta^{18}O$. Air humidity is used due to the assumption that it is a relevant factor controlling stomatal conductance. In a first step the change in relative humidity (rH), the ratio between vapour pressures in the atmosphere and the intercellular spaces ($e_a / e_i \approx$ rH), is deducted. In the case of dry air, reduced rH, $\delta^{18}O$ in the leaf water increases. Secondly, $\delta^{13}C$ values explain changes in c_i. The third step includes the evaluation of the before found information and the selection of the A_{max} (photosynthetic activity) and g_1 (stomatal conductance). These assumptions need to be made because of the photosynthetic characteristics of plants: In the atmosphere carbon exists as ^{12}C, but also as ^{13}C. C_3 plants, including trees, prefer the lighter ^{12}C because of discrimination of Rubisco against the heavier ^{13}C. If the needed amount of ^{12}C is not available for photosynthesis, ^{13}C can also be used. There are mostly two cases where ^{13}C increases its enrichment in tissues due to photosynthesis:

1. Either, the environment is dry and the stomata is closed, so only the air that is already in the plant can be used for photosynthesis. First the trees deplete the ^{12}C before using the ^{13}C.
2. Or the stomata are open, but the photosynthesis rate is higher than normal. Then, the trees also use the ^{12}C first, but the air around the trees then gets a higher ratio of ^{13}C and due to fast photosynthesis and high need of carbon, trees also assimilate ^{13}C.

By analysing the ratio of ^{12}C and ^{13}C, it can be said that high $\delta^{13}C$ values show that the stomata was closed or that the photosynthesis rate was enormously high. To distinguish these two cases, the oxygen isotope has to be included in the analysis. Trees and plants are determined by the rH, and therefore water, which holds ^{18}O and ^{16}O. Usually, the lighter ^{16}O is transpired. But if transpiration rate is higher than normal, ^{18}O is also transpired and $\delta\ ^{18}O$ values get larger. The transpiration rate correlates with temperature and drought due to the rH. Combining the two stable isotope ratios one is able to get a meaningful statement about $A_{\max}$ and g_l (Scheidegger et al. 2000).



	a)		b)		c)		d)		e)		f)		g)		h)	
δ18O	≈		↑		↑		↑		≈		↓		↓		↓	
rH	≈		↓		↓		↓		≈		↑		↑		↑	
δ13C	↑		↑		≈		↓		↓		↓		≈		↑	
ci	↓		↓		≈		↑		↑		↑		≈		↓	
	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
Amax	↑	≈	↑	≈	↑	↓	≈	↓	≈	↓	≈	↓	↑	↓	↑	≈
gl	≈	↓	≈	↓	↑	↓	↑	≈	↑	≈	↑	≈	↑	↓	≈	↓
Selection based on rH change	x			x		x		x		x	x		x		x	

Fig. 5.1: Conceptual model of Scheidegger et al. (2000)

6 Results

6.1 Ring Width

The following section gives an overview of the tree-ring widths at the different sites. In a first part, the measurements at the NNF are visualised and described, in a second part, the samples form HRN and PPN, the two sites in eastern Nebraska, are presented. All the measurements presented are raw measurements, before standardisation was performed. The *Gleichläufigkeit* (Glk) and the crossdating index (CDI) for the measurements are noted below the figures.

6.1.1 Ring Widths NNF

The following Figures show parts of cores taken at the NNF to illustrate the measured ring width patterns of *P. ponderosa* and *J. virginiana* at the NNF. The black arrows show examples of outstanding years with narrow rings, which often represent pointer years.

Fig. 6.1: *Pinus ponderosa*, core NNF

Fig. 6.2: *Juniperus virginiana*, core NNF

NNF *P. ponderosa* sparse

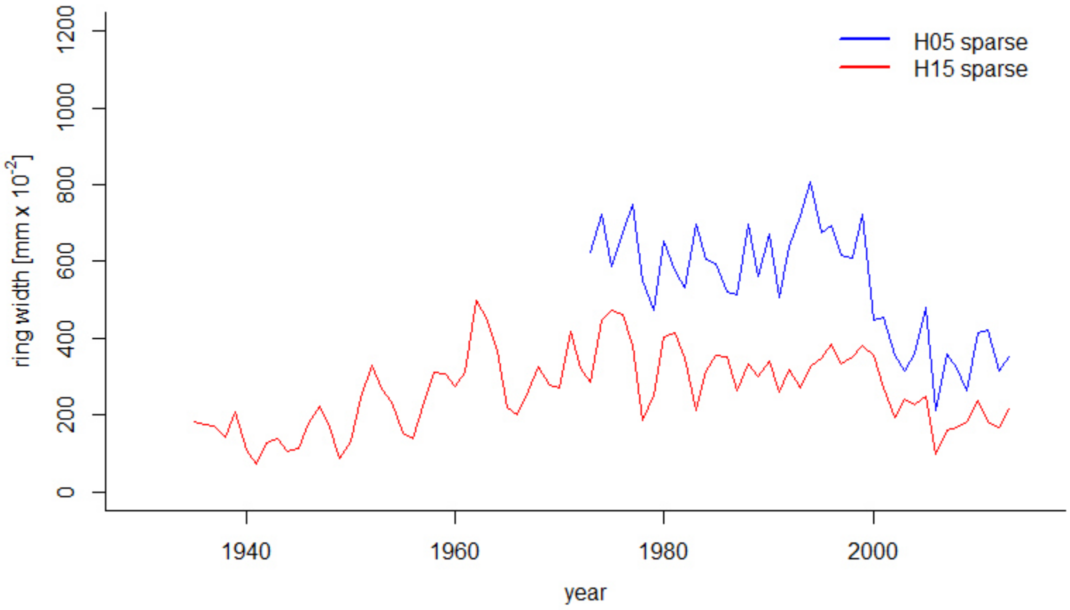


Fig. 6.3: NNF *P. ponderosa* sparse H05 and H15; Glk 58, CDI 23

Comparing the two sites where *P. ponderosa* in a sparse forest was sampled it is visible that the trees at sample site H05 are younger than the ones at H15. From 1979 they show a similar growth pattern whereby H05 shows a higher growth rate than H15. Some pointer years are clearly visible, as in 1987, 1988, 1989, 1990, 1991 and 2006.

NNF *P. ponderosa* mid

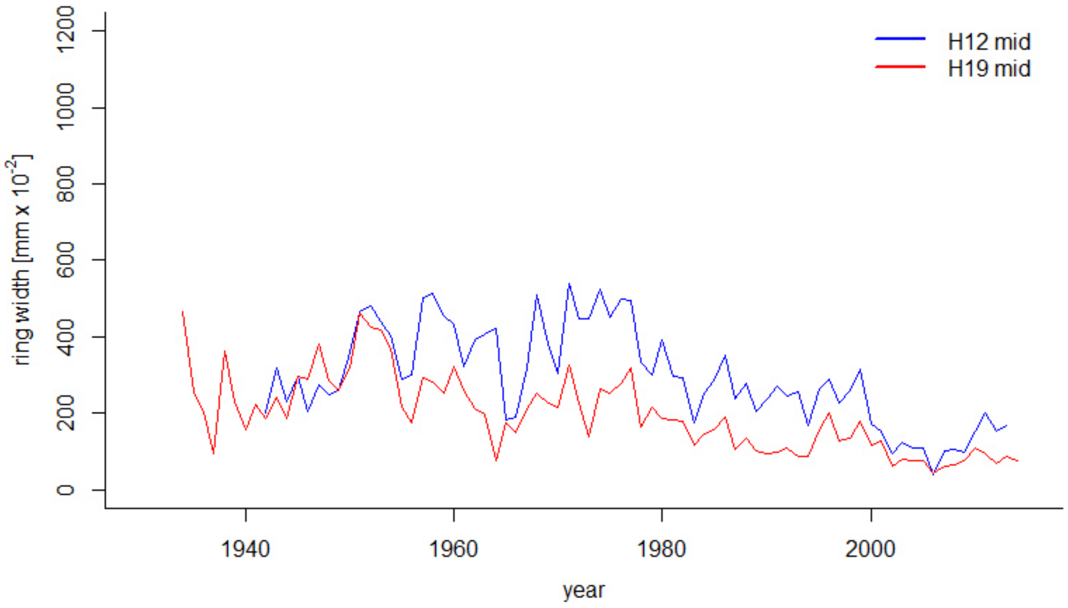


Fig. 6.4: NNF *P. ponderosa* mid H12 and H19; Glk 69***, CDI 39

Figure 6.4 shows the means of *P. ponderosa*'s tree-ring width in a mid density forest. The two chronologies seem to have a similar growth pattern. Pointer years in both curves are visible in 1971, 1983, 1986, 1987, 2002 and 2006. H12 shows a larger growth than H19, and both flatten off in the last 15 years.

NNF *P. ponderosa* dense

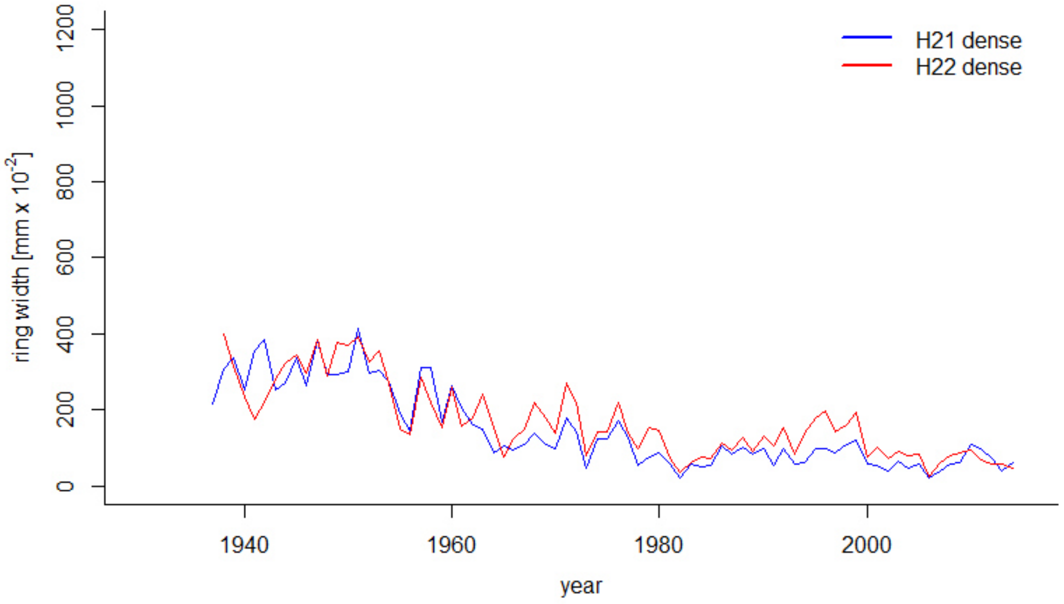


Fig. 6.5: NNF *P. ponderosa* dense H21 and H22; Glk 82***, CDI 87

The two curves of site H21 and H22 show a similar growth pattern apart from the first years. Their variability is small, both curves are complacent and they decline towards 2014. Clear pointer years can be emphasized in 1956, 1970, 1971, 1973, 1982, 1991, 1992, 2000 and 2006.

NNF *P. ponderosa* site chronologies

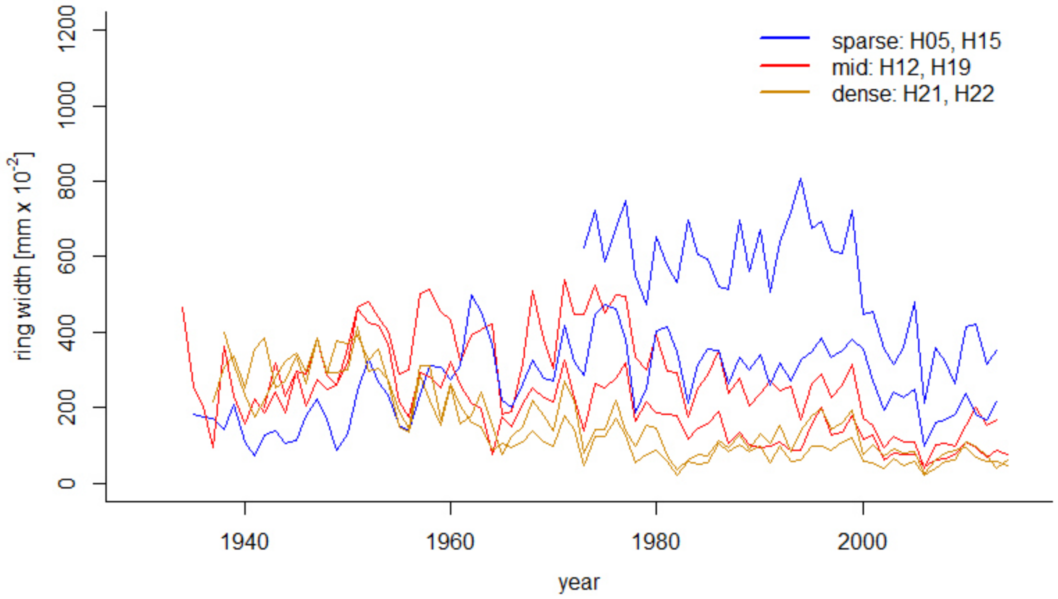


Fig. 6.6: NNF *P. ponderosa* site chronology; Glk 65**, CDI 34

Comparing the ring width of *P. ponderosa* sparse, mid and dense stands with each other, sparse shows the highest sensitivity and mid shows a higher sensitivity than dense. Dense stands were the most complacent. This fact can be attributed to the forest density and not to age, given that sparse is of similar age as mid and dense. Older trees were less sensitive than younger ones. *Pinus ponderosa* shows a clear pointer year in 2006 in all the different density sites. Also, in 1973 and 1982 clear pointer years are detected in *P. ponderosa* dense. The NOAA recorded recent droughts in the years 2002 and 2006; in these years pointer years are detectable in *P. ponderosa* and also *J. virginiana* (see following section). In general, all curves are well synchronised.

NNF *J. virginiana* sparse and mid

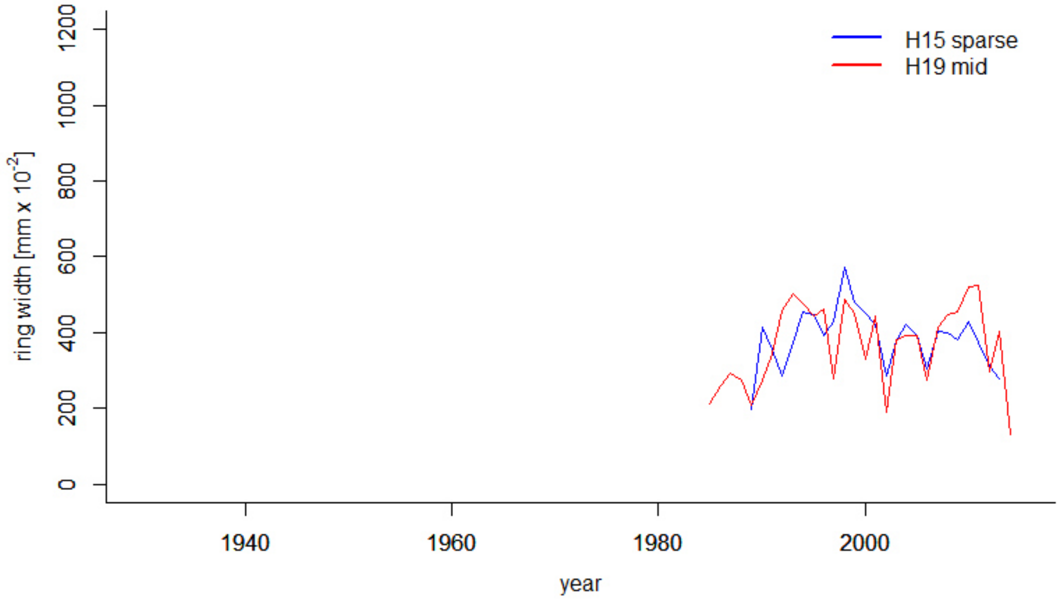


Fig. 6.7: NNF *J. virginiana* sparse H15 and mid H19; Glk 54, CDI 19

Figure 6.7 shows *J. virginiana* in the NNF at sparse and mid site together because no comparable sites were available and despite the different forest densities they show a similar growth pattern. The trees at site H19 established within a *P. ponderosa* forest whereas the trees at H15 grew in the open prairie. In both curves the years 2002 and 2006 stand out as pointer years.

NNF *J. virginiana* dense

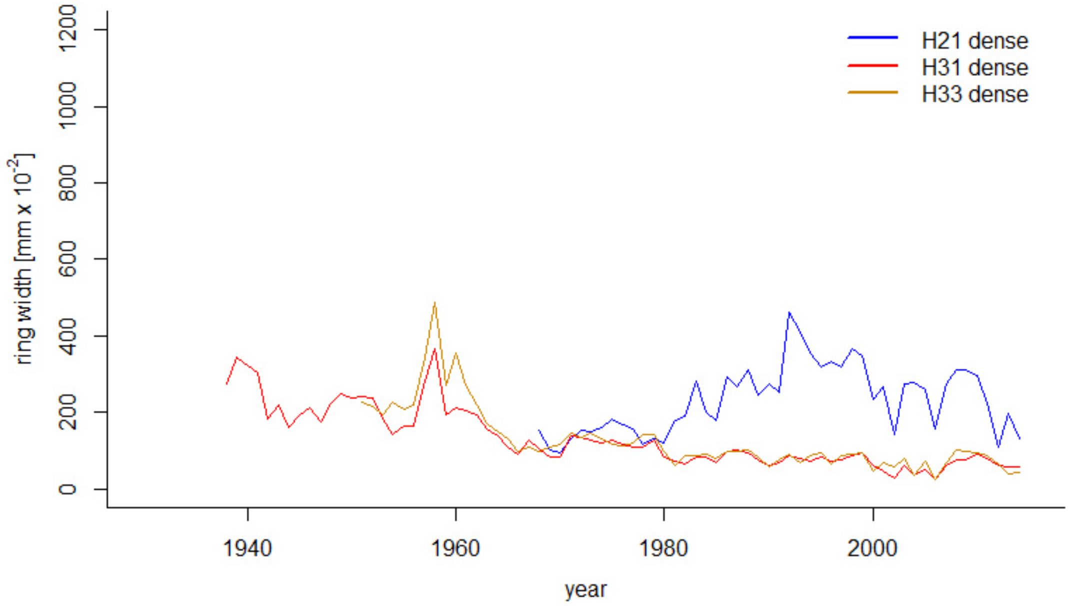


Fig. 6.8: NNF *J. virginiana* dense H21, H31 and H33; Glk 68**, CDI 20

The curves of site H31 and H33 show a high correlation and their variability is small. The variability and growth rates of H21 are much higher. H21 shares the pointer years in 2002 and 2006 with H31 and H33, but the growth rate at H21 is much higher and the growth pattern does not match perfectly with the other two curves. Furthermore the trees at site H21 are younger than the ones from the other two sites. The trees at site H21 are growing between *P. ponderosa* trees. Sites H31 and H33 are stands composed only of *J. virginiana*.

NNF *J. virginiana* site chronologies

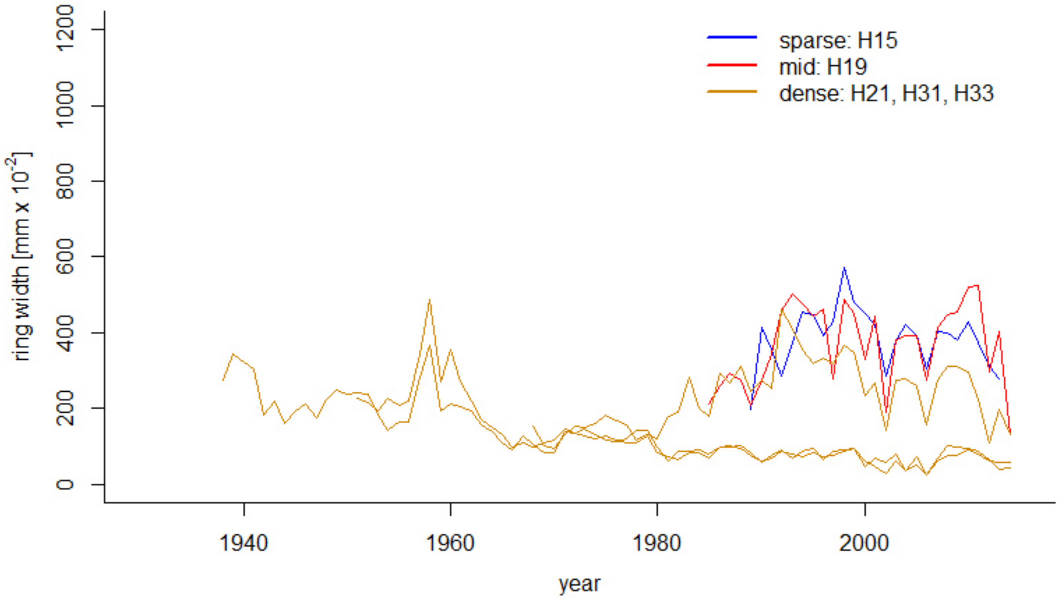


Fig. 6.9: NNF *J. virginiana* site chronology; Glk 54, CDI 17

The five sites with *J. virginiana* can be divided into two age groups. The older group is more complacent than the younger, but they have a quite similar growth pattern.

In general, *J. virginiana* does not show a clear relation between sensitivity and forest density as *P. ponderosa* does, but *J. virginiana* sparse and mid have a higher sensitivity than dense. *Juniperus virginiana* sparse and mid are younger than *J. virginiana* dense at plot H31 an H33. *Juniperus virginiana* sparse shows clear pointer years in and 1997, 2002, 2006 in which 2006 is the most pronounced one. *Juniperus virginiana* mid also shows these pointer years, but 2002 is more pronounced than 1997 and 2006. Plot H21, which is growing within a *P. ponderosa* stand, is similar to *J. virginiana* mid. The years 2002 and 2006 are also pointer years in *J. virginiana* dense, but less extremely narrow than in *J. virginiana* mid, sparse and in H21. In *J. virginiana* dense, the pointer year 1997 is not clearly visible. Overall, compared to *J. virginiana* sparse and mid, *J. virginiana* dense is complacent, as it was found in *P. ponderosa* stands.

Comparison NNF sparse

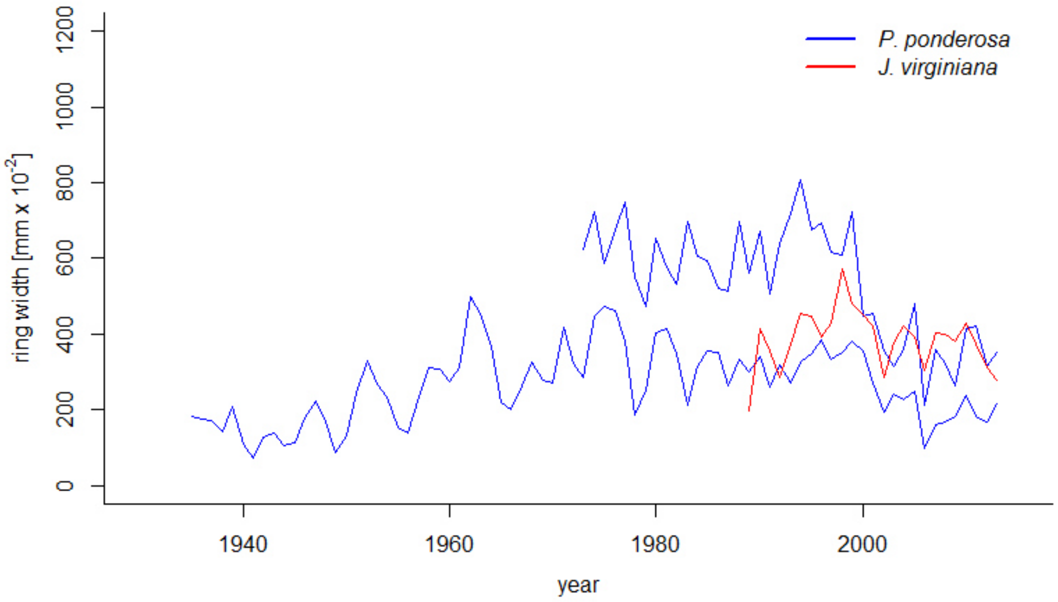


Fig. 6.10: Comparison NNF sparse

The comparison between the two species in a sparse forest indicates a difference in age. While the growth of the oldest *P. ponderosa* started in 1935, *J. virginiana* only starts to grow in 1989. It has to be taken into account that the first growth years of a tree usually are individual for each tree and cannot be used for exact comparison. Due to the relatively short lifetime of *J. virginiana*, no significant statements can be made about the variability of both species. *Pinus ponderosa* individually shows a relative high variability. Both species have 2006 as a clearly visible pointer year.

Comparison NNF mid

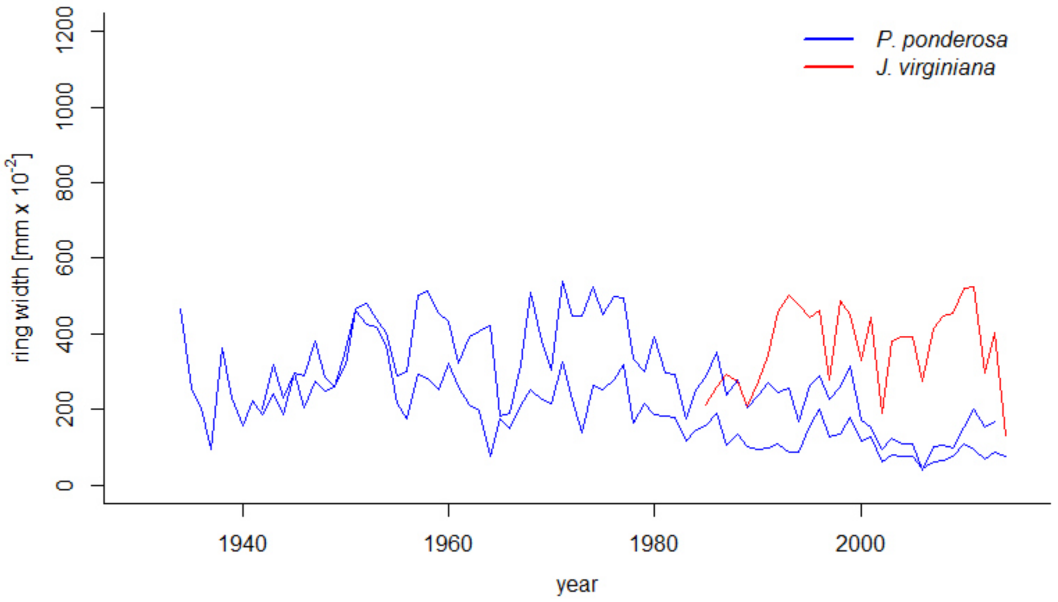


Fig. 6.11: Comparison NNF mid

In mid density stands, all trees of *J. virginiana* are younger than the *P. ponderosa*, as it is also the case at the sparse sites. As mentioned above, the first years of *J. virginiana* do not fit into the growth pattern of *P. ponderosa* due to the age trend. From 1996 on the two species show a highly correlating growth pattern whereby *J. virginiana* has a higher variability compared to *P. ponderosa*. Regarding the whole chronology of *P. ponderosa* it can be said that the variability was higher until 1978. Afterwards it flattens out. *J. virginiana* shows clearer pointer years than *P. ponderosa* but they are visible in both chronologies. The years 1997, 2002, 2006 and 2012 can be identified as pointer years.

Comparison NNF dense

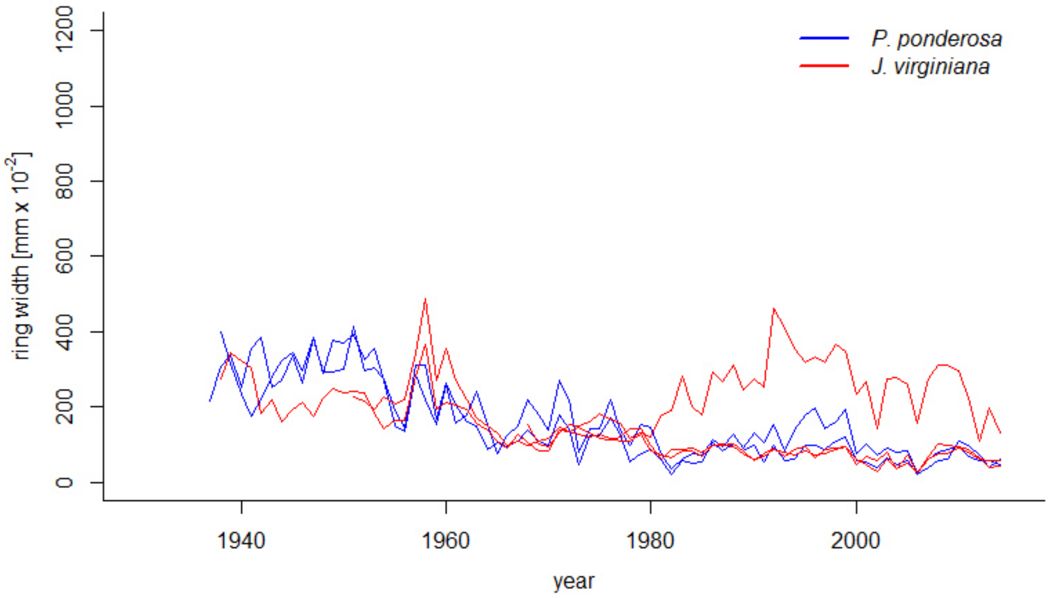


Fig. 6.12: Comparison NNF dense

In the first part of the chronology the two species in a dense forest show a different growth pattern while the second part correlates highly. In both species the variability is low, apart from one *J. virginiana* plot. This plot established between *P. ponderosa* trees. Pointer years do not stand out clearly. Comparing sparse, mid and dense forest among each other it can be determined that sparse and mid forests show a higher variability than dense forests.

6.1.2 Ring Widths HRN and PPN

The following Figures show parts of cores taken at HRN and PPN to illustrate the measured ring width patterns. Black arrows stand as an example for narrow rings, which often represent pointer years.

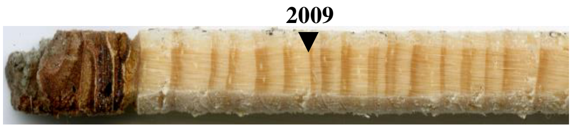


Fig. 6.13: *Pinus ponderosa*, core PPN

Fig. 6.14: *Juniperus virginiana*, core HRN

HRN *P. ponderosa* dense

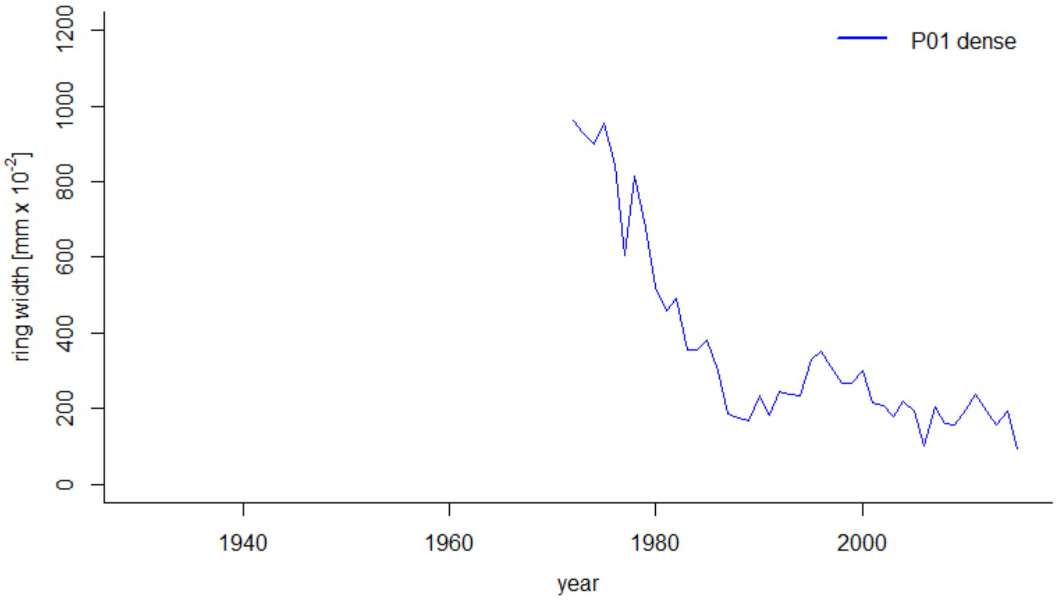


Fig. 6.15: HRN *P. ponderosa* dense

Plot P01 shows a clear age trend. Whereas in the first years the ring widths are very high and the trees seem to be very sensitive, they decrease towards the sampling date. Only one pointer year, in 2006, is visible. Unfortunately there is no comparable plot in eastern Nebraska, but further down this plot will be compared to sparse *P. ponderosa* plots at PPN.

HRN *J. virginiana* dense

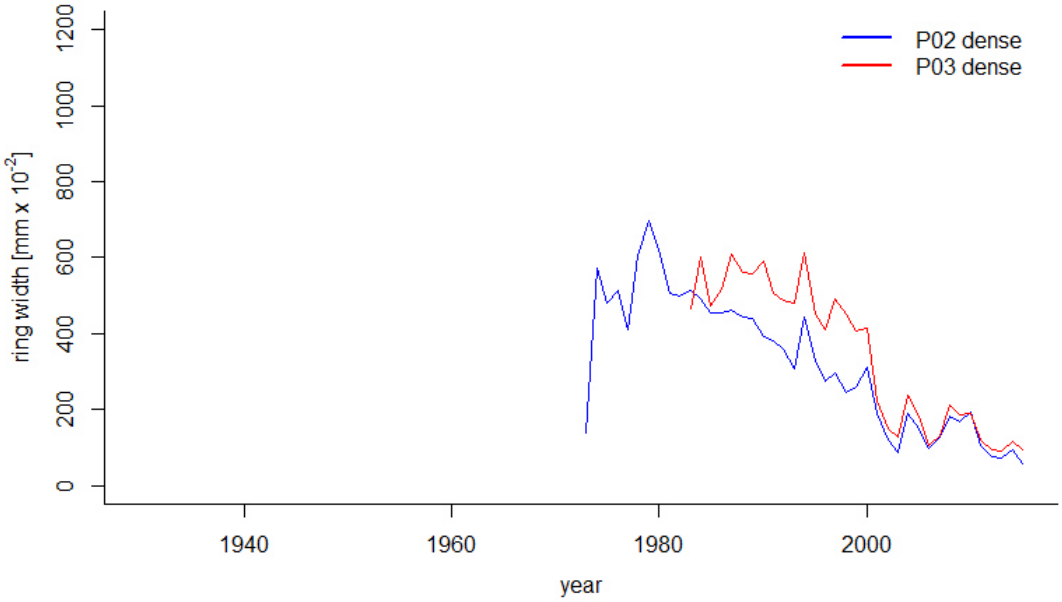


Fig. 6.16: HRN *J. virginiana* dense P02 and P03; Glk 62, CDI 27

Apart from the first years of growth, the trees at plot P02 and P03 show almost identical growth patterns. The sensitivity of the tree ring's widths is high, but decreases with increasing age. Pointer years are detectable in 1996, 2002, 2003 and 2006.

PPN *P. ponderosa* sparse

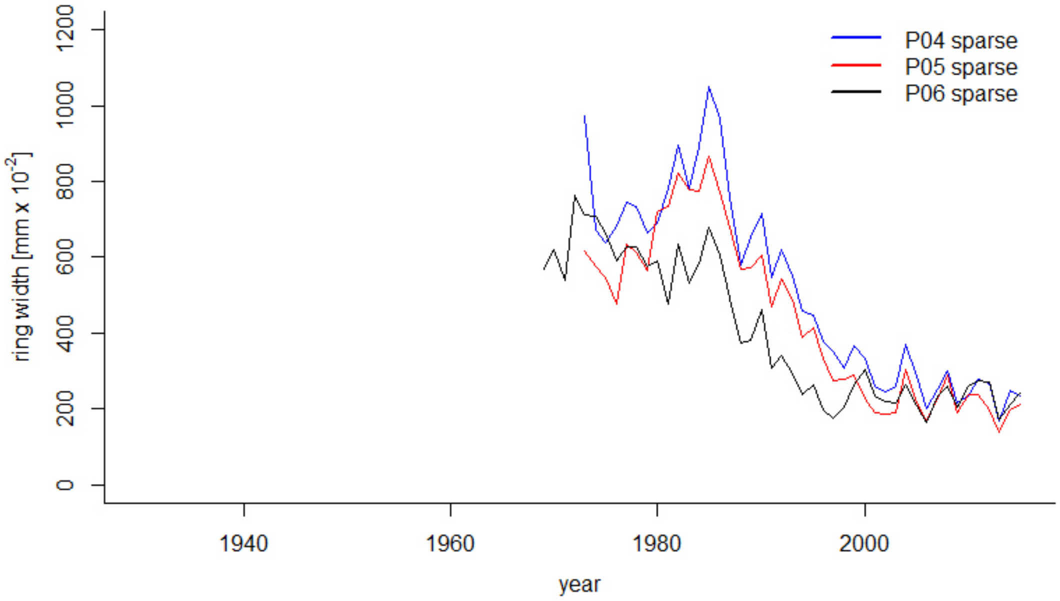


Fig. 6.17: PPN *P. ponderosa* sparse P04, P05 and P06; Glk 90***, CDI 88

Apart from the first years, the averages of P04, P05 and P06 show similar growth patterns. With increasing age, the sensitivity seems to decline and the growth patterns are getting more alike. After

2003 the growth is almost identical. No clear pointer years are visible, neither in the single tree series, nor in the means.

Comparison *P. ponderosa* HRN and PPN

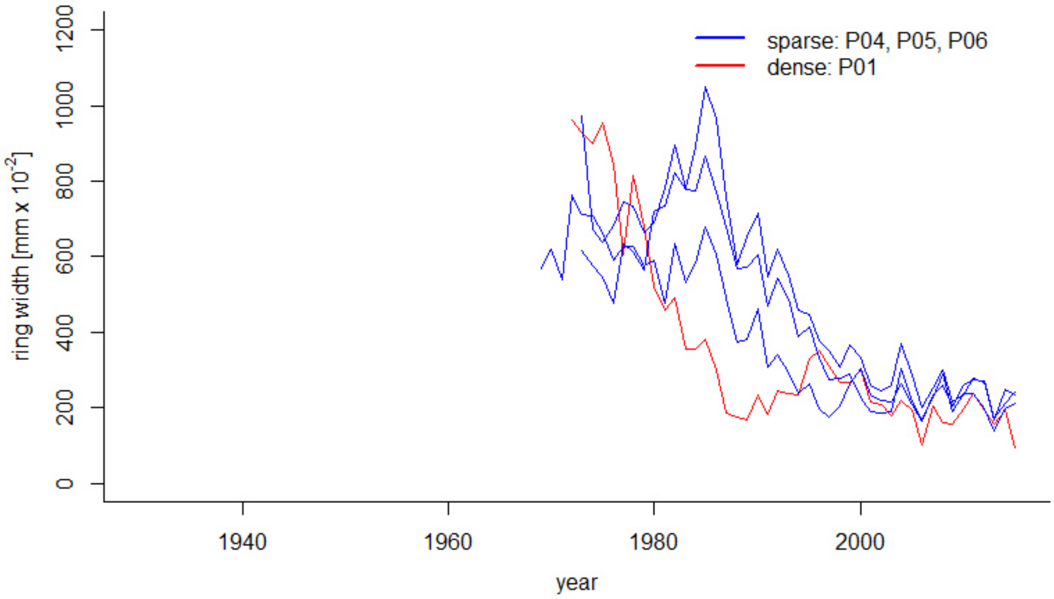


Fig. 6.18: HRN and PPN *P. ponderosa*; Glk 71**, CDI 24

Comparing the means of all *P. ponderosa* plots at HRN and PPN, a similar growth pattern can be found. In the first years, the trees at PPN (P04, P05 and P06) show a higher sensitivity over a longer time period than *P. ponderosa* at HRN (P01). At HRN, on the other side, the sensitivity is decreasing faster. From 1995 until the date of sampling, all the sites show a very resembling growth pattern even though plot P01 shows a higher stand density than the other plots.

6.2 Standardisation

Since correlations between tree-ring widths and climate have to be calculated to investigate the influence of the climate to the growth of the trees, the tree-ring widths need to be standardised. Otherwise, the broader rings of the first years of growth of the tree lead to wrong correlations, which results in not significant data which do not lead back to climate but to the biological trend of growth (Biondi & Qeadan 2008). The standardisation was done with all the measured samples, because afterwards correlations between climate and all of them were calculated. Figure 6.19 shows eleven samples of plot P01, representative for all samples, before and after the standardisation. The black lines indicate the tree-ring widths before the standardisation, the blue lines after standardisation.

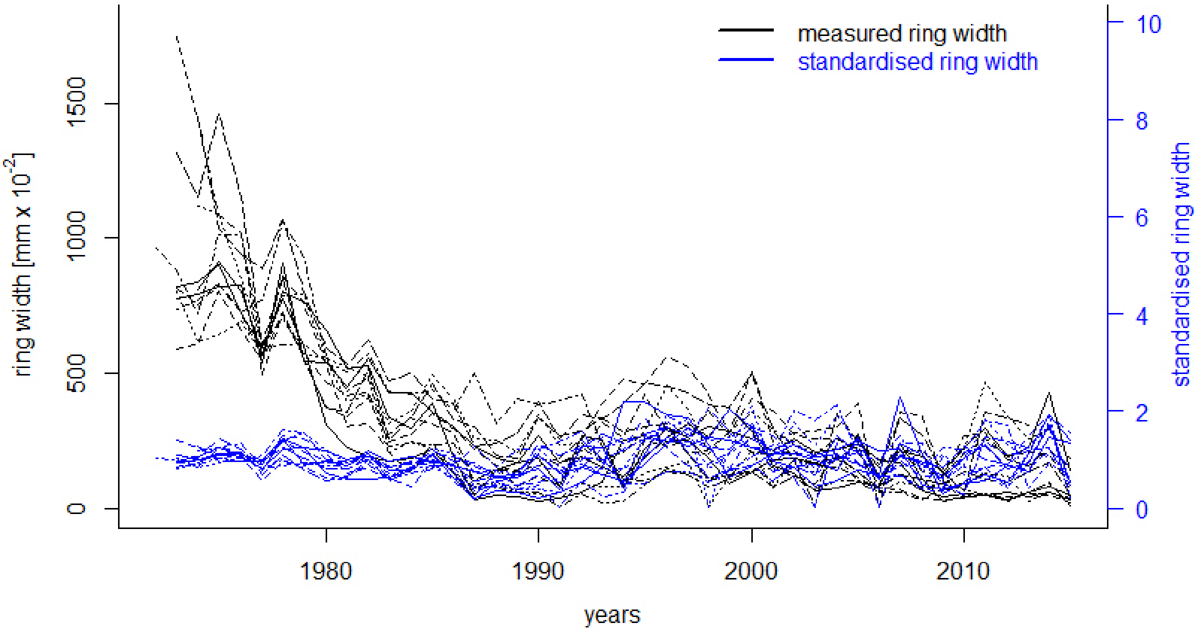


Fig. 6.19: Effect of standardisation

While the development of the measured ring widths shows a decrease, the standardised ring widths do not. So the higher values before standardisation, caused by the biological growth and age trend, are removed and the data is ready for the calculation of correlations.

6.3 Correlation Climate

Precipitation

The following section shows the results from the calculated correlations between tree-ring width and precipitation. First, the results of *P. ponderosa* are presented, followed by the calculations of *J. virginiana*. For all the presented tables the minuscule "p" stands for 'precipitation in the previous year', the capital letter "P" stands for 'precipitation in the actual year'. Precipitation data shows a melt season in January, February and March and a wet season in April, May and June when around 70 percent of precipitation occurs. July and August represent the dry season. In September and October no clear precipitation pattern is detectable, whereas precipitation in November and December mostly occurs in the form of snow (Eggenmeyer et al. 2006). Therefore the correlations were calculated using the means of each investigated time period.

6.3.1 Correlation Climate at the NNF

NNF *P. ponderosa*

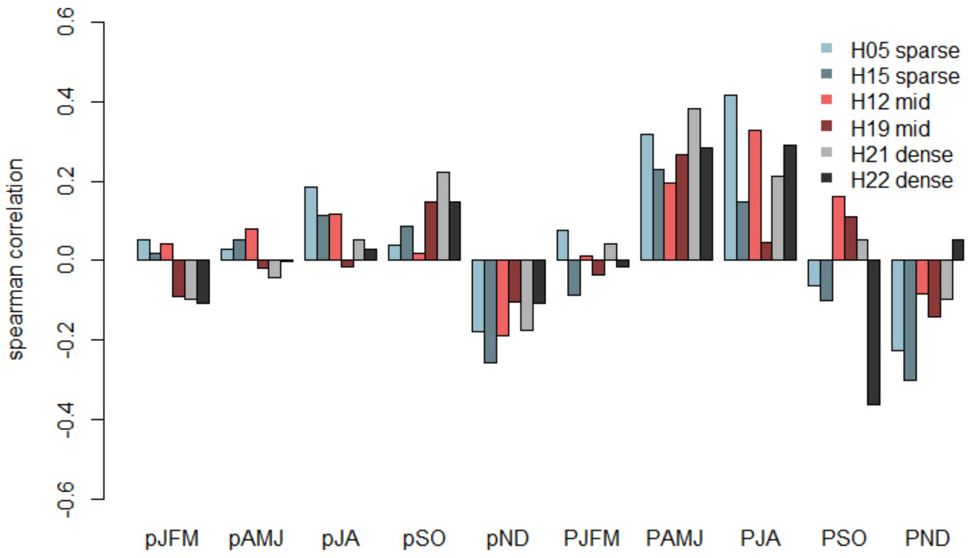


Fig. 6.20: NNF *P. ponderosa* correlation precipitation

Figure 6.20 and Table 6.1 show the results of the calculated correlations between precipitation and ring width of *P. ponderosa* in the NNF. The influence of the previous year precipitation on tree-ring widths is smaller than the influence of the actual year. All correlation values of the actual year are higher than the ones of the previous year. The previous as well as the actual year indicate a positive correlation between precipitation and ring width in June, August, September and October, whereas in November and December the correlations are negative for all stand densities. Even though values in November and December of the actual year show a significant negative correlation, they can be ignored because then tree-ring growth has already stopped for this year. At sparse sites significant values were found in November and December of the previous year at H15. At H05 no significant values for the previous year were found. In April, May, June, July, August, November and December of the actual year, significant values were calculated for H05 and in July, August, November and December for H15, respectively. For *P. ponderosa* at mid density sites, significant values were found in July, August, November and December at H12 of the actual year and in April, May, June, November and December for H19, respectively. At dense sites significant values were found in April, May and June for H21 in the actual year, and in April, May, June, July and August for H22. Comparing the three stand densities, in all of them significant correlation values were detected. They are either in the wet period April, May and June of the actual year or in the dry season in July and August of the actual year. Further, on the sparse plot H15 a significant value resulted in November and December of the previous year. No other plot showed significant values for the previous year. As a result the above seen pattern in Figure 6.20 can be affirmed by the correlations presented in the following Table 6.1.

Table 6.1: NNF *P. ponderosa* correlations precipitation

months	H05 sparse	H15 sparse	H12 mid	H19 mid	H21 dense	H22 dense
pJFM	0.054	0.019	0.043	-0.090	-0.098	-0.106
pAMJ	0.027	0.052	0.081	-0.018	-0.044	-0.002
pJA	0.184	0.113	0.117	-0.014	0.052	0.029
pSO	0.038	0.087	0.017	0.149	0.222	0.147
pND	-0.179	-0.258*	-0.188	-0.103	-0.176	-0.106
PJFM	0.077	-0.087	0.011	-0.037	0.043	-0.014
PAMJ	0.317*	0.23	0.197	0.267**	0.384***	0.285**
PJA	0.416**	0.148**	0.328**	0.047	0.213	0.292**
PSO	-0.062	-0.045	-0.056	0.161	0.111	0.054
PND	-0.362*	-0.227*	-0.303*	-0.083	-0.142	-0.098

Significance levels are shown as follows: $P < 0.05$*, $P < 0.01$**, $P < 0.001$***.

NNF *J. virginiana*

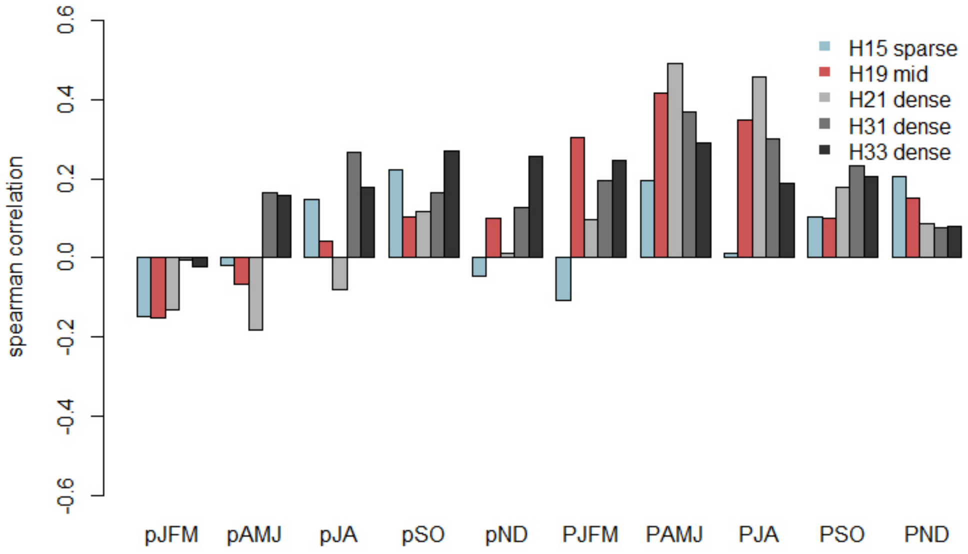


Fig. 6.21: NNF *J. virginiana* correlation precipitation

Investigating the correlation between tree-ring width of *J. virginiana* in the NNF and precipitation it is obvious that at almost all plots the precipitation is positively correlated with the tree-ring width. Only some values, mostly in the previous year, are negatively correlated, but none of them significantly. Precipitation influences ring growth favourably. The following Table 6.2 shows the significance of the calculated correlations. For the sparse plot H15, no significant values resulted from the calculations. At mid density stand H19 significant values were only found in April, May and June of the actual year. At the dense sites most significant values were found, not only of the actual year, but also of the previous year. Significant values were found in April, May and June of the actual year in all dense plots and in July and August of the actual year in H21 and H31. Further H31 shows significant values in July and August of the previous year and in September and October of the actual year. Moreover plot H33 shows significant values in September, October, November and December of the previous year and in January, February and March and as all the other dense plots in April, May and June in the actual year. Comparing the three stand densities, not in all of them significant values were detected. The sparse plot H15 did not show any significant values, whereas the mid plot H19 only showed one. In contrast, all dense plots showed more than one significant or even highly significant value. So, precipitation seems to highly influence the growth of *J. virginiana* in dense stands. Not only the precipitation of the actual year, but also the one of the previous year had an influence on the tree growth in dense stands.

Table 6.2: NNF *J. virginiana* correlation precipitation

months	H15 sparse	H19 mid	H21 dense	H31 dense	H33 dense
pJFM	-0.148	-0.151	-0.132	-0.006	-0.024
pAMJ	-0.019	-0.066	-0.183	0.165	0.157
pJA	0.149	0.042	-0.081	0.267*	0.178
pSO	0.224	0.104	0.118	0.164	0.270*
pND	-0.045	0.099	0.01	0.127	0.258*
PJFM	-0.109	0.306	0.096	0.197	0.248*
PAMJ	0.196	0.417*	0.492***	0.37***	0.292*
PJA	0.01	0.349	0.458***	0.302**	0.19
PSO	0.102	0.099	0.179	0.234*	0.204
PND	0.205	0.15	0.087	0.075	0.08

Significance levels are shown as follows: P < 0.05*, P < 0.01**, P < 0.001***.

Temperature

The following section shows the results from the calculated correlations between tree-ring width and temperature. First, the results of *P. ponderosa* are presented, followed by the calculations of *J. virginiana*. For all the following tables the minuscule "t" stands for temperature in the previous year, the capital letter "T" stands for temperature in the actual year. The analysis was conducted at the basis of months.

NNF *P. ponderosa*

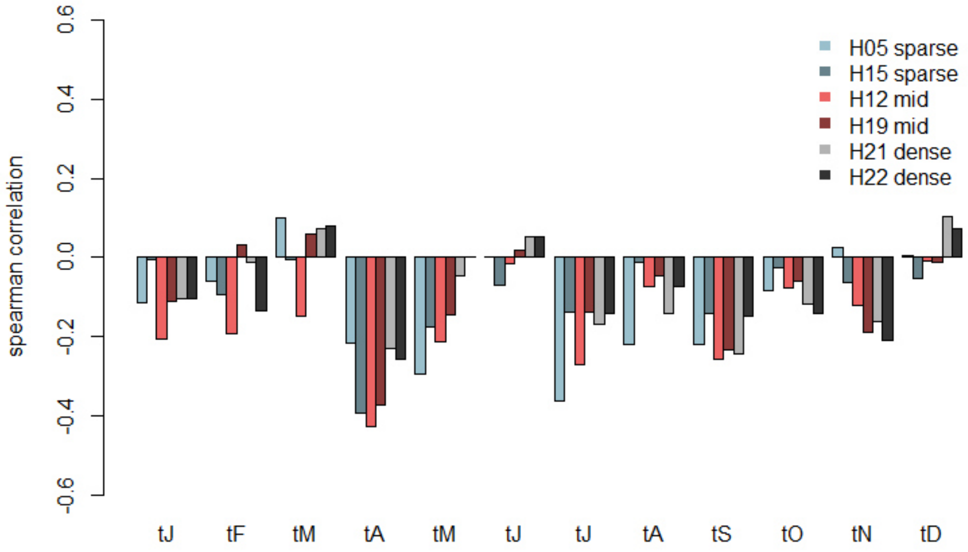


Fig. 6.22: NNF *P. ponderosa* correlation temperature previous year

Figure 6.22 shows the correlations between tree-ring width and temperature of the previous year at the *P. ponderosa* stands in the NNF. Temperature shows a negative correlation with tree-ring width. Temperature in April and July of the previous year highly influences tree-ring growth in a negative way.

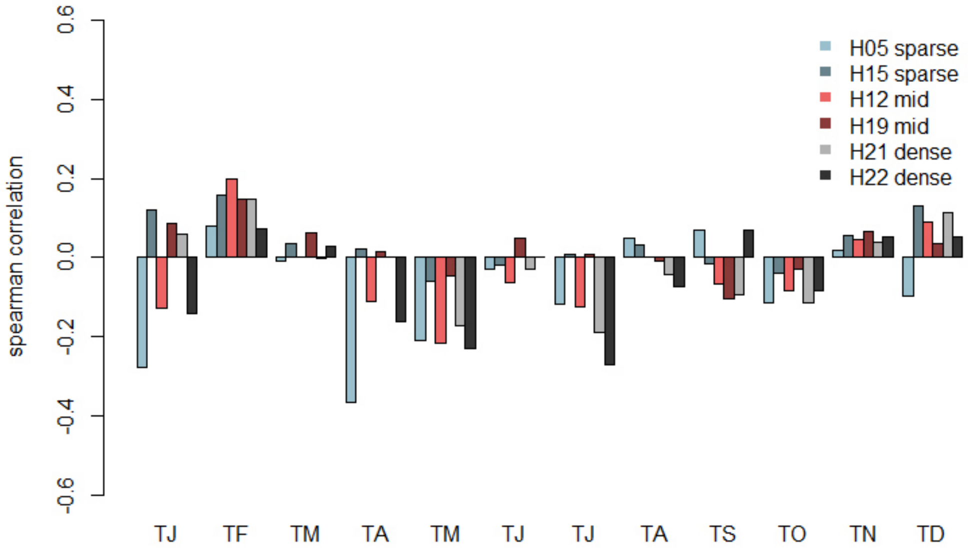


Fig. 6.23: NNF *P. ponderosa* correlation temperature actual year

The correlations between tree-ring width and temperature of the actual year are slightly different from the correlations of the previous year. There are more values correlating positively, but only three of them are significant. At H05 significant values were found in July of the previous year and in April of the actual year, whereas at H15 significant values were only found in April of the previous year. At mid density stands, H12 and H19, significant values for both were calculated in April and September of the previous year and in addition for H12 in July of the previous year. The dense plots H21 and H22 also show significant values in April of the previous year and H21 in September as well. In addition the ring widths of plot H22 is significantly correlating with temperature in May and July of the actual year. Summing up, temperature in the previous year is highly negatively correlated and temperature of the actual year is mainly negatively correlated but not as significant as in the previous year.

Table 6.3: NNF *P. ponderosa* correlation temperature

month	H05 sparse	H15 sparse	H12 mid	H19 mid	H21 dense	H22 dense
tjanuary	-0.113	-0.006	-0.205	-0.111	-0.104	-0.105
tfebruary	-0.06	-0.093	-0.194	0.031	-0.011	-0.136
tmarch	0.099	-0.004	-0.148	0.059	0.074	0.081
tapril	-0.218	-0.392***	-0.428***	-0.373***	-0.231*	-0.258*
tmay	-0.294	-0.177	-0.212	-0.144	-0.046	0
tjune	0	-0.07	-0.017	0.019	0.054	0.051
tjuly	-0.362*	-0.139	-0.271*	-0.138	-0.17	-0.142
taugust	-0.22	-0.012	-0.073	-0.047	-0.143	-0.072
tseptember	-0.219	-0.142	-0.257*	-0.233*	-0.245*	-0.148
toctober	-0.084	-0.027	-0.077	-0.061	-0.118	-0.14
tnovember	0.024	-0.064	-0.122	-0.188	-0.163	-0.211
tdecember	0.004	-0.054	-0.008	-0.013	0.103	0.072
Tjanuary	-0.277	0.12	-0.127	0.086	0.058	-0.141
Tfebruary	0.08	0.159	0.2	0.148	0.148	0.074
Tmarch	-0.009	0.037	0.003	0.061	-0.003	0.03
Tapril	-0.368*	0.022	-0.112	0.016	0.001	-0.162
Tmay	-0.211	-0.059	-0.215	-0.047	-0.171	-0.231*
Tjune	-0.029	-0.02	-0.062	0.048	-0.03	0.002
Tjuly	-0.118	0.009	-0.125	0.009	-0.19	-0.27*
Taugust	0.05	0.033	0.001	-0.009	-0.044	-0.075
Tseptember	0.069	-0.015	-0.067	-0.103	-0.095	0.07
Toctober	-0.114	-0.041	-0.083	-0.029	-0.114	-0.085
Tnovember	0.02	0.055	0.047	0.067	0.039	0.053
Tdecember	-0.098	0.131	0.09	0.035	0.115	0.052

Significance levels are shown as follows: $P < 0.05$*, $P < 0.01$**, $P < 0.001$***.

NNF *J. virginiana*

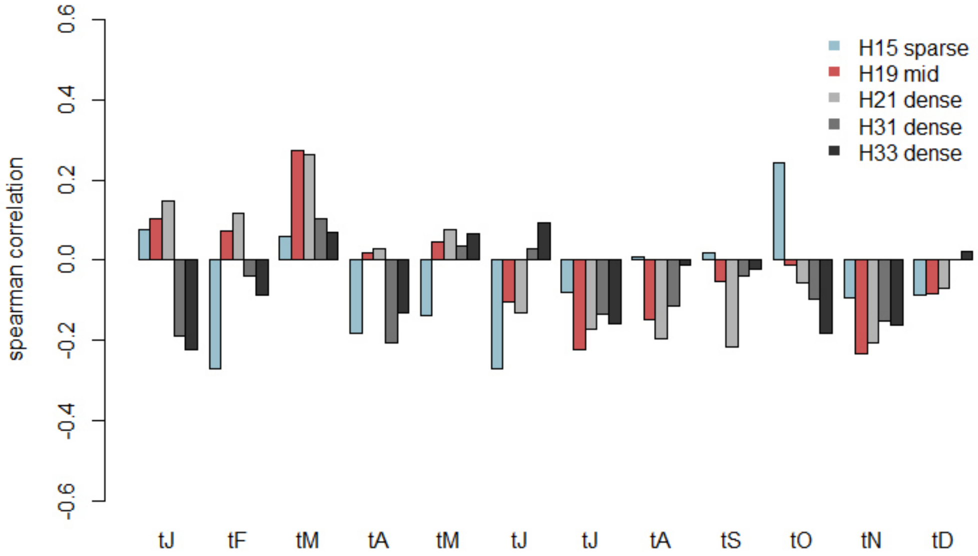


Fig. 6.24: NNF *J. virginiana* correlation temperature previous year

Figure 6.24 shows the correlations between tree-ring width and temperature of the previous year at the *J. virginiana* stands in the NNF. Temperature in the previous year mostly shows a negative correlation with tree-ring width with some exceptions which are not significant. None of the values for the previous year correlate significantly.

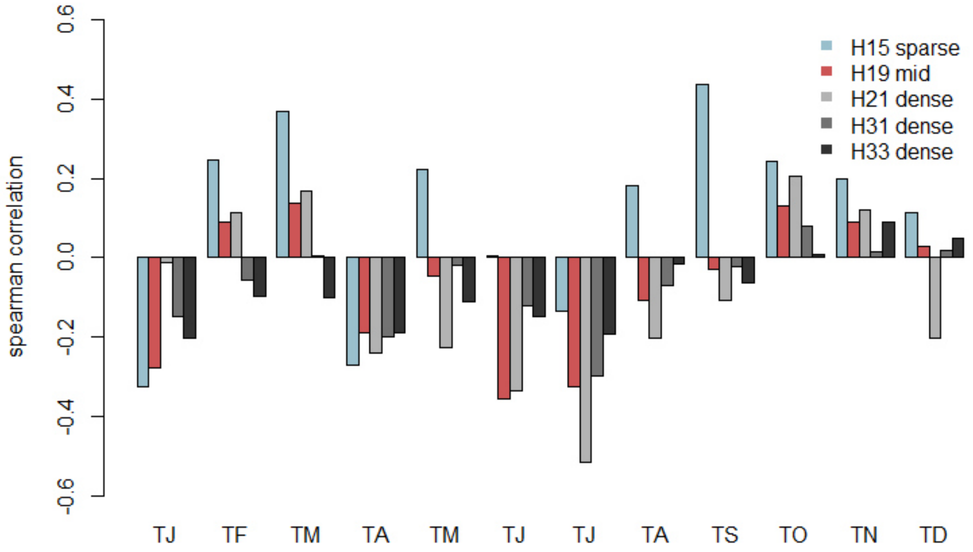


Fig. 6.25: NNF *J. virginiana* correlation temperature actual year

Temperature in the actual year influences the tree-ring growth also rather negatively, but depends on the stand densities. The correlations are negative, mostly at dense sites, whereas at sparse and mid sites more positive correlations are attributed. Overall the explanatory power is low because only three values are significant: in the actual year in September at H15, in June and July at H21 and in July at H31.

Table 6.4: NNF *J. virginiana* correlation temperature

month	H15 sparse	H19 mid	H21 dense	H31 dense	H33 dense
tjanuary	0.075	0.104	0.147	-0.191	-0.223
tfebruary	-0.272	0.073	0.118	-0.041	-0.087
tmarch	0.06	0.274	0.265	0.104	0.071
tapril	-0.184	0.017	0.029	-0.206	-0.132
tmay	-0.137	0.047	0.075	0.035	0.066
tjune	-0.27	-0.105	-0.133	0.029	0.092
tjuly	-0.08	-0.225	-0.172	-0.135	-0.158
taugust	0.008	-0.148	-0.195	-0.116	-0.012
tseptember	0.018	-0.053	-0.217	-0.038	-0.021
toctober	0.244	-0.012	-0.057	-0.098	-0.184
tnovember	-0.095	-0.235	-0.205	-0.151	-0.162
tdecember	-0.088	-0.085	-0.069	0.003	0.021
Tjanuary	-0.324	-0.279	-0.011	-0.15	-0.204
Tfebruary	0.248	0.09	0.114	-0.058	-0.099
Tmarch	0.369	0.136	0.168	0.005	-0.102
Tapril	-0.271	-0.191	-0.24	-0.198	-0.188
Tmay	0.222	-0.046	-0.228	-0.019	-0.11
Tjune	0.004	-0.356	-0.337*	-0.12	-0.148
Tjuly	-0.136	-0.324	-0.517***	-0.297**	-0.192
Taugust	0.182	-0.106	-0.202	-0.069	-0.016
Tseptember	0.436*	-0.029	-0.106	-0.024	-0.065
Toctober	0.242	0.131	0.205	0.079	0.008
Tnovember	0.2	0.089	0.122	0.015	0.091
Tdecember	0.113	0.028	-0.202	0.018	0.05

Significance levels are shown as follows: $P < 0.05$*, $P < 0.01$**, $P < 0.001$***.

6.3.2 Correlation Climate at HRN

Precipitation

HRN *P. ponderosa*

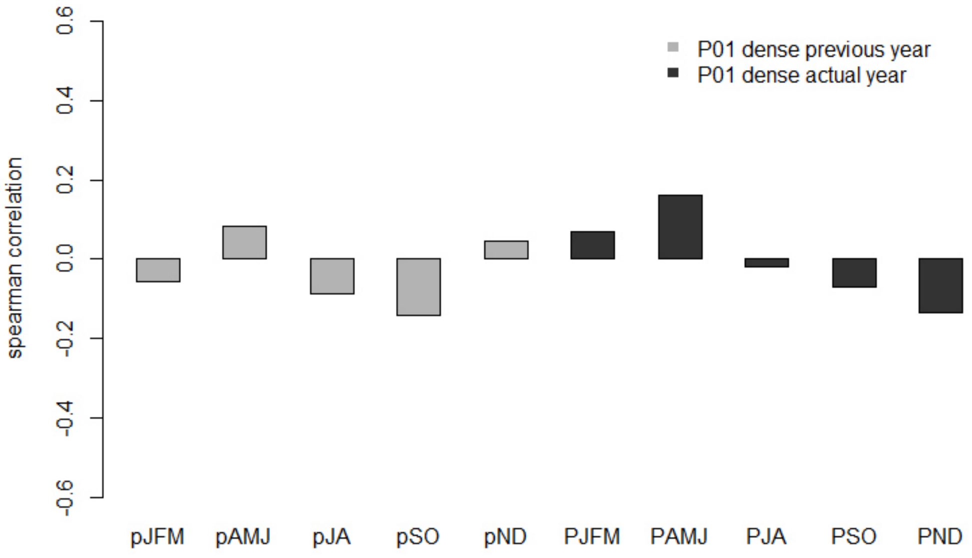


Fig. 6.26: HRN *P. ponderosa* correlation precipitation

Figure 6.26 shows the correlations between tree-ring width and precipitation of the previous and actual year of *P. ponderosa* at HRN. The correlations are low and no significant values were found. Precipitation has only little influence on *P. ponderosa*'s tree-ring width at HRN.

Table 6.5: HRN *P. ponderosa* correlation precipitation

months	P01
pJFM	-0.055
pAMJ	0.082
pJA	-0.088
pSO	-0.141
pND	0.044
PJFM	0.068
PAMJ	0.163
PJA	-0.020
PSO	-0.069
PND	-0.134

Significance levels are shown as follows: $P < 0.05^*$, $P < 0.01^{**}$, $P < 0.001^{***}$.

HRN *J. virginiana*

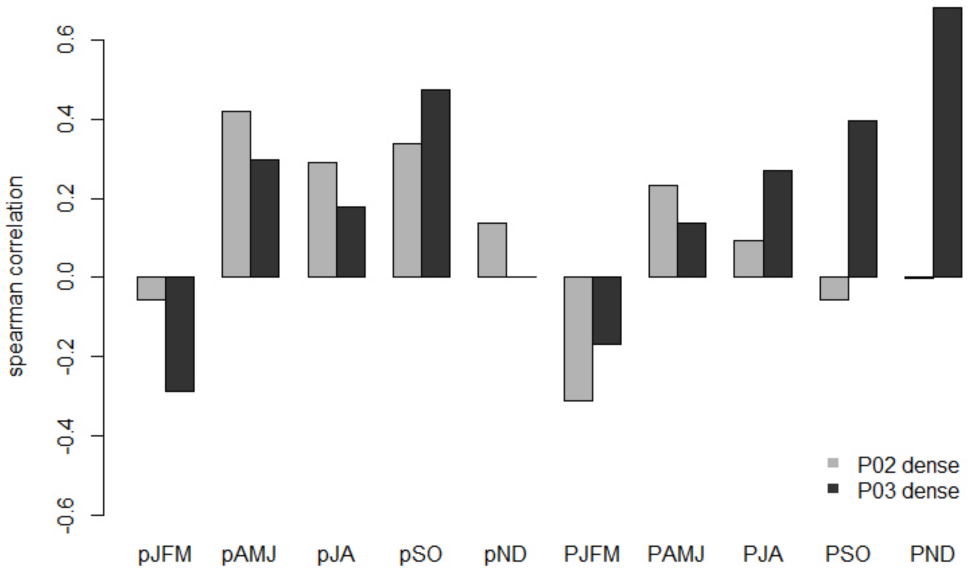


Fig. 6.27: HRN *J. virginiana* correlation precipitation

Figure 6.27 shows the correlations between tree-ring width and precipitation of the previous and actual year of *J. virginiana* at HRN. The correlations are mostly positive apart from January, February and March of the previous and the actual year at both plots and of P02 in September and October of the actual year; but only P02 in January, February and March of the actual year is significantly correlated. Other significant values can be detected in September and October of the previous year at both plots, and in September, October and November of the actual year. It is noteworthy to compare *J. virginiana* with *P. ponderosa* at HRN. Between *P. ponderosa* and precipitation no significant values were found at HRN, whereas *J. virginiana* showed some significant and verifiable values.

Table 6.6: HRN *J. virginiana* correlation precipitation

months	P02	P03
pJFM	-0.055	-0.287
pAMJ	0.421**	0.298
pJA	0.290	0.178
pSO	0.337*	0.474**
pND	0.136	0.000
PJFM	-0.313*	-0.169
PAMJ	0.234	0.136
PJA	0.094	0.271
PSO	-0.056	0.397*
PND	-0.001	0.683***

Significance levels are shown as follows: $P < 0.05$*, $P < 0.01$**, $P < 0.001$***.

Temperature

HRN *P. ponderosa*

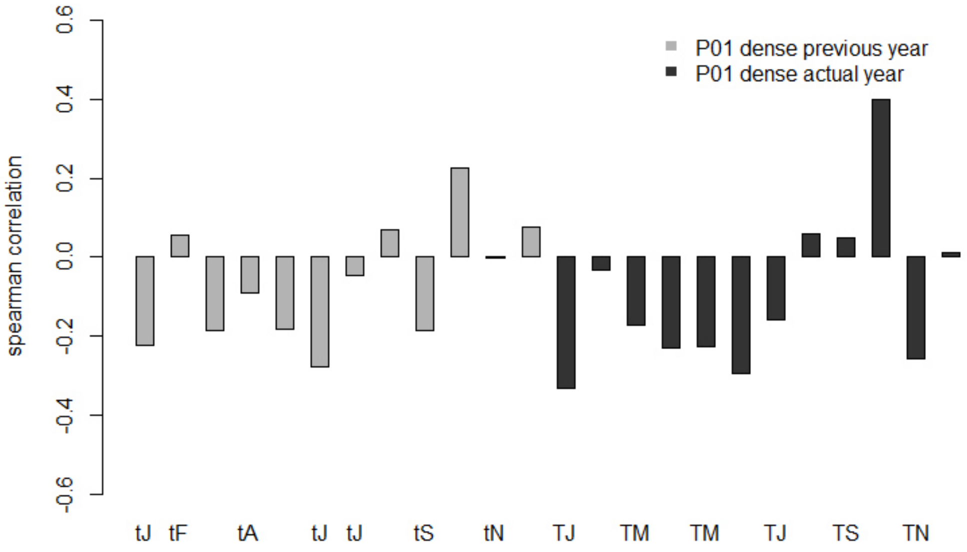


Fig. 6.28: HRN *P. ponderosa* correlation temperature previous and actual year

Figure 6.28 shows the correlations between temperature and tree-ring width at the *P. ponderosa* plot at HRN for the previous and the actual year. Predominantly the correlation is negative and only a few significant values were found as for January and October of the actual year.

Table 6.7: HRN *P. ponderosa* correlation temperature

Previous year		Actual year	
month	P01	month	P01
tjanuary	-0.225	Tjanuary	-0.334*
tfebruary	0.057	Tfebruary	-0.032
tmarch	-0.187	Tmarch	-0.171
tapril	-0.091	Tapril	-0.231
tmay	-0.184	Tmay	-0.226
tjune	-0.278	Tjune	-0.295
tjuly	-0.046	Tjuly	-0.159
taugust	0.069	Taugust	0.060
tseptember	-0.187	Tseptember	0.049
toctober	0.225	Toctober	0.399**
tnovember	-0.002	Tnovember	-0.256
tdecember	0.075	Tdecember	0.011

Significance levels are shown as follows: $P < 0.05$*, $P < 0.01$**, $P < 0.001$***.

HRN *J. virginiana*

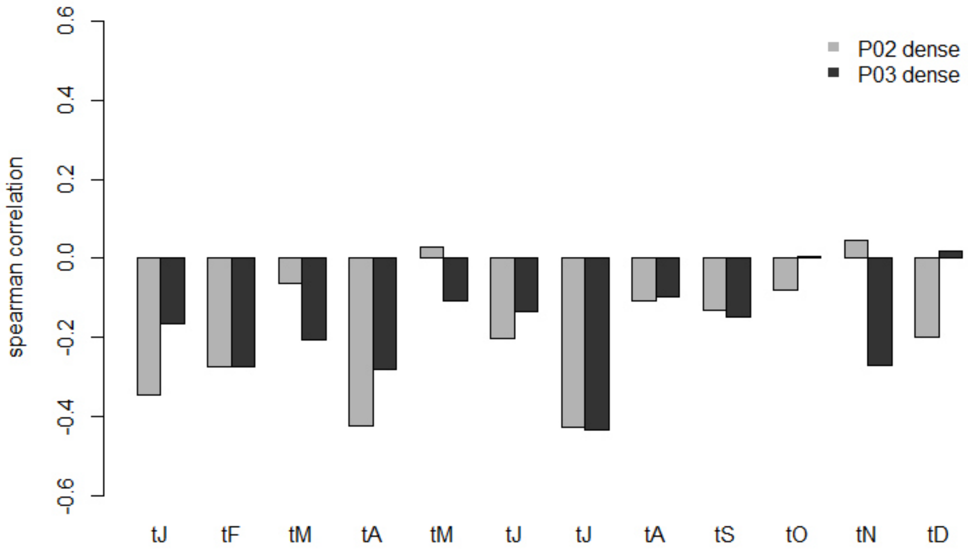


Fig. 6.29: HRN *J. virginiana* correlation temperature previous year

The influence of temperature of the previous year on *J. virginiana* at HRN appears negative. In regard to the significance, this can be confirmed. Significant values were found in January and April at P02 and in July for P02 and P03; all were negative.

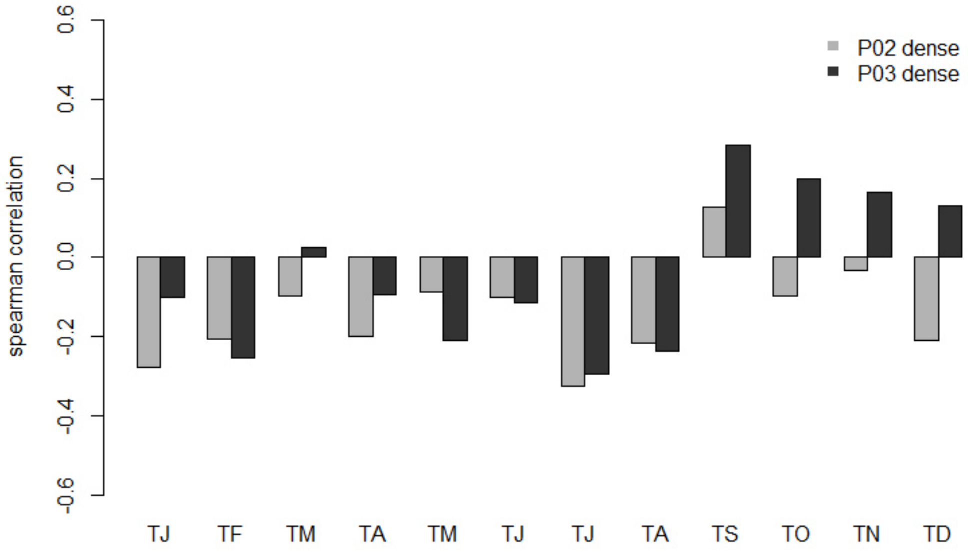


Fig. 6.30: HRN *J. virginiana* correlation temperature actual year

The correlations of the actual years are less pronounced compared to the correlations of the previous year. Only one significant value was found; namely at P02 in July.

Table 6.8: HRN *J. virginiana* correlation temperature

Previous year			Actual year		
month	P02	P03	month	P02	P03
tjanuary	-0.347*	-0.164	Tjanuary	-0.277	-0.102
tfebruary	-0.274	-0.276	Tfebruary	-0.205	-0.254
tmarch	-0.065	-0.205	Tmarch	-0.098	0.024
tapril	-0.426**	-0.283	Tapril	-0.201	-0.095
tmay	0.027	-0.108	Tmay	-0.086	-0.209
tjune	-0.202	-0.136	Tjune	-0.100	-0.115
tjuly	-0.427**	-0.434*	Tjuly	-0.327*	-0.295
taugust	-0.106	-0.096	Taugust	-0.215	-0.236
tseptember	-0.130	-0.147	Tseptember	0.127	0.285
toctober	-0.081	0.006	Toctober	-0.099	0.198
tnovember	0.044	-0.270	Tnovember	-0.031	0.165
tdecember	-0.198	0.018	Tdecember	-0.211	0.131

6.3.3 Correlation Climate at PPN

Precipitation

PPN *P. ponderosa*

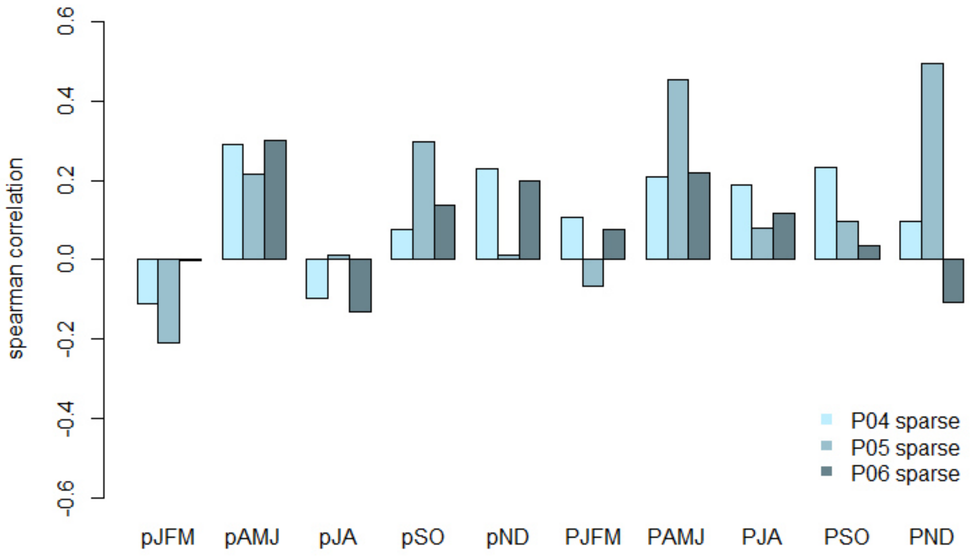


Fig. 6.31: PPN *P. ponderosa* correlation precipitation previous and actual year

Figure 6.31 shows the correlations between tree-ring width and precipitation at *P. ponderosa* plots at PPN. In most months the correlation is positive apart from some exceptions, which are not significant. Significant correlations only can be found at P05 in April, May, June, November and December of the actual year and at P06 in April, May and June of the previous year.

Table 6.9: PPN *P. ponderosa* correlation precipitation

months	P04	P05	P06
pJFM	-0.111	-0.210	-0.003
pAMJ	0.292	0.215	0.301*
pJA	-0.097	0.010	-0.131
pSO	0.077	0.296	0.138
pND	0.229	0.010	0.200
PJFM	0.107	-0.067	0.077
PAMJ	0.209	0.453**	0.219
PJA	0.189	0.081	0.118
PSO	0.233	0.096	0.036
PND	0.098	0.494***	-0.106

Significance levels are shown as follows: $P < 0.05$*, $P < 0.01$**, $P < 0.001$***.

Temperature

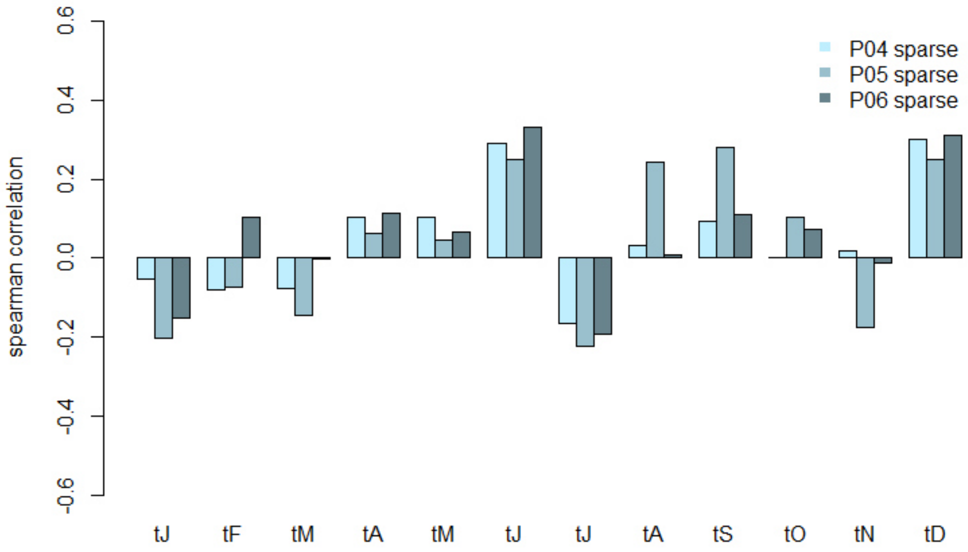


Fig. 6.32: PPN *P. ponderosa* correlation temperature previous year

Temperature of the previous year influences tree-ring growth positively and negatively but only positive values at P04 in December, at P05 in September and at P06 in June and December are significant.

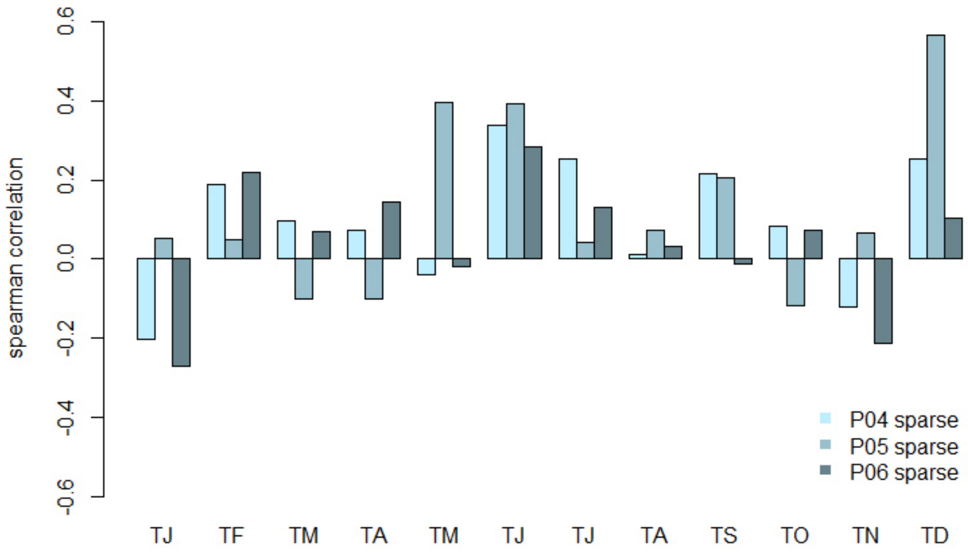


Fig. 6.33: PPN *P. ponderosa* correlation temperature actual year

Temperature in the actual year has a different influence on tree-ring widths than temperature of the previous year. Significant values were found at P04 in June and at P05 in May, June and December. The significance level of these values is almost always higher than in the previous year.

Table 6.10: PPN *P. ponderosa* correlation temperature

Previous year				Actual year			
month	P04	P05	P06	month	P04	P05	P06
tjanuary	-0.052	-0.203	-0.152	Tjanuary	-0.202	0.053	-0.270
tfebruary	-0.080	-0.073	0.102	Tfebruary	0.189	0.050	0.219
tmarch	-0.076	-0.145	-0.003	Tmarch	0.097	-0.102	0.068
tapril	0.102	0.063	0.115	Tapril	0.073	-0.101	0.146
tmay	0.103	0.046	0.066	Tmay	-0.038	0.395**	-0.020
tjune	0.292	0.251	0.331*	Tjune	0.337*	0.393**	0.283
tjuly	-0.167	-0.225	-0.192	Tjuly	0.254	0.041	0.131
taugust	0.031	0.243	0.009	Taugust	0.010	0.073	0.033
tseptember	0.094	0.279*	0.111	Tseptember	0.215	0.206	-0.013
toctober	-0.000	0.103	0.073	Toctober	0.083	-0.119	0.073
tnovember	0.019	-0.177	-0.011	Tnovember	-0.122	0.066	-0.213
tdecember	0.301*	0.250	0.312*	Tdecember	0.255	0.566***	0.102

Significance levels are shown as follows: $P < 0.05$*, $P < 0.01$**, $P < 0.001$***.

In general, for all sample areas, precipitation of the previous year seems to have less influence than precipitation of the actual year. For the NNF the most significant values were found in April, May, June, July and August of the actual year. All of them showed a positive correlation between tree-ring width and precipitation. April, May and July represent the wet season, whereas July and August stand for the dry season. The responses of *P. ponderosa* were less pronounced compared to *J. virginiana*. At HRN no correlations for *P. ponderosa* were found, but for *J. virginiana* significant values were found in the previous as well as in the actual year, but mostly not in the same months as it was the case at the NNF. At PPN, for *P. ponderosa*, ring widths were significantly correlated in April, May and June, as in NNF, but less pronounced. In general precipitation of the actual year has higher influences to the growth than precipitation of the previous year. In addition, *P. ponderosa*'s response to precipitation was less pronounced than *J. virginiana*'s, but both species showed positive correlations between tree-ring width and precipitation. Temperature does not show such a clear pattern as precipitation does. In the NNF at *P. ponderosa*'s plot, particularly temperature of the previous year influenced tree-ring growth negatively. For *J. virginiana* no significant correlations of the previous year values were found and just a few for the actual year, mostly at dense plots. A similar pattern can be found at HRN for *P. ponderosa*. However, *J. virginiana* showed significant negative correlations between ring width and temperature especially in the previous year. At PPN only positive significant correlations are detectable, in the previous, as well as in the actual year. Temperature influences all sample sites and as the two species react differently to this influence, no direct comparison can be made.

6.4 Palmer Drought Index (PDI)

The following tables show the results of the calculated correlations between the standardised tree-ring widths and the PDI. The results from the NNF are presented, followed by the ones from HRN and PPN.

Table 6.11: PDI *P. ponderosa* NNF

month	H05 sparse	H15 sparse	H12 mid	H19 mid	H21 dense	H22 dense
JAN	0.309*	0.041	0.134	0.149	0.226*	0.21
FEB	0.306	0.065	0.16	0.162	0.25*	0.22
MAR	0.282	0.037	0.132	0.15	0.27*	0.212
APR	0.33*	0.032	0.198	0.191	0.309**	0.272*
MAY	0.406**	0.11	0.283**	0.259**	0.342**	0.304**
JUN	0.397**	0.105	0.222	0.213	0.356***	0.291**
JUL	0.408**	0.071	0.215	0.17	0.347**	0.305**
AUG	0.424**	0.046	0.224	0.164	0.322**	0.32**
SEP	0.342*	-0.017	0.174	0.172	0.277**	0.249*
OCT	0.279	-0.04	0.166	0.16	0.217	0.214
NOV	0.23	-0.023	0.142	0.154	0.183	0.195
DEC	0.157	-0.074	0.072	0.123	0.126	0.13

Significance levels are shown as follows: P < 0.05*, P < 0.01**, P < 0.001***.

The two sparse sites show a completely different pattern; while at H05 the tree-ring widths during the whole growing season highly correlate with the PDI, in H15 no significant correlation values resulted from the calculations. In H05 a significant correlation in January was found. The stands with mid forest density, H12 and H19 only show significant values in May, and therefore in the wet season. The dense plots show similar results as H05. Plot H21 also shows significant values in February and March, however H22 does not. Plot H22 shows significant values during the whole growing season.

Table 6.12: PDI *J. virginiana* NNF

month	H15 sparse	H19 mid	H21 dense	H31 dense	H33 dense
JAN	0.195	0.382*	0.15	0.327**	0.368**
FEB	0.213	0.38*	0.134	0.338**	0.379**
MAR	0.182	0.442**	0.189	0.383***	0.429***
APR	0.255	0.486**	0.21	0.414***	0.488***
MAY	0.332	0.581***	0.285	0.465***	0.551***
JUN	0.387	0.623***	0.428**	0.456***	0.519***
JUL	0.414*	0.692***	0.489***	0.525***	0.542***
AUG	0.371	0.662***	0.521***	0.474***	0.468***
SEP	0.28	0.63***	0.513***	0.424***	0.413***
OCT	0.322	0.642***	0.498***	0.392***	0.373**
NOV	0.373	0.674***	0.498***	0.387***	0.358**
DEC	0.322	0.606***	0.477***	0.349**	0.283**

Significance levels are shown as follows: P < 0.05*, P < 0.01**, P < 0.001***.

The samples from the sparse forest density H15 only show a significant value in July. Plot H15 sparse is the only plot that does show just one significant value. Plot H19 shows significant values the whole year around similar to H31 and H33. In plot H21 significant values only resulted from June to December.

Table 6.13: PDI *P. ponderosa* and *J. virginiana* HRN and PPN

P. ponderosa					*J. virginiana*	
month	P01	P04	P05	P06	P02	P03
JAN	-0.031	0.033	0.069	0.031	0.309*	0.153
FEB	0.01	0.059	0.097	0.065	0.286	0.166
MAR	-0.013	0.105	0.058	0.116	0.209	0.093
APR	0.075	0.104	0.023	0.107	0.194	0.086
MAY	0.194	0.093	0.11	0.101	0.059	0.091
JUN	0.178	0.162	0.243	0.146	0.174	0.254
JUL	0.208	0.222	0.266	0.121	0.169	0.29
AUG	0.164	0.289	0.278	0.143	0.128	0.238
SEP	0.065	0.305*	0.226	0.11	-0.043	0.166
OCT	0.074	0.278	0.114	0.094	-0.098	0.047
NOV	0.11	0.232	0.122	0.023	-0.092	0.091
DEC	0.035	0.314*	0.261	0.047	-0.098	0.22

Significance levels are shown as follows: $P < 0.05$*, $P < 0.01$**, $P < 0.001$***.

The *P. ponderosa* plots at HRN and PPN show less significant values than the plots at the NNF. Only P04 shows significant values in September and December. All the other plots show no significant values. The two *J. virginiana* plots at HRN only show one significant value at P02 in January. No other significant values are identifiable.

In general it can be said that highly significant values resulted for the plots in the NNF. There, *J. virginiana* shows more significant values and many of them have a higher significance than *P. ponderosa*. The significant values at the *P. ponderosa* plots can mostly be found during the growing season from April to September. The other plots do not show such a correlation with the growing season. The plots at HRN and PPN do not show high values and there is no clear difference between the species.

6.5 Stepwise Linear Regression Modelling (SLRM)

The following Table 6.14 shows the results of the SLRM. Temperature and precipitation were analysed.

Table 6.14: results SLRM

site	density	plot	species	R^2	adjusted R^2
HRN	dense	p03	*J. virginiana*	0.9168	0.8669
HRN	dense	p02	*J. virginiana*	0.9156	0.8134
PPN	sparse	p05	*P. ponderosa*	0.8367	0.7635
PPN	sparse	p06	*P. ponderosa*	0.7503	0.6519
NNF	dense	H21	*J. virginiana*	0.6978	0.6243
NNF	mid	H19	*J. virginiana*	0.671	0.4882
PPN	sparse	p04	*P. ponderosa*	0.5493	0.4592
NNF	dense	H31	*J. virginiana*	0.4818	0.3846
NNF	dense	H33	*J. virginiana*	0.4586	0.3683
HRN	dense	p01	*P. ponderosa*	0.4359	0.3444
NNF	dense	H22	*P. ponderosa*	0.3878	0.3055
NNF	sparse	H15	*J. virginiana*	0.3872	0.2996
NNF	sparse	H15	*P. ponderosa*	0.3492	0.2748
NNF	mid	H12	*P. ponderosa*	0.3265	0.241
NNF	dense	H21	*P. ponderosa*	0.2784	0.2283
NNF	mid	H19	*P. ponderosa*	0.2295	0.1556
NNF	sparse	H05	*P. ponderosa*	0.1997	0.1365

Table 6.14 shows the results of the SLRM. Values at R^2 show the explanatory power of the input variables, whereas adjusted R^2 additionally take the number of input values into account, resulting in lower values than R^2. For more accuracy due to the consideration of the number of input variables, the focus will be on adjusted R^2. The results can be divided into two main groups: One with adjusted R^2 below 0.5, indicating that less than half of the variation in tree-ring width is explainable by climatic factors and the second group with adjusted R^2 above 0.5, indicating that more than half of the variation in tree-ring width is related to the climatic factors used in the analysis.

Climatic factors can explain more than half of the tree-ring width variations at five sites. Two of them are at HRN, two at PPN and only one at the NNF. The plots at the NNF and at HRN are both dense, whereas at PPN they are sparse. At twelve sites, climatic factors explain less than half of the tree-ring width variations. For all but one plot at the NNF less than half of the tree-ring widths can be explained only by climatic factors. At the sites in eastern Nebraska, HRN and PPN, for all but one plots of each sample site, climatic conditions exert the main influence on tree-ring width.

6.6 Stable Isotopes

The following figures give an overview of the stable isotope analysis. In the first part, $\delta^{18}O$ is investigated, followed by $\delta^{13}C$. In the second part, the WUE is presented and in the third part the $\delta^{13}C$ / $\delta^{18}O$ ratios are shown.

6.6.1 $\delta^{18}O$

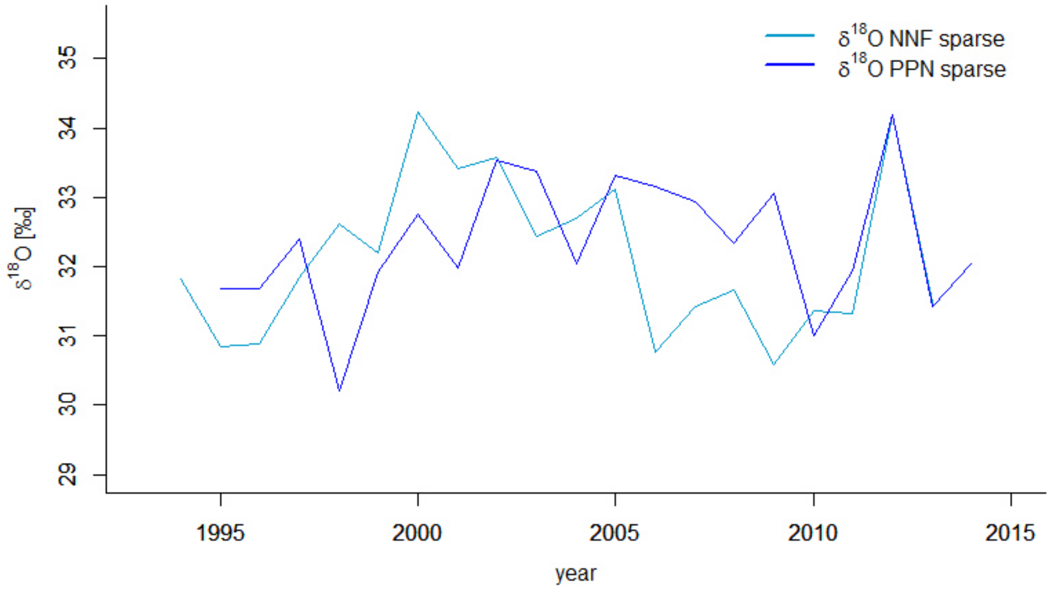


Fig. 6.34: $\delta^{18}O$ NNF and PPN sparse

Figure 6.34 shows the measured $\delta^{18}O$ at sparse sites at the NNF and at PPN. Even though the values are in the same range and the correlation value is 0.15, no significant statement can be made.

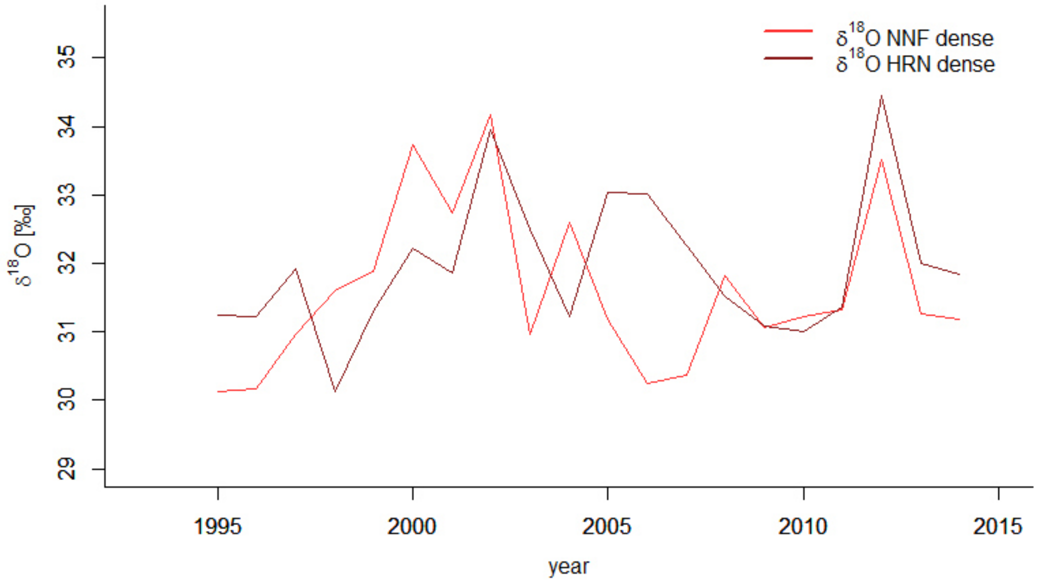


Fig. 6.35: $\delta^{18}O$ NNF and HRN dense

Figure 6.35 shows the measured $\delta^{18}O$ at dense sites at the NNF and at HRN. The values are in the same range, and the curves show some similarity. The correlation value is 0.31, but statistically not significant.

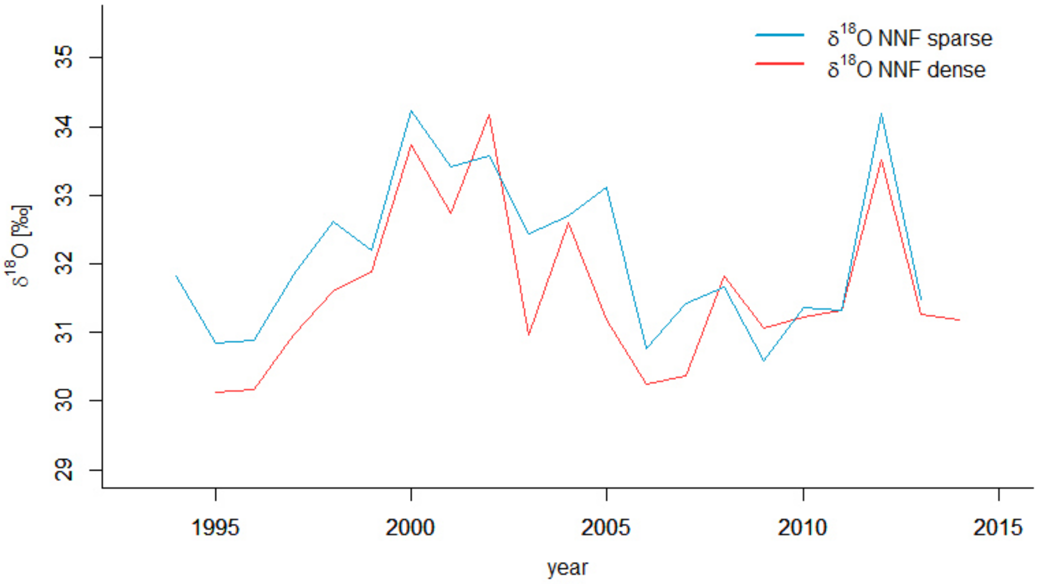


Fig. 6.36: $\delta^{18}O$ NNF sparse and NNF dense

Figure 6.36 shows the $\delta^{18}O$ values for sparse and dense sites at the NNF. Their correlation is highly significant ($p < 0.001$), with a correlation coefficient of 0.86.

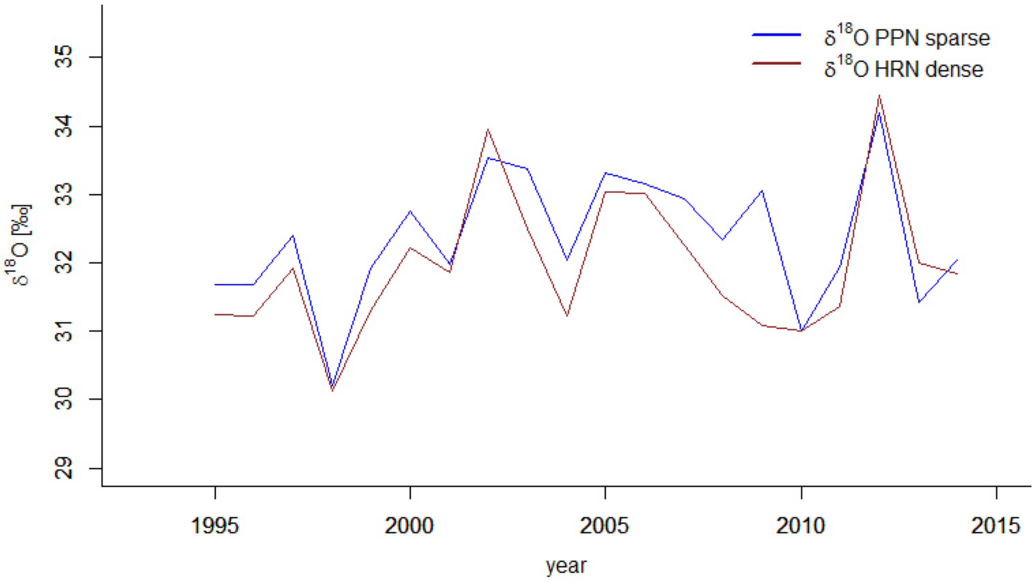


Fig. 6.37: $\delta^{18}O$ PPN sparse and HRN dense

Figure 6.37 shows the measured $\delta^{18}O$ at the eastern Nebraska sites, PPN and HRN. Their correlation is highly significant ($p < 0.001$) with a correlation value of 0.85.

Comparing the correlations of $\delta^{18}O$ at the different sample sites, significant values were not influenced by stand density, but by sample area. The samples within the NNF correlate significantly and so do the samples in eastern Nebraska, at PPN and HRN.

6.6.2 $\delta^{13}C$

The following figures present the results of the $\delta^{13}C$ investigations.

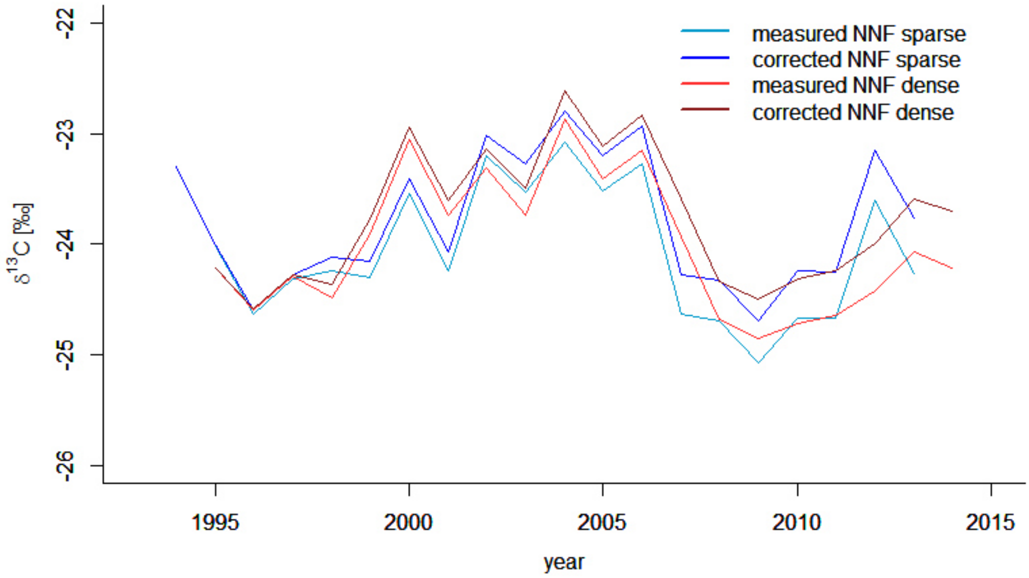


Fig. 6.38: $\delta^{13}C$ / $\delta^{12}C$ NNF sparse and dense

Figure 6.38 shows the $\delta^{13}C$ / $\delta^{12}C$ ratio of sparse and dense sites at the NNF. The curves run parallel to each other and no significant differences can be detected. The correlation of the measured and the corrected values are highly significant ($p < 0.001$) and their strong correlation value is 0.85.

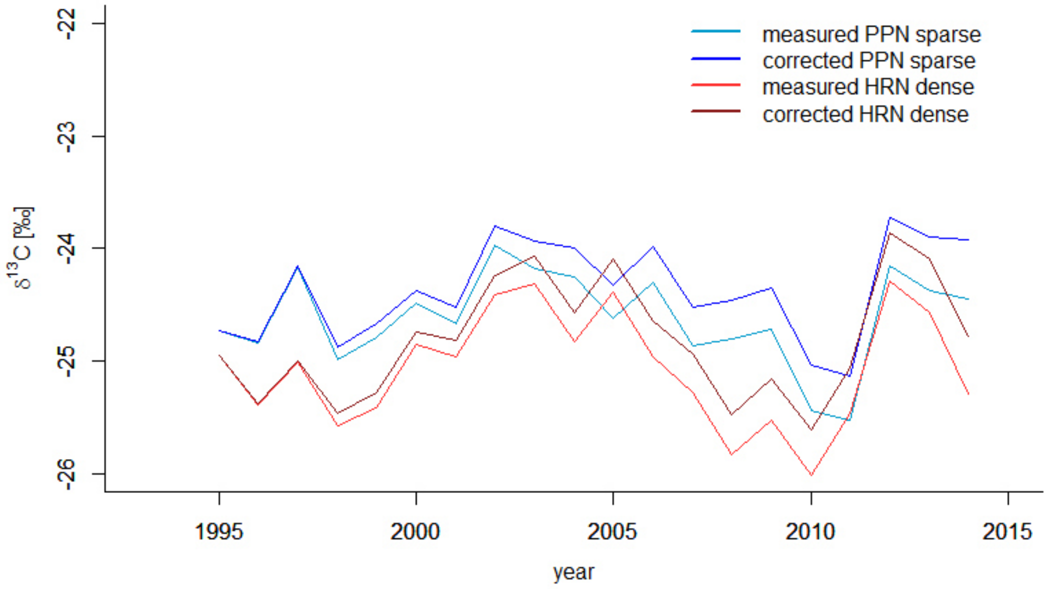


Fig. 6.39: $\delta^{13}C$ / $\delta^{12}C$ PPN sparse and HRN dense

Figure 6.39 shows the measured and atmospherically corrected values of the $\delta^{13}C$ / $\delta^{12}C$ ratio at PPN and HRN. The curves' patterns are mostly similar and both sample sites show a growing difference between measured and corrected values up until now. The correlations are highly significant ($p < 0.001$) with a correlation coefficient of 0.77.

6.6.3 WUE

The following figures show the results of the WUE and additionally display the measured increase in atmospheric CO_2. The calculations of the WUE are based on the results of the stable isotope analysis and were examined as described in the method section. First, the results from the NNF, second, the ones from HRN and PPN, and third, a comparison between all the sites are presented.

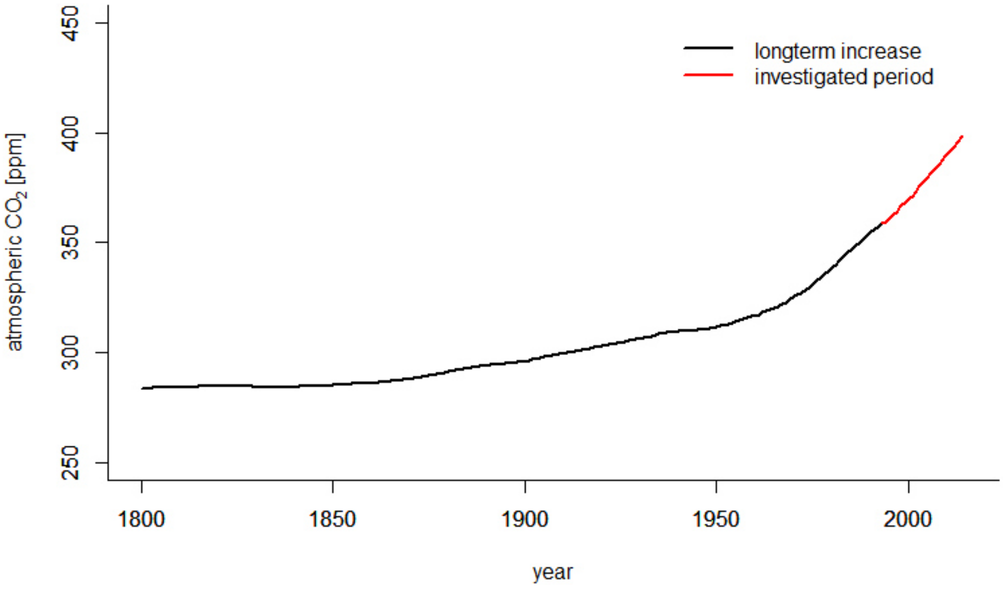


Fig. 6.40: atmospheric CO_2 increase

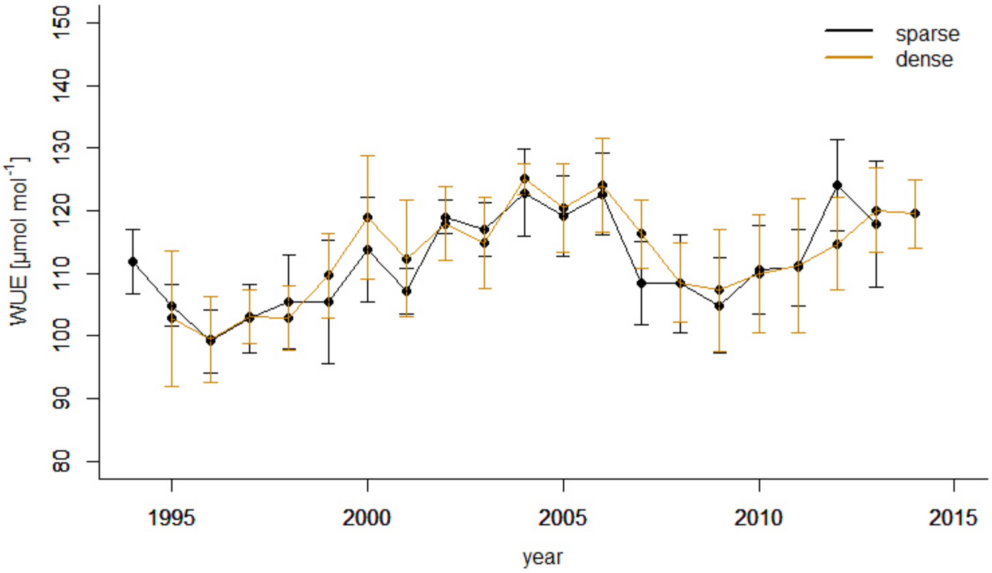


Fig. 6.41: WUE *P. ponderosa* NNF

Figure 6.41 shows the means of the WUE in the Sandhills at sparse and dense sites for *P. ponderosa*. Both lines show an increase in the WUE, mostly between 2001 and 2006. After 2006, a decrease is detectable. Still the values do not go deeper than they were before 2001. Subsequently again an increase follows towards 2014. The curves look quite similar, but mostly the dense sites show slightly higher values than the sparse sites, but they do not differ significantly.

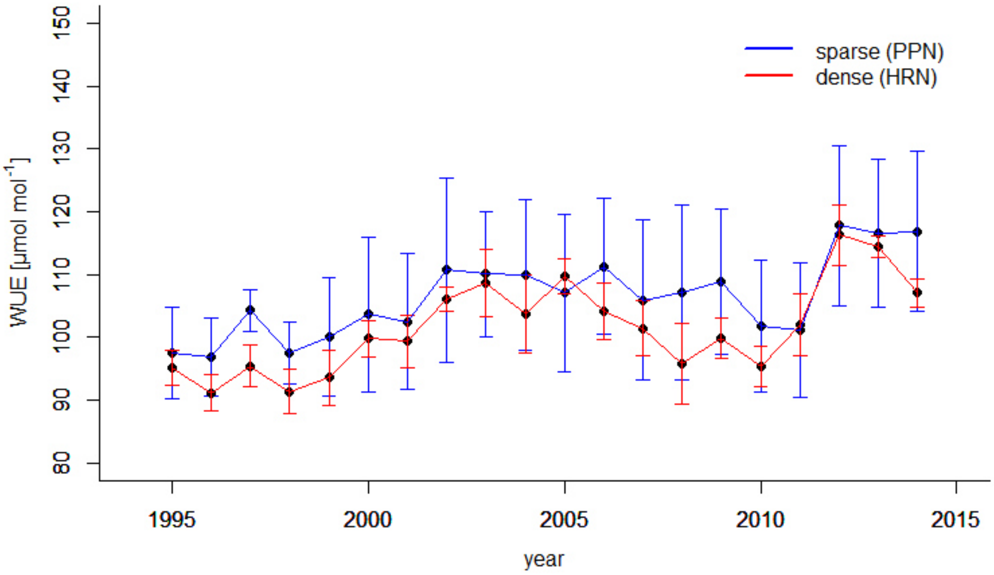


Fig. 6.42: WUE *P. ponderosa* HRN and PPN

Figure 6.42 shows the means of the WUE at HRN and PPN. The curves increase from 1995 until 2005; afterwards they slightly decrease until 2010 and then strongly increase again until they reach the highest values in 2012 before decreasing again. The trees at the sparse site show higher values than the trees at the dense site, but the curves mostly show an analogue curve progression and do not vary significantly.

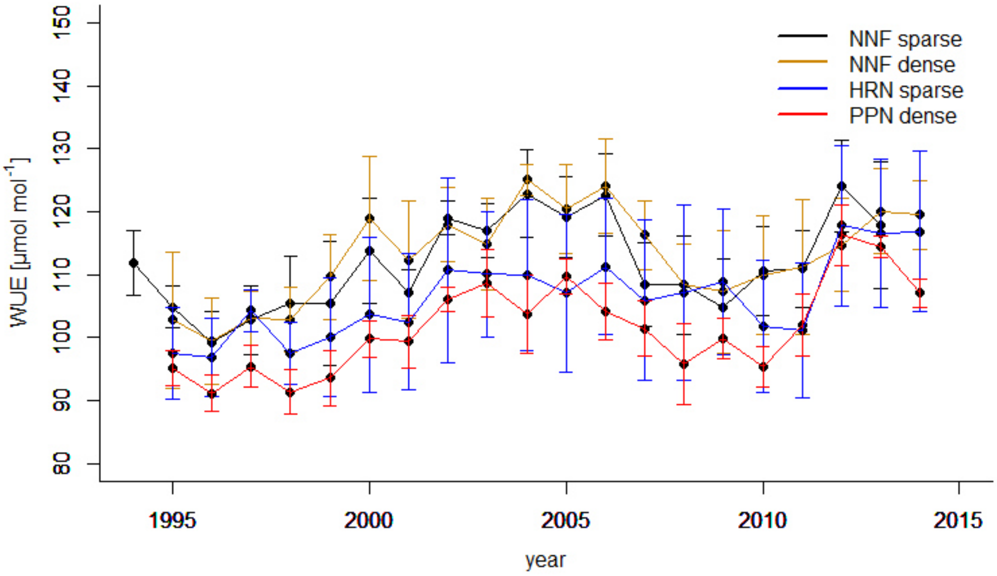


Fig. 6.43: WUE *P. ponderosa* NNF, HRN and PPN

Figure 6.43 shows the means of the WUE in NNF at sparse and dense sites as well as sparse sites at PPN and dense sites at HRN. All curves show quite similar curve characteristics: An increase in the first half of the investigated time period, followed by a moderate decrease, which is then again followed by an increase. It is notable that the WUE of the trees at HRN and PPN is mostly lower than the

WUE of the trees in the NNF. When comparing the WUE at all sites with the increase in atmospheric CO_2, the increase in CO_2 is larger compared to the one of WUE; the rise is not parallel.

6.6.4 $\delta^{18}O$ / $\delta^{13}C$ Relations

In the following section, the $\delta^{18}O$ / $\delta^{13}C$ values are plotted together to investigate their relations, referring to the conceptual model of Scheidegger et al. (2000), shown in Figure 5.1 (see Material & Methods). In addition the PDI values and the results of the correlation between climate and $\delta^{13}C$ for the investigated time period are presented to link the resulting $\delta^{18}O$ / $\delta^{13}C$ relations to climate and especially to droughts.

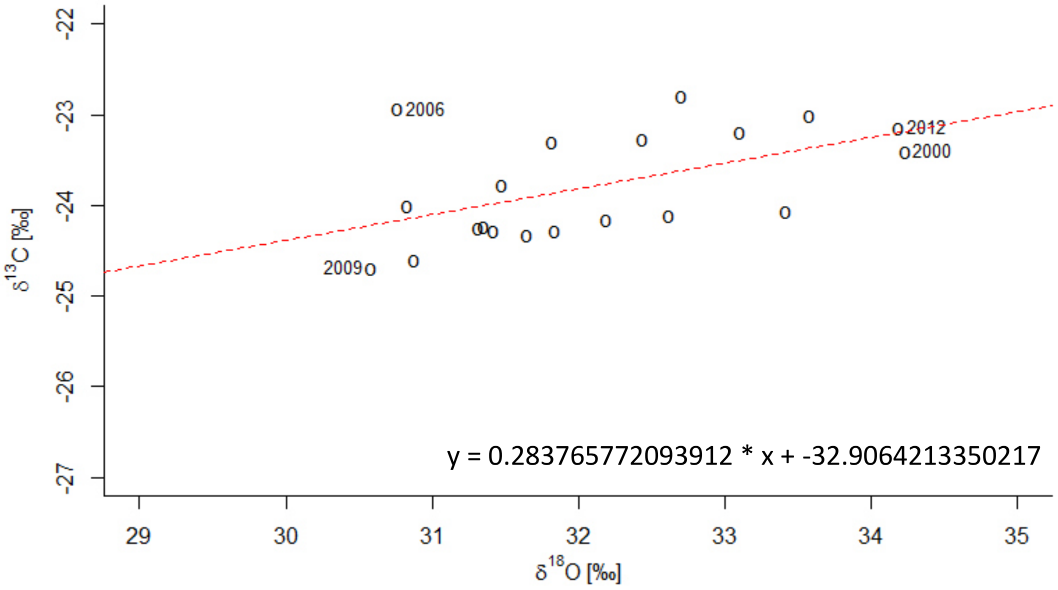


Fig. 6.44: $\delta^{18}O$ / $\delta^{13}C$ relation *P. ponderosa* sparse, NNF

The values show a slightly increasing trend, indicated by the red line. The correlation between $\delta^{18}O$ and $\delta^{13}C$ is little significant ($p < 0.05$) with a correlation value of 0.536*. Due to the low significance Fig. b or Fig. c of the conceptual model may be selected. The data distribution is more alike the one of *P. ponderosa* dense at the NNF than sparse at PPN and dense at HRN. Thus Fig. c was defined as appropriate representation. Thus an enhancement in $\delta^{18}O$ and a decrease in rH together with statistically consistent $\delta^{13}C$ and c_i values, lead to a decrease in A_{max} and g_1. This indicates that in dry periods A_{max} and g_1 are low to reduce the loss of water. Taking the PDI values from the two years with highest $\delta^{18}O$ values into account this can be approved. The two highest values of the $\delta^{18}O$ / $\delta^{13}C$ relation are measured in 2000 and 2012. For 2000 PDI values are, in six months of the year (March, April, May, June, July and October) lower than -2, indicating six months were of moderate drought. In addition two months (August and September) hold values lower than -4, indicating extreme drought. The lowest values were measured in 2006 and 2009. In 2006 two months (September and October) with moderate, three (May, June and November) with severe and two (July and August) with extreme drought were measured. Despite these high values, $\delta^{18}O$ values were low. In 2009 no droughts were recorded.

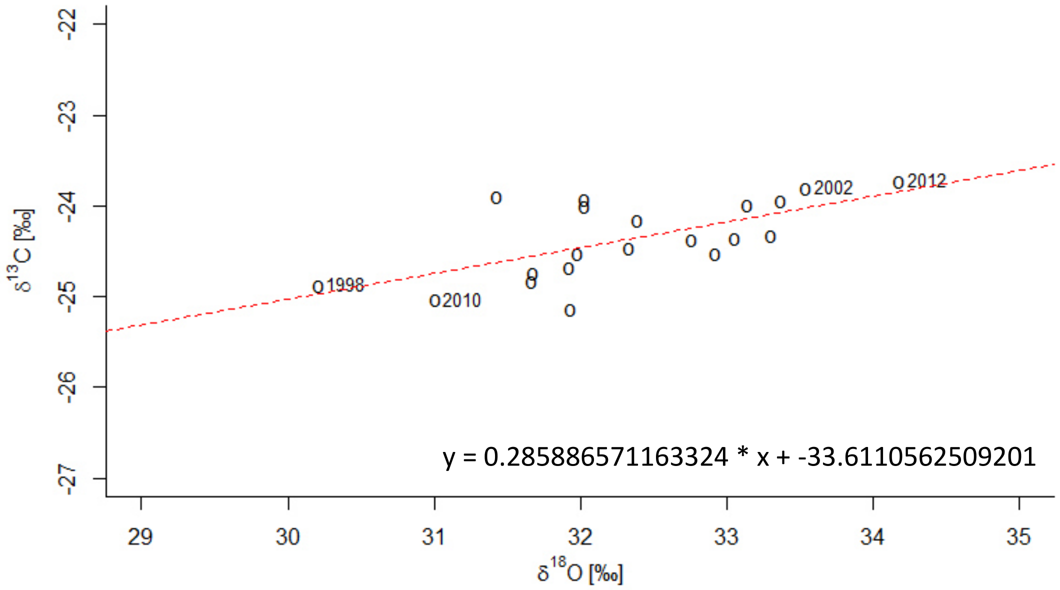


Fig. 6.45: $\delta^{18}O$ / $\delta^{13}C$ relation *P. ponderosa* sparse, PPN

The values show a slightly increasing trend, indicated by the red line. The correlation between $\delta^{18}O$ and $\delta^{13}C$ is significant ($p < 0.01$) with a correlation value of 0.638**. Due to the significance, an increased transpiration rate and relating thereto higher $\delta^{18}O$ values can be expected. Fig. b was chosen, which stands for an enhancement in $\delta^{18}O$ and a decrease in rH. This, together with statistically increasing $\delta^{13}C$ and decreasing c_i values, leads to a constant A_{max} and a decreasing g_1. Indicating that in dry periods A_{max} is still high but g_1 is lower to reduce the loss of water. In regard to the PDI values from the two years with highest $\delta^{18}O$ values this conclusion can be validated. The two highest values of the $\delta^{18}O$ / $\delta^{13}C$ relation are measured in 2002 and 2012. For 2002 PDI values are, in three months (July, August and December); lower than -2, which means three months were of moderate drought and in one month (September) lower than -3, indicating a severe drought. The two years with the lowest values are 1998 and 2010. In both years no droughts were recorded.

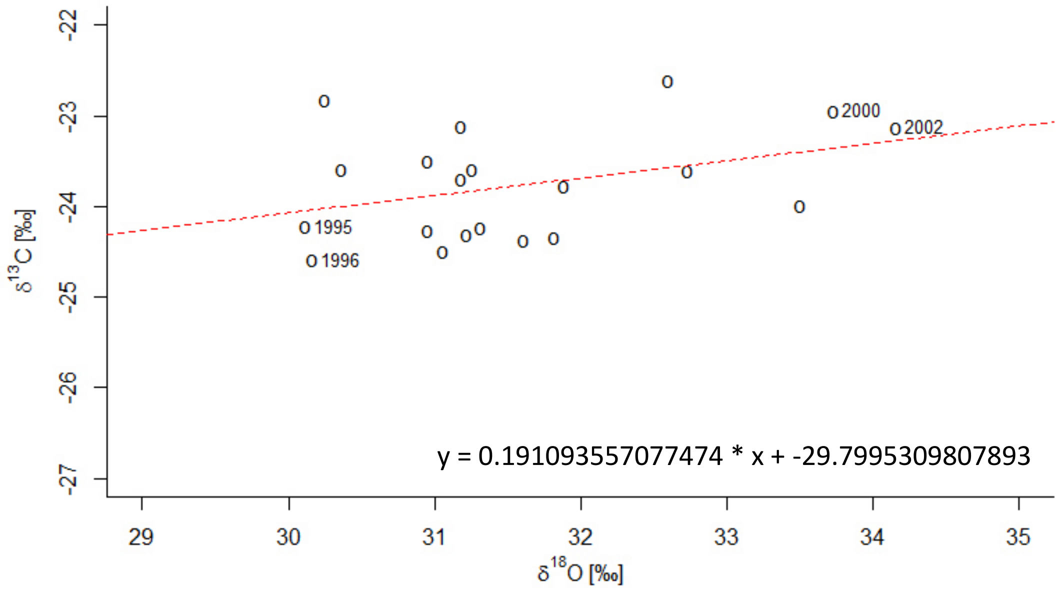


Fig. 6.46: $\delta^{18}O$ / $\delta^{13}C$ relation *P. ponderosa* dense, NNF

The values show a slightly increasing trend, indicated by the red line. The correlation between $\delta^{18}O$ and $\delta^{13}C$ is not significant with a correlation value of 0.377. Due to no statistical significance between the values, an increased transpiration rate and relating thereto higher $\delta^{18}O$ values can be expected. Thus Fig. c was selected which means an enhancement in $\delta^{18}O$ and a decrease in rH together with statistically consistent $\delta^{13}C$ and c_i values, leading to a decrease in A_{max} and g_1. This indicates that in dry periods A_{max} and g_1 are low to reduce the loss of water. Taking into account the PDI values from the two years with highest $\delta^{18}O$ values this assumption can be supported. The two highest values of the $\delta^{18}O$ / $\delta^{13}C$ relation are measured in 2000 and 2002. For 2000 PDI values are, in six months of the year (March, April, May, June, July and October) lower than -2, which means six months were of moderate drought. Additionally, for 2002 PDI values are, in one month (May) lower than -2, which means this month was of moderate drought and in one month (October) lower than -3, indicating a severe drought. In 1995 and 1996 lowest $\delta^{18}O$ values were measured but they are not listed as years with droughts. Lowest $\delta^{18}O$ values were measured in 1995 and 1996, both years without recorded droughts.

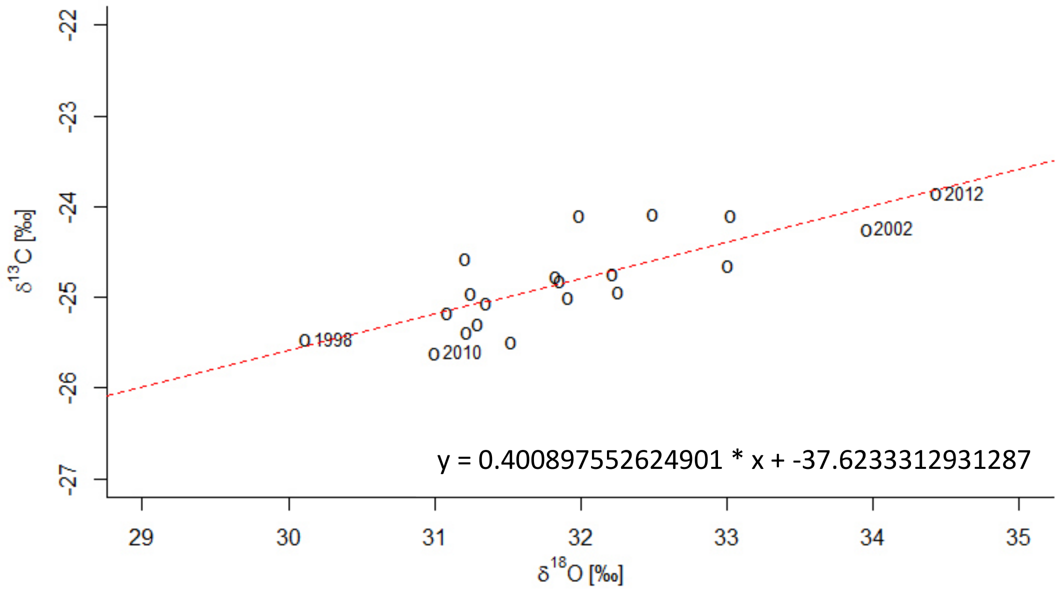


Fig. 6.47: $\delta^{18}O$ / $\delta^{13}C$ relation *P. ponderosa* dense, HRN

The values show a moderate increase, indicated by the red line. The correlation between $\delta^{18}O$ and $\delta^{13}C$ is highly significant ($p < 0.001$) with 0.794***. Due to the high significance, as in *P. ponderosa* sparse PPN, an increased transpiration rate and relating thereto higher $\delta^{18}O$ values can be expected. Therefore Fig. b was chosen, which stands for an enhancement in $\delta^{18}O$ and a decrease in rH together with statistically increasing $\delta^{13}C$ and decreasing c_i values, leading to a constant A_{max} and a decreasing g_1. This indicates that in dry periods A_{max} is still high but g_1 is lower to reduce the loss of water. In regard to the PDI values from the two years with highest $\delta^{18}O$ values this assumption can be reinforced. The two highest values of the $\delta^{18}O$ / $\delta^{13}C$ relation are measured in 2002 and 2012, the same year as at *P. ponderosa* sparse at PPN. Therefore the values are the same: For 2002 PDI values are in three months (July, August and December) lower than -2, which indicates moderate drought and in one month (September) lower than -3, which indicates a severe drought. In 1998 and 2010 the lowest $\delta^{18}O$ values were recorded and both years were not affected by droughts.

Comparing all four sample plots, it is noticeable that the $\delta^{18}O$ / $\delta^{13}C$ correlations at *P. ponderosa* sparse (0.536*) and *P. ponderosa* dense (0.377) in the NNF are less significant than at *P. ponderosa* sparse at PPN (0.638**) and at *P. ponderosa* dense at HRN (0.794***). In addition, less pronounced PDI values were measured at PPN and HRN. So the reduced rH, together with the other factors of the conceptual model, trigger the closure of stomata and a reduced A_{max} at NNF. Plots at HRN and PPN do not show such a strong reaction. The g_1 decreases but A_{max} mostly stays constant. As a result, water availability highly influences A_{max} and g_1 and therefore also tree-ring growth.

Table 6.15: PDI in the NNF, colours according to severity: white = no exceptional drought, yellow = moderate drought, orange = severe drought, red = extreme drought (NOAA 2017)

year	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEP	OCT	NOV	DEC
1995	2.22	1.88	2.70	3.87	5.79	5.33	4.47	3.29	4.20	4.97	4.17	3.32
1996	3.95	3.01	2.23	1.21	3.32	1.55	0.68	1.08	3.41	3.12	3.15	2.79
1997	2.37	2.32	0.67	1.70	1.36	0.71	1.83	2.14	2.33	3.17	2.32	1.84
1998	1.42	0.98	1.91	1.52	1.37	2.97	3.27	3.48	1.90	3.80	4.32	3.71
1999	3.31	3.32	3.04	3.90	3.49	3.93	3.45	2.46	3.01	0.95	-1.11	-1.67
2000	-1.69	-1.64	-2.07	-2.36	-2.34	-2.47	-2.65	-4.03	-4.22	-2.59	-1.43	-1.54
2001	-0.19	0.15	-0.57	2.18	1.37	-0.74	-0.09	-0.13	0.01	-0.78	0.36	-0.70
2002	-0.98	-1.35	-1.50	-1.98	-2.66	-4.29	-5.82	-5.45	-5.32	-3.27	-4.15	-4.26
2003	-3.99	-3.91	-3.97	-3.72	-3.54	-2.33	-3.49	-4.66	-4.86	-5.06	-4.77	-4.52
2004	-4.43	-4.19	-4.26	-4.56	-4.68	-4.59	-4.21	-4.36	-2.17	-2.00	-1.83	-2.52
2005	-2.42	-2.82	-2.69	-0.83	0.21	2.24	0.17	0.53	-0.85	-1.30	-1.17	-1.31
2006	-1.62	-1.82	-0.95	-1.36	-3.08	-3.38	-4.63	-4.30	-2.10	-2.25	-3.10	-0.56
2007	-0.51	0.51	0.89	1.77	2.57	2.05	-0.06	1.21	0.06	1.66	-0.11	0.94
2008	0.30	-0.21	-0.80	-0.43	1.37	1.69	1.69	1.87	2.26	3.88	3.61	3.49
2009	3.56	3.86	3.81	4.15	2.68	4.32	4.59	5.71	5.19	6.58	5.34	5.75
2010	5.49	5.37	5.26	5.24	4.81	6.63	6.71	6.51	5.97	5.36	4.24	3.88
2011	4.36	4.29	4.08	3.96	4.54	5.09	5.24	5.82	4.79	5.16	4.06	3.29
2012	2.46	3.69	0.85	1.54	-0.79	-3.08	-4.65	-5.63	-6.36	-6.30	-6.39	-5.94
2013	-5.74	-5.07	-5.07	-4.64	-2.65	-3.13	-3.04	-1.02	-1.47	0.36	0.29	0.29
2014	-0.06	0.01	-0.40	-0.70	-1.43	2.00	1.18	2.91	2.78	2.09	1.55	2.53

Table 6.16: PDI at HRN and PPN, colours according to severity: white = no exceptional drought, yellow = moderate drought, orange = severe drought, red = extreme drought (NOAA 2017)

year	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEP	OCT	NOV	DEC
1995	0.21	-0.33	-0.06	0.42	3.10	1.74	0.86	-0.11	-1.01	-1.69	-1.94	-2.27
1996	-2.21	-2.64	-2.94	-2.85	1.07	-0.04	0.18	1.32	1.32	0.65	2.23	1.63
1997	1.33	1.96	0.37	1.42	0.90	1.08	0.51	-0.23	-0.55	0.63	0.98	1.35
1998	1.37	1.67	2.43	2.40	-0.02	1.12	2.06	1.21	-0.11	-0.21	1.31	0.50
1999	0.53	0.07	-0.62	1.16	1.85	1.96	0.37	-0.49	-1.29	-2.08	-2.57	-2.81
2000	-3.18	-2.98	-3.23	-3.64	-4.51	-4.27	-3.45	-4.40	-4.92	-4.70	-4.39	-4.26
2001	-3.71	-1.32	-1.38	-1.89	1.77	2.00	2.24	0.84	1.87	1.67	0.66	-0.22
2002	-0.35	-0.60	-0.76	-1.01	0.53	-1.39	-2.37	-2.41	-3.07	-0.07	-1.16	-2.20
2003	-2.50	-2.37	-2.66	-2.35	-1.99	0.11	-2.11	-2.54	-1.88	-2.35	-1.48	-1.57
2004	-0.83	-0.56	0.87	-0.72	0.55	-0.33	0.39	-0.50	-0.97	-1.61	-1.70	-2.02
2005	-1.79	-0.34	-1.21	-0.31	-1.55	-1.56	-1.44	-1.35	-2.19	-2.14	-2.36	-2.57
2006	-2.84	-3.24	-3.20	-3.08	-3.49	-3.99	-4.07	-2.70	-1.45	-1.65	-2.72	-0.92
2007	-0.54	0.05	0.18	0.88	1.94	0.87	-0.38	1.71	1.13	2.43	1.22	2.61
2008	2.23	1.95	1.58	2.62	3.01	3.30	3.22	2.03	2.12	3.59	3.41	3.20
2009	2.70	2.26	1.07	1.28	-0.55	0.10	-0.55	-0.22	-0.87	0.93	0.70	1.47
2010	1.47	1.50	1.73	1.38	1.31	2.24	2.06	1.45	1.89	-0.17	0.14	-0.82
2011	-0.61	-0.67	-1.19	-0.88	0.34	-0.10	-0.11	0.83	-0.64	-1.23	-1.06	0.35
2012	-0.28	0.81	-0.64	-0.55	-1.52	-1.53	-2.65	-3.17	-3.76	-3.45	-3.97	-3.86
2013	-3.81	-3.83	-3.98	-2.43	0.39	-0.95	-1.84	-2.25	-2.65	-1.04	-0.92	-1.36
2014	-1.87	-1.96	-2.52	-2.42	-2.81	-0.47	-1.36	0.12	0.25	1.24	0.28	0.70

The following Table 6.17 shows the results of the calculated correlations between $\delta^{13}C$ and climate at the NNF, HRN and PPN. For NNF significant values between $\delta^{13}C$ and climate only resulted when considering the PDI. Therefore only results of the calculations including PDI are shown. For HRN and PPN no significant values were calculated. Climate at these two sites seems not to influence $\delta^{13}C$ significantly.

Table 6.17: Correlation $\delta^{13}C$ and climate

month	NNF sparse	NNF dense	PPN sparse	HRN dense
PDIjanuary	-0.479*	-0.493*	-0.147	0.054
PDIfebruary	-0.566**	-0.539*	-0.092	0.022
PDImarch	-0.499*	-0.483*	-0.172	0.035
PDIapril	-0.594**	-0.491*	-0.186	-0.026
PDImay	-0.493*	-0.461*	-0.075	-0.078
PDIjune	-0.39	-0.408	-0.213	-0.187
PDIjuly	-0.445*	-0.425	-0.275	-0.154
PDIaugust	-0.383	-0.396	-0.161	0.03
PDIseptember	-0.241	-0.291	-0.045	0.1
PDIoctober	-0.236	-0.249	-0.019	0.165
PDInovember	-0.219	-0.244	-0.053	0.193
PDIdecember	-0.158	-0.209	0.063	0.311

Significance levels are shown as follows: $P < 0.05$*, $P < 0.01$**, $P < 0.001$***.

Significant correlations at the NNF were found for both, sparse and dense sites from January to May and additionally in July at sparse sites. The winter months and the beginning of the growing season (April and May) were correlating significantly with $\delta^{13}C$.

In addition the correlations between $\delta^{18}O$ and climate were calculated. Significant results were only found with precipitation, at the NNF for sparse and dense sites and at PPN.

Table 6.18: correlation $\delta^{18}O$ and climate

month	NNF sparse	NNF dense	PPN sparse	HRN dense
Pjfm	0.135	-0.005	0.111	0.238
Pamj	0.223	0.212	-0.538**	-0.346
Pja	-0.426	-0.299	-0.222	-0.023
Pso	0.146	0.446*	0.237	0.383
Pnd	0.58**	0.576**	0.089	-0.142

Significance levels are shown as follows: $P < 0.05$*, $P < 0.01$**, $P < 0.001$***.

7 Discussion

7.1 Ring Widths

By the means of dendrochronology, the ring widths of *J. virginiana* and *P. ponderosa* were measured to investigate their growth characteristics as a function of stand density and response to precipitation gradients and drought.

7.1.1 Ring Widths NNF

Pinus ponderosa growth patterns at the NNF showed clear reactions depending on their stand density. Trees at sparse sites showed more individual growth pattern and the chronologies correlated less than at mid and dense sites. The Glk and CDI increased from sparse to mid stands and at dense sites highest values were measured. Highest sensitivity was measured at sparse sites and lowest at dense sites. At sparse sites, trees respond individually, because their nearby environment is slightly different at every sample site. Different light, temperature, precipitation, competition, wind and soil conditions, or limited root space, cause different microclimates which result in diverse growth patterns (Fritts 1976; Schweingruber 1996; Stiell 1970). At mid density sites, similar growth pattern and significant Glk were found, indicating that the surrounding of all the trees is more similar than at sparse sites and they are affected by the same influences at the same level. At dense sites this fact is reinforced due to the low variability of site conditions from tree to tree. At all densities, the growth pattern was highly influenced by droughts. Pointer years mostly appeared in years when droughts occurred. Then, narrow tree rings were detected.

It can be said that at the NNF stand density is strongly reflected in the ring widths of *P. ponderosa*. Additionally, extreme dry years were obvious in tree-ring width, independent of stand density. But the identification of single factors causing these effects is not possible by ring width measurements.

Same dependences of tree-ring widths, stand density and droughts were detected for most of the *J. virginiana* plots at the NNF. One exception was found at the mid density plot H19, where *J. virginiana* grew within a *P. ponderosa* stand. There, *J. virginiana* mid showed the same curve characteristics as at sparse plots. These trees react as individually as trees at sparse sites do. At sparse sites the main competitor is prairie grass, while at H19, *P. ponderosa* trees are the competitors. However *J. virginiana* trees at H19 do not seem to be stronger influenced by *P. ponderosa* than by prairie grass at the sparse site.

This can be attributed to the root depth and the plasticity of *J. virginiana* to reach different soil layers depending on different climate and competition conditions (see also Discussion Stable Isotopes) (Eggenmeyer et al. 2006). The same responses explain the less complacent growth of the dense plot H21, where trees also grow between *P. ponderosa*. Additionally, the age trend may explain the different growth pattern compared to other dense plots at the NNF, because trees at H21 are younger than the trees at the other dense sites at the NNF (Fritts 1976; Schweingruber 1996).

To sum up, the stand density at *J. virginiana* sites is not as clearly reflected in the tree-ring widths as it was at *P. ponderosa* sites. But the influence of dry years is still visible in tree-ring widths.

7.1.2 Ring Widths PPN and HRN

Pinus ponderosa at PPN and HRN showed the same growth patterns and responses to drought even though their stand density was different. Additionally, at HRN, the Missouri River is closely situated and ground water may be available for trees. Local factors such as understory, nutrient and water availability and the above mentioned climatic influences seem not to influence tree growth strongly.

At HRN all *J. virginiana* trees at dense plots showed the same curve characteristics. Their environment is similar and the plots are affected by the same limitations. Pointer years were detected in extraordinary dry years. Groundwater availability, provided by the nearby Missouri River, may have caused these similar growth patterns.

To conclude, the different tree-ring widths and curve patterns at all the investigated sites are related to the microclimate which is characterised by light, temperature, precipitation, wind and soil conditions, limited root space, water availability, nutrient supply, soil characteristics and competition (Fritts 1976; McDowell et al. 2003; Schweingruber 1996; Stiell 1970). Studies give evidence that out of all the different factors, soil water content is one of the most important components in regard of tree-ring widths. If soil moisture was high, increased growth was measured and wider rings were built (Eggenmeyer et al. 2006; Saurer et al. 1997). At dense sites, soil moisture is often limited which explains the more complacent structure of the ring widths compared to other densities. This fact was proofed in thinning experiments showing that soil moisture and tree growth increased after thinning (McDowell et al. 2003). Other factors such as less light availability at dense sites, therefore lower photosynthetic input and bad growth conditions may have influenced the growth (Stiell 1970). All the mentioned factors are subject to competition. In general, the competition between individual trees at sparse sites is low and gets higher with increasing density, whereas the competition between trees and understory is high at sparse sites and gets lower with increasing density. These effects are mainly due to different proportions in water availability, light, nutrient and rooting space limitations. Since soil moisture is closely related to drought, it is not surprising that most of the pointer years coincided with extraordinary dry years. Further investigations are still needed to understand the proportions of the different factors influencing ring widths and the dependencies between age and competition. Moreover, one tree ring stands for one entire year and no intra-annual differences are detectable. In addition, tree-ring widths alone do not give evidence of influences of previous years which also could play an important role in ring width formation (Fritts 1966; Sander 1970).

7.2 Correlation Climate

To investigate the influence of temperature and precipitation to tree-ring width, correlations of tree-ring widths with temperature, precipitation and the PDI were calculated at a monthly basis for each sample plot. In addition, to identify climate variables which influenced the tree growth the most, a SLRM was applied.

7.2.1 Correlations NNF

Precipitation patterns at the NNF are characterised by melt season in March, followed by a wet season in April, May and June, when around 70 percent of precipitation occurs (Eggenmeyer et al. 2006). July and August are usually dry, whereas September and October are moderate and in January, February, November and December precipitation occurs mostly as snow. For both species, precipitation of the previous year poorly influenced tree-ring width. In the actual year, precipitation positively influenced tree-ring width during the initial period of the growing season, in April, May and June mostly at mid and dense sites. The dry season, July and August, also showed a positive influence. This is not explainable by the amount of precipitation in July and August, but on the one hand by the precipitation, fallen in the wet season and stored in the soil. On the other hand, tree growth is delayed and therefore the positive correlation may be still attributed to wet season precipitation. Climate correlations at the NNF showed that *P. ponderosa* is highly influenced by precipitation, independent of stand density. In contrast, *J. virginiana* showed stronger correlations with climate with increasing density.

As already seen in the tree-ring widths, water availability and soil moisture are the crucial factors for tree-ring growth, because cambial activity is reduced when water availability and soil moisture are limited (Fritts 1976; McDowell et al. 2003; Oberhuber et al. 1998; Saurer et al. 1997). Self-thinning and therefore less competition, and stand density reduction experiments have identified changes in water availability and soil moisture after thinning. Tree-ring patterns then were similar to the ones in periods of wetter than normal climate and showed broader tree rings (McDowell et al. 2003; Murrell 2009; Westoby 1984). The reaction of *J. virginiana* supports these findings. With increasing density, less water and soil moisture is available and therefore the dependence on precipitation gets higher.

Analysing the correlations between temperature and ring width for most of the plots in the NNF showed clear visible patterns. High temperatures in January and February were positively correlated with ring width. March also showed this effect, but not as strong as January and February did. In April, May, June and July high temperatures were highly negatively correlated to ring widths. August and September did not show clear correlations. Some plots showed a slightly positive correlation while others showed a negative one. In October, the correlations were negative but not significant. In November temperature and ring width was positively correlated at all plots, but no significant values were detectable. In December the correlations were somewhat higher, but not significant as well. Apart from one plot (H05 sparse) a positive correlation could be found.

According to Fritts (1976), the nine-to-ten-month period before the start of the growing season has high impacts on tree-ring growth. Above-average temperature and a small number of frost days in these months lead to better growth conditions. Due to high temperatures in winter and spring, the cambial activity is initiated early in the year and lead to the formation of wide rings (Fritts 1976). This explains the positive correlations between temperature and ring width from November of the previous year to March of the actual year. Different studies have shown that droughts during the growing season highly influence tree growth negatively (Fritts 1966; Fritts 1976; Seiler et al. 2017; Woodhouse et al. 2001). Therefore, temperatures from April to July are highly negatively correlated with ring widths. Temperature correlations did not show a clear pattern between the different stand densities at the NNF. For *P. ponderosa*, previous year temperature influenced the growth more than actual year temperature. *Juniperus virginiana* was only significantly correlated with temperature in the actual year. Overall the validity of temperature influencing ring width is low.

7.2.2 Correlations PPN and HRN

At HRN, *P. ponderosa* showed no correlations with precipitation, but *J. virginiana* did. In April, May, June, September and October of the previous year, from January to March and from September to December of the actual year significant correlations were calculated. At PPN, *P. ponderosa*'s ring widths were correlating with precipitation but only at one plot in April, to June and December and November of the actual year. Presumably, correlations from September to December in the actual year are coincidences, because the growing season had already finished.

At HRN, *P. ponderosa* only showed significant values in January and October of the actual year, while *J. virginiana* correlated stronger with temperature of the previous year. At PPN, significant values resulted for the previous year in May, September and December and in the actual year in May, June and December.

Mostly for precipitation, significant correlations were more frequent and showed a higher significance level at the NNF compared to PPN and HRN. Mainly due to the fact that less precipitation occurs at the NNF than at HRN and PPN (Wilhite & Hubbard 1998). Precipitation and soil moisture therefore are limiting factors at the NNF. The observed responses may also be influenced by the trees' age. At PPN and HRN trees are younger than at the NNF. Even though standardisation was performed, younger trees express climate influences differently than older trees. Thus, age and density structures, in association with competition and cooperation, result in different reactions to climate (Carrer & Urbinati 2004; Schweingruber 1996; Smedley et al. 1991).

7.2.3 Species-Specific Response to Climate

In addition to the above mentioned influences on ring width correlations and climate, species-specific responses also define tree-ring pattern and their relations to climate (Fritts 1966).

Juniperus virginiana, for instance, built false rings when environmental stresses such as droughts occur. It was found that in Nebraska, when summer months were exceptionally dry, but followed by an autumn with high precipitation, resulted in intra-annual density fluctuation being built. Due to drought, water is limited and fewer cells for water transport are used. Then cells with thick walls for stabilisation are built. After drought, when water was available again, cells with thin walls for water transport were built. The pattern of a thin-walled cells to tick-walled cell and thin-walled cells again result in an additional tree ring. The ring boundary triggered by drought is unsharp. This smooth change allows the differentiation of intra-annual density fluctuations and annual rings. Annual rings show abrupt changes between thin-walled cells early wood and thick-walled cells in late wood. In dry years, *J. virginiana* showed false rings in mostly all the stand densities (Cherubini et al. 2003; De Micco et al. 2016; Edmondson 2010). However*, P. ponderosa* did not show false rings.

For *P. ponderosa*, water availability, which is connected to precipitation, stand density and ground water availability, were identified as the dominant factors over tree-ring width, whereas temperature only plays a subordinate role (Kusnierczyk & Ettl 2002; McDowell et al. 2003). For *J. virginiana*, in their experiment, Volder et al. (2010) modified temperatures and precipitation regimes as a simulation of future climate scenarios for investigating the reactions of *J. virginiana* and three other species. They redistributed 40 percent of precipitation during summer to spring and autumn to intensify summer drought. During all treatments, survival of *J. virginiana* remained high and no mortality related to droughts was measured. The growth of *J. virginiana* therefore could relate to water availability and temperature at the same degree (Volder et al. 2010).

7.2.4 Palmer Drought Index (PDI)

Not only correlations between tree-ring widths and precipitation and temperature were found, but also with the PDI. The most numerous and most significant correlations resulted for *J. virginiana* at mid and dense plots at the NNF, followed by *P. ponderosa* also at the NNF, at one sparse and two dense plots. At HRN and PPN only three significant values resulted, indicating that these two sites are less limited by droughts. At HRN and PPN, temperatures are slightly higher, but mean annual precipitation is much higher than at the NNF (Wilhite & Hubbard 1998). Therefore trees at the NNF are more exposed to drought. This is supported by the PDI, which shows more years with extreme droughts at the NNF compared to HRN and PPN. Most significant values were found from April to September. Since the PDI is composed of different factors such as runoff, soil recharge, deep percolation, soil moisture conditions and evapotranspiration, which are closely linked to precipitation and temperature, the findings that drought during growing season has a high negative impact on tree growth, is underpinned (Eggenmeyer et al. 2006; Eggemeyer et al. 2009; Fritts 1976; Palmer 1965; Seiler et al. 2017; Wilhite & Hubbard 1998). In regard to the stand density, mostly dense plots showed higher correlations.

There, water availability may be limited due to competition. At sparse plots local factors as exposition, slope, aspect, depth to groundwater or competition with other species seem to have a strong influence (Belsky 1994; Gosselin et al. 1999; Gosselin et al. 2006; Kusnierczyk & Ettl 2002; McDowell et al. 2003).

7.2.5 Stepwise Linear Regression Modelling (SLRM)

Investigating the explanatory power of precipitation and temperature, the influence of other factors on tree-ring width can be estimated. By analysing the explanatory power of temperature and precipitation the results from the SLRM give additional significance to the calculated correlations between tree-ring width, climate and PDI.

The strongest explanatory power was found for two plots at HRN, followed by two at PPN and one at the NNF. At these plots more than the half of ring width was statistically explainable by temperature and precipitation. At all other plots temperature and precipitation were only able to explain less than the half of ring width.

Growth of trees at the eastern Nebraska sites, HRN and PPN are more climatically dominated than at the NNF, even though at the NNF precipitation is lower. At HRN and PPN, due to the soil properties, the supply of nutrients and water is high, influence of fires is negligible and monitoring and interventions to improve trees' health are perhaps more frequent (Schweingruber 1996). As a result competition in regard to the mentioned factors is low, resulting in tree-ring widths dominated strongly by climate factors. At the NNF, limiting factors are more numerous: High competition in water availability, soil moisture, aspect, slope, shading, radiation, drought stress, disturbance of fires and cattle and low nutrient availability due to the soil properties result in weakened explanatory power of temperature and precipitation (Fritts 1966; Fritts 1976; Oberhuber et al. 1998; Seiler et al. 2017). Mostly water availability may dominate the correlations. The hydrological settings are remarkably different on dunes and also between interdunal valleys, even over short distances due to water accumulation in topographic depressions and the slope of the local relief (Gosselin et al. 1999; Gosselin et al. 2006). In regard to the results of the SLRM, climatic factors influence tree-ring growth in all sample areas. But the competition for the other mentioned factors, disturbances and influence of topography on water availability at the NNF are higher than at HRN and PPN. Therefore plots at the NNF showed lower adjusted R^2 values. Other studies also found no strong correlations between tree-ring width, temperature and precipitation. When cores were taken from locations, where no clear limiting factor exists, local conditions and predominantly not climatic factors seem to influence the tree-ring growth (Oberhuber et al. 1998; Seiler et al. 2017).

7.3 Stable Isotopes

The stable isotopes were analysed to investigate the water-use efficiency (WUE) of *P. ponderosa* and to link stable isotopes with stomatal conductance and photosynthetic capacity. To understand the relations between climate and stable isotopes the conceptual model of Scheidegger et al. (2000) was applied. In addition, correlations with climate were calculated to evaluate the reliance of stable isotopes on climate.

7.3.1 WUE

The stable isotope of carbon, ^{13}C, in tree rings was analysed to investigate water-use efficiency (WUE) variations and the adaptation of *P. ponderosa* to dry environmental conditions. This is possible due to the well-established relationship between WUE and carbon isotope fractionation during photosynthesis (Farquhar, Ehleringer & Hubick 1989).

The curves of the WUE in the NNF at sparse and dense sites only showed small differences. Dense sites showed slightly higher values than sparse sites. That could be a sign of higher competition for water. At the sparse site PPN, higher WUE, compared to HRN was found, but none of them was significant. Comparing the WUE at the NNF with HRN and PPN, higher WUE values were found for the NNF. At all sample sites, the tendency to increased WUE over time exists. This increase is most likely related to the increase in atmospheric CO_2.

Various studies have shown a relation between WUE and increased atmospheric CO_2 levels. CO_2 is linked to air temperature and temperature is an important climatic factor determining WUE (Altieri et al. 2015). Three main influences of elevated CO_2 to WUE can be summarised: Firstly, increased CO_2 and therefore increased air temperatures lead to decreasing g_1 and resulted in lower transpiration rates. Stomata tend to close to reduce water loss. This closure usually results in increased WUE. Secondly, A_{max} can be increased due to elevated CO_2. This fact was predominantly observed in short term studies. Thirdly, the combination of declining g_1 and increased A_{max} lead to strongly enhanced WUE. Other studies have reinforced this assumption: forests were artificially fumigated with CO_2 which resulted in increased WUE. Moreover, changes in temperature and CO_2 concentration together with climate change lead to a restricted function of stomata or stomatal density reduction. Responses to increased CO_2 are species and tree-specific and depend on their ability to use water and nutrients efficiently. Other factors such as temperature, soil moisture and other microclimate differences affected WUE of each tree differently (Battipaglia et al. 2013; Bégin et al. 2015; Eamus 1991; Field et al. 1995). At the NNF precipitation is lower than at HRN and PPN. This fact, together with the generally increased temperature and atmospheric CO_2 in the region and lower available moisture, can explain the differences at the sample sites. Subsequently the increase in A_{max} due to elevated CO_2 and the decrease in g_1 extend the WUE. On the other hand, the higher temperatures and lower precipitation, together with the CO_2 concentration increase may have reduced the stomatal function and density at the NNF more pronounced than at HRN and PPN (Eamus 1991).

In the water limited environment at the NNF, presumably dense stands would have shown much higher WUE compared to sparse plots as a result of higher competition. In the present case, however, this fact is not as pronounced as it could have been assumed. Thinning studies by McDowell et al. (2003) and by Skov et al. (2004) have shown a decreasing WUE. Due to the thinning, increased light and nitrogen availability, together with lower competition for water caused a greater increase in A_{max} and g_1 and therefore lower WUE. At the NNF no significant differences between sparse and dense stands were found. Probably, trees at dense, as well as at sparse sites need a high WUE to survive in the dry area of the NNF anyway. Competition, light and nitrogen availability, other microclimatic influences and also the stand density only play a subordinate role (Battipaglia et al. 2013; Bégin et al. 2015). Competition is also reduced because of groundwater at the study area at around 7 m depth. *Pinus ponderosa* reaches the groundwater due to a rooting depth of around 12 m (Burns & Honkala 1990; Eggenmeyer et al. 2006; Richard & Stephan 2008).

Further, in regard to the ongoing increase of atmospheric CO_2, an increasing WUE would be expected. However, no significant increases resulted at HRN, PPN, as well as in the NNF. Studies have shown that recently a saturation of the WUE adaptation to atmospheric CO_2 took place in mature trees at a level of about 380 ppm. The increase in atmospheric CO_2 does not rise in line with WUE and therefore, increasing CO_2 does not necessarily lead to increased WUE and increased growth. Nutrient limitations are presumed to additionally drive the saturation of WUE to increasing CO_2 (Peñuelas et al. 2008; Peñuelas et al. 2011; Waterhouse et al. 2004).

7.3.2 δ^{18}O / δ^{13}C Relations

The δ^{18}O / δ^{13}C relation is determined simultaneously by g_1 and A_{max} which are influenced by environmental and plant intern factors (Scheidegger et al. 2000). The isotopic ratio at dry sites is characterised by enhanced stomatal resistance, therefore higher δ^{13}C and higher oxygen isotope enrichment in leaf water, which results in higher δ^{18}O of organic matter. Increased δ^{13}C results of periods of low precipitation or water stress, whereas δ^{18}O represents the prevailing humidity and soil water conditions, but also temperature. Values of δ^{13}C are mostly influenced by macroclimate (Bégin et al. 2015; Saurer et al. 1995; Saurer et al. 1997). Analysing both, δ^{13}C and δ^{18}O therefore help separating photosynthesis-related and water-related influences on trees.

Values of δ^{13}C were higher at the NNF than at HRN and PPN almost every year. At the NNF, stomatal conductance must have been reduced or photosynthetic capacity increased. Since it is known that drought stress results in higher δ^{13}C values, trees at the NNF seem to suffer more from droughts than trees at HRN and PPN (Eggenmeyer et al. 2006; Scheidegger et al. 2000).

In regard to δ^{18}O, no significant differences between the NNF, HRN and PPN could be found. It can be assumed that stomata were more often closed at the NNF, due to dry air which triggers stomata closure and trees at the NNF suffer more from water stress and drought than trees at HRN and PPN (Scheidegger et al. 2000). These findings agree with the correlations between tree-ring width and climate. Correlations were more frequently significant and reactions to climate were more pronounced at the NNF compared to HRN and PPN.

Within the NNF, differences depending on stand density were small. The sparse sites showed more samples with high $\delta^{18}O$ values than dense sites. The same pattern was detectable for HRN and PPN. At PPN the $\delta^{18}O$ values were higher than at HRN. Since the values of ^{18}O are higher in rainfall than in deep, long stored groundwater (Allison & Hughes 1983), sparse sites at the NNF and at PPN presumably do not use as much groundwater as trees at dense sites in the NNF and at HRN do. Water availability in upper soils at sparse sites seems to be higher than at dense sites. This observation corresponds with the soil moisture measurements of Eggenmeyer et al. (2006): They showed that soils until a depth of 3 m were dryer at dense sites than in open areas. Saurer et al. (1997) support these findings. They found that isotopic ratios are related to soil moisture and that higher ratios resulted at drier sites. At dense sites competition is higher and therefore to succeed, trees have to take up water from deeper lying layers earlier than at sparse sites.

The depth of water taken up by plants is closely related to seasonal variations in groundwater depth and their root structure. Different rooting patterns are understood as adaptations to competitive environmental strategies (Ehleringer et al. 1991; Roden & Ehleringer 2007). The success of trees to survive in the NNF depends on soil moisture, root structure and their ability to reach different soil layers (Schenk & Jackson 2002). At the NNF, in the upper soil, grasses are the most competitive species, but trees' roots reach deeper soil layers or even groundwater (Belsky 1994). During wet season, predominantly water from the upper soil and so from the actual precipitation is taken up by lateral roots. A smaller amount is taken from deeper lying layers by the plants' tap root. On the contrary, in dry seasons, groundwater is the dominant source of water, taken up by the tap root (Dawson et al. 1996).

Eggenmeyer et al. (2009) found similar patterns for *P. ponderosa* and *J. virginiana* at the NNF. Both species are able to take up water from different depths, depending on the environmental conditions. During winter, water was predominantly taken up from deep layers (below 0.9 m depth). In spring, if precipitation occurs, mostly water in the upper layers was used by the trees, and newly built lateral roots are found, taking up the water from upper layers. During growing season, different strategies were used by the species. *Pinus ponderosa* preferentially took water from 0.05-0.9 m, whereas *J. virginiana* acquired water from 0.05-0.5 m. Later, water was mostly taken up from soil layers between 0.5-0.9 m and therefore the dependence of precipitation during growing season decreased. In September, when soil moisture and precipitation were at their minimum, water was taken from below 0.9 m (Eggenmeyer et al. 2009).

In the present study only *P. ponderosa* was investigated isotopically. As seen in wet seasons, mostly water from upper soil layers was used. During dry periods water from deeper layers was taken up. Therefore differences in $\delta^{18}O$ values between the sample sites and the densities are expectable. The plasticity to take water from different soil depth and the groundwater availability allow the trees in the

NNF to survive and to recover from drought stress (Eggenmeyer et al. 2006; Scheidegger et al. 2000). Moreover this explains the small differences between the NNF and HRN and PPN in $\delta^{18}O$ values.

7.3.3 Correlations $\delta^{13}C$ and Climate

To evaluate the reliance of $\delta^{13}C$ on climate, correlations were calculated. Only for the PDI at the NNF, significant values ($p < 0.05$) were found. January, February, March, April at dense sites and January, February, March, April and July at sparse sites were correlated significantly to the PDI. No significant correlations resulted for HRN and PPN. Thus, values of $\delta^{13}C$ at dry sites are higher and more strongly influenced by climate than $\delta^{13}C$ values at more humid sites (Saurer et al. 1995). It can be confirmed that trees at the NNF suffer more from droughts than trees at HRN and PPN. This fact is supported by the calculations of the correlation between climate, tree-ring width and the PDI. These correlations showed a higher frequency of extreme droughts in the region of that at the NNF, compared to HRN and PPN. At the NNF, seven years of extreme droughts within the investigated 20 years were reported, whereas at HRN and PPN only two years were extremely dry.

7.3.4 Correlations $\delta^{18}O$ and Climate

To investigate the dependences of $\delta^{18}O$ and climate, correlations were calculated. Significant values only resulted for precipitation of the actual year. They were found from September to December at the NNF and in April, May and June at PPN. No clear patterns in regard to the stand densities were found. As a result, $\delta^{18}O$ values do not rely much on climate and stand density. The influence of storage time may dominate $\delta^{18}O$ values. If trees alternatively used precipitation or groundwater no consistent relationship to climate may be expected.

7.3.5 Outstanding $\delta^{18}O$ and $\delta^{13}C$ Values

The two highest $\delta^{18}O$ values, which also showed outstanding $\delta^{13}C$ values, now can be set in the context of the discussed results. During dry periods with water stress $\delta^{13}C$ values increased. The $\delta^{13}C$ / $\delta^{18}O$ relations are dependent on soil moisture, and therefore the dryer a site is, the higher are the isotopic ratios (Saurer et al. 1997). At the NNF in the years 2000, 2002 and 2012 the highest ratios were measured. These isotope ratios are consistent with extreme droughts recorded in these years. To reduce water loss, g_1 was decreased whereas A_{max} maintained and WUE increased (see also Results WUE). At HRN and PPN, the years 2002 and 2012 showed the highest $\delta^{18}O$ values and also high $\delta^{13}C$ values. The PDI for 2002 showed extreme droughts whereas in 2012 no extreme droughts were measured but five consecutive months with severe drought. In these years increased WUE was measured also for HRN and PPN.

Apart from NNF sparse, all $\delta^{13}C$ values were part of the lowest values in all the measurements. That means no severe water stress strained the trees. At the NNF in 2006 and 2009 the lowest $\delta^{18}O$ were measured. In 2009, low $\delta^{13}C$ values were also measured, whereas 2006 was higher with $\delta^{13}C$. In 1998 and 2010 lowest values were measured at HRN and PPN. According to the PDI, all years apart from 2006, were not affected by droughts. In 2006 extreme drought was reported and tree rings were unusually narrow (Eggenmeyer et al. 2006). Presumably growth was heavily limited due to water stress, as expressed in high $\delta^{13}C$ values, which significantly correlated with the PDI. Not even groundwater was taken up and trees were unable to recover.

7.4 Future Climate Change

Due to the ongoing climate change, presumably droughts will occur more often. To understand how *P. ponderosa* and *J. virginiana* will react to them, the findings from above will be set in the context of ongoing studies.

In regard to future climate changes, precipitation, temperature and competition will be the determining factors. The behaviour of *P. ponderosa* is uncertain, because of the high dependence on precipitation which is hard to predict (Kusnierczyk & Ettl 2002). *Juniperus virginiana*, as shown by Volder et al. (2010), is able to adapt to changes in precipitation and temperature regime. The species is very competitive, drought-resistant and is able to maintain physiological activity under water stress over a longer time than *P. ponderosa* (Bihmidine et al. 2010; Briggs et al. 2002; Burns & Honkala 1990).

At the NNF, trees' main competitors are prairie grasses. Trees are only successfully surviving if they take up water from different layers as the prairie grasses do. If trees get established, grasses suffer from shade, competition in nutrients and in physical space. Due to the high adaptability of *J. virginiana* to future climate scenarios and due to the high plasticity in water up take from different soil depths, presumably grasses will be supressed and disappear from areas where trees are prevalent (Awada et al. 2013; Eggenmeyer et al. 2006; Eggemeyer et al. 2009; Polley et al. 2013; Volder et al. 2010). This is supported by models from Daly et al. (2000), which showed that deeply rooted trees, using water from deep soil layers, are highly competitive to grasses. Their simulations concluded with the absence of fire, trees will dominate over grass lands.

Increasing temperatures together with decreasing precipitation or enlarged dry periods will reduce soil moisture predominantly in the upper soil. There, grasses take water up. Then, they will suffer from water stress and more competitive trees will grow and shade them. This, in turn reduces their growth again. If trees are rooting at same depths as grasses, grasses will dominate. Additionally, if summers are getting dryer, herbaceous vegetation will be a very successful competitor to trees (Ehleringer et al. 1991).

Climate change brings warmer temperatures, higher amounts of ozone in the atmosphere, less and modified precipitation patterns and increases in atmospheric CO_2 as scenarios. Then, fires may be more frequent despite human control, which allows grassland to extend and eventually get higher survival rates than trees (Hulbert 1988; Polley et al. 2013). Further, the interactions of droughts with ozone influences the stomata closure and reinforce water stress what in turn affects WUE and survival rate of the trees.

Comparing these findings with the NNF, ground water has to be taken into account. Since it is known that net photosynthesis is highly correlated with stomatal conductance, temperature and soil water, as long as groundwater is available for trees, they presumably will be able to survive even extreme droughts and regenerate fast (Kaul 1998; Panek & Goldstein 2001; Wilhite & Hubbard 1998) Short term droughts may have small impact on Sandhills ecosystem because of the groundwater reservoir (Bleed 1998). If droughts occur more often and precipitation amounts get lower, shift in ecotones, invasion of non-native species and water demand of vegetation and humans rise. In addition the hydrological cycle may change and groundwater reserves may decrease. Since groundwater is the main driver for economy and ecosystems in the Sandhills, momentous effects and losses have to be expected with increasing water demand (Archer 1995; Archer et al. 2000; Bleed 1998; Briggs et al. 2002; Briggs et al. 2005; Brooks et al. 2004; Brown & Carter 1998; Engle & Moseley 1996; O'Connor et al. 2014).

A positive effect of the high potential of tree species surviving in the Sandhills is that elevated CO_2 in the air may be reduced by woody plant encroachment, because forests can act as sinks for carbon. This would lead to more incorporated carbon, which is desired to reduce the magnitude of climate change (Archer et al. 2000; McKinley & Blair 2008). The existing trees may not act as a beneficial carbon sink because their growth is not linearly coupled with increasing atmospheric CO_2 (Peñuelas et al. 2008; Waterhouse et al. 2004). A negative effect of high temperature, not found in the analysis of tree-ring width but in other studies, is the mortality of seedlings under high temperatures. If they additionally suffer from root competition, their taproot development is not rapid enough to reach deep lying water to overcome competition and high temperatures (Kolb & Robberecht 1996).

To conclude, different driving forces such as climate change, land management or other disturbances may facilitate plant invasion, resulting in a shift in plant communities, biodiversity and soil properties. This, in turn, leads to modified litter composition, rooting pattern and vegetation cycle. Further, soil moisture, local hydrology and nutrient availability are affected, leading to shifts in ecosystems with socioeconomic impacts, as for instance the Dust Bowl and the thereby caused economic crisis in 1930 (Archer et al. 2000; Briggs et al. 2005; Knapp et al. 2008; Ramankutty 2008).

All in all, the stated hypotheses are supported by the results of the present thesis: The reactions of *P. ponderosa* to droughts were less pronounced than the reactions of *J. virginiana*. For both species, the response to drought was stronger in dense plots than in sparse plots, presumably due to the high competition with other trees. In regard to the WUE and the stable isotope analysis, *P. ponderosa* and also *J. virginiana*, were able to take up water from different soil depths, depending on the prevalent soil moisture conditions and competition with other vegetation species. Their root structure, comprising of a massive taproot and small roots, allow this plasticity. By comparing the sample sites at the NNF with the sites in eastern Nebraska, HRN and PPN, the abundance of tree-ring growth with precipitation and soil moisture stands out. In the NNF, more limiting factors exist due to soil characteristics, precipitation and temperature pattern and competition. Therefore, plots at the NNF were more frequently and stronger correlated with climate than HRN and PPN. The explanatory power of temperature and precipitation was smaller at the NNF than at HRN and PPN because of the additional limiting factors at the NNF. Nutrient and water availability, light, wind, rooting space, soil, fire, air pollution, slope, aspect, influences of human and animals, the WUE and the stomatal regulation and competition for all the mentioned factors with the understory and other tree species, were elected as limiting factors. While analysing the results, it has to be noted that at the NNF, depending on the exact location of trees in the dune landscape, varying groundwater is available and may distort correlations and the influence of competition (Gosselin et al. 1999; Gosselin et al. 2006).

Exact predictions about the behaviour of the tree species under future climate change are difficult to make, because knowledge about the groundwater availability, climate change scenarios on a regional scale, expansion of exotic and invasive species, interactions between grazing, fire regime and soil type, interactions between climate and soil water and land use managements is limited (Polley et al. 2013). Further research is needed to overcome these uncertainties.

8 Conclusions

The performed investigations led to interesting insights in the ongoing climate change, the shifts in ecotones and their consequences for vegetation, climate and humans. By the example of the two invasive species, *P. ponderosa* and *J. virginiana*, these processes were examined. Starting with humans, who supported the implementation and encroachment of invasive species by planting them as shelter belt to be protected from soil and wind erosion, by extensively raise them in the Nebraska National Forest and also by suppressing fire which would control the dispersal to a certain degree. With the investigations in the Sandhills it could be shown that *P. ponderosa* and *J. virginiana* are able to adapt to changing climate and other changing environment conditions, as competition, nutrient and water availability. Their reactions were species specific, but up to now both were able to survive in the Sandhills, despite extreme drought and a drastically limited environment with high competition.

The survival of *P. ponderosa* and *J. virginiana* in the Sandhills of Nebraska and their further outspread is likely, as long as groundwater is available and fire rarely occurs. If temperatures rise, groundwater reserves deplete and the likelihood of fire increases. As a result, prairie grasses will become a strong competitor.

Encroachments of trees and shifts in ecotones are not processes isolated to the Sandhills. All over the globe, such change can be identified. How such areas develop, and the consequences for mankind and the ecosystem will have to endure, is unknown. It is also uncertain if trees, which are often seen as carbon sinks in the terrestrial carbon cycle, will fulfil the expectations of lowering the atmospheric CO_2 and therefore decelerate and lower climate change. These interactions are subject to actual research, but it is almost certain that vegetation will find a way to survive, even in the Sandhills of Nebraska.

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Personal Declaration

I hereby declare that the submitted thesis is the result of my own, independent work. All external sources are explicitly acknowledged in the thesis.

Rahel Aus der Au

Place / Date

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Signature

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