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Tree Rings of *Pinus ponderosa* and *Juniperus virginiana* Show Different Responses to Stand Density and Water Availability in the Nebraska Grasslands

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ABSTRACT.—Changes in climate, land use and management have led to an increase in woody species encroachment into grasslands, threatening key ecosystem services and resilience. This study uses dendroecological techniques to investigate acclimation strategies of two native woody species, *Juniperus virginiana* and *Pinus ponderosa*, to spatial and temporal variability in precipitation and stand density in Nebraska (NE). Two locations in Eastern NE and one in Western NE, were selected and tree cores for ring-width measurements were collected. Stable Isotope ratios of carbon were analysed to investigate water use efficiency (WUE), and stable isotope ratios of oxygen were used to understand stomatal conductance and control. Our results showed trees in dense stands exhibited less intra-specific variability in response to climate and narrower tree rings than sparse open stands, with *P. ponderosa* being more responsive to density and climate variability than *J. virginiana*. Populations in the drier Sandhills grasslands of Western NE were more dependent on intra- and inter-annual precipitation and generally more impacted by drought events than those in the East. Eastern NE trees were less limited by drought and displayed lower WUE relative to Western location, even though temperatures were slightly higher, but this was compensated for by the overall higher precipitation levels in the East. Generally, above average winter temperatures were positively correlated with ring widths, while temperature extremes during the growing season were negatively correlated. Although years of extreme drought events were visible in the tree-ring width patterns for both species independent of stand density and location, it seems that once the trees are established and have access to soil moisture, the current climate variability and extremes in NE do not limit or cause a permanent decline in growth of either species.

INTRODUCTION

Changes in climate, land use, and anthropogenic management, such as fire regime and livestock grazing, have contributed to an increase in woody species encroachment into grassland and

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savanna ecosystems across the globe (Archer, 1995; Archer *et al.*, 2000; Briggs *et al.*, 2002a). This trend has accelerated in recent decades, leading to directional and sometimes persistent shifts from grasslands to open and, in some cases, closed canopy forests (Wilcox, 2010; Awada *et al.*, 2013; Nippert *et al.*, 2013). Grasslands provide significant socio-economic and ecological services (Briggs *et al.*, 2005) and contribute to around 35% of global net primary productivity (Chapin *et al.*, 2011). Encroachment of woody species into grassland ecosystems has modified and, in some instances, threatened key ecosystem services (Wilcox, 2010; Twidwell *et al.*, 2013), such as forage production, biogeochemical and ecohydrological cycles, fire regime, wildlife habitat, and the overall resilience of the ecosystem (Archer, 1995; Archer *et al.*, 2000; Briggs *et al.*, 2002b; Brooks *et al.*, 2004; Briggs *et al.*, 2005; Awada *et al.*, 2013; O'Connor *et al.*, 2014; Msanne *et al.*, 2017).

In the Great Plains of North America, several woody species have contributed to the shift from grass-dominated communities to savannas and wooded areas. For example mesquite (*Prosopis glandulosa* Torr.) has been encroaching and replacing grass species in Texas (Archer, 1995), whereas ponderosa pine (*Pinus ponderosa* P. & C. Lawson) has been expanding from its historical grassland-woodland ecotone into grasslands in the Black Hills of South Dakota (Shinneman and Baker, 1997) and the Pine Ridge and Niobrara Valley of Nebraska (Steinauer and Bragg, 1987). Eastern redcedar (*Juniperus virginiana* L.) has been expanding at an alarming rate across the Great Plains (McKinley and Blair, 2008). It can now be found in every state east of the 100th meridian (McKinley and Blair, 2008; Starks *et al.*, 2014) and has encroached into 7 million ha of grasslands, savannas, and riparian forests (Willson *et al.*, 2008; Eggemeyer *et al.*, 2009; Msanne *et al.*, 2017).

The semiarid grasslands of the Nebraska Sandhills cover an area of 50,000 km² and are considered the largest stabilized formation of sand dunes in the Western Hemisphere. They make up a unique and fragile ecosystem that provides economically (*i.e.*, livestock production) and ecologically important services. The Sandhills are, like other areas in the Great Plains, experiencing an encroachment of the two native woody species, *J. virginiana* and *P. ponderosa*. Both species have been shown to grow under a wide range of soil-water conditions and found to follow different adaptive and acclimation strategies to succeed in semiarid grasslands. *Juniperus virginiana* behaves like a drought-tolerant species and is able to maintain physiological activity at lower soil-water content, whereas *P. ponderosa* adopts a drought-avoidance strategy with strong stomatal control (Bihmidine *et al.*, 2010). What is not clear is how these species perform or how they respond to several consecutive years of drought, which are common in the Great Plains and the Nebraska Sandhills.

The few studies that have addressed the responses of *J. virginiana* and *P. ponderosa* to the environment in the Sandhills have mainly focused on ecophysiological and hydrological responses, and plant-soil processes as impacted by climate and stand density (*e.g.*, Eggemeyer *et al.*, 2006, 2009; Awada *et al.*, 2013; Msanne *et al.*, 2017). None of them has used tree rings to analyse the physiological performance and growth of woody species under different precipitation regimes over time.

To investigate the impacts of anthropogenic management and climatic variability and extremes on the performance of woody species in temperate regions such as the Nebraska Sandhills, woody species annual ring growth and the stable isotope composition of carbon (C) and oxygen (O) can be used (McCarroll and Loader, 2004) to study formation and growth of tree rings as influenced by factors, such as stand density (Aussenac and Granier, 1988; Bréda *et al.*, 1995; Canellàs *et al.*, 2004; Di Matteo *et al.*, 2010), site characteristics including precipitation pattern and gradient, management practices, soil nutrients, and the species growth habit, age, and genetics (Fritts, 1966; Schweingruber, 1996). The isotopic

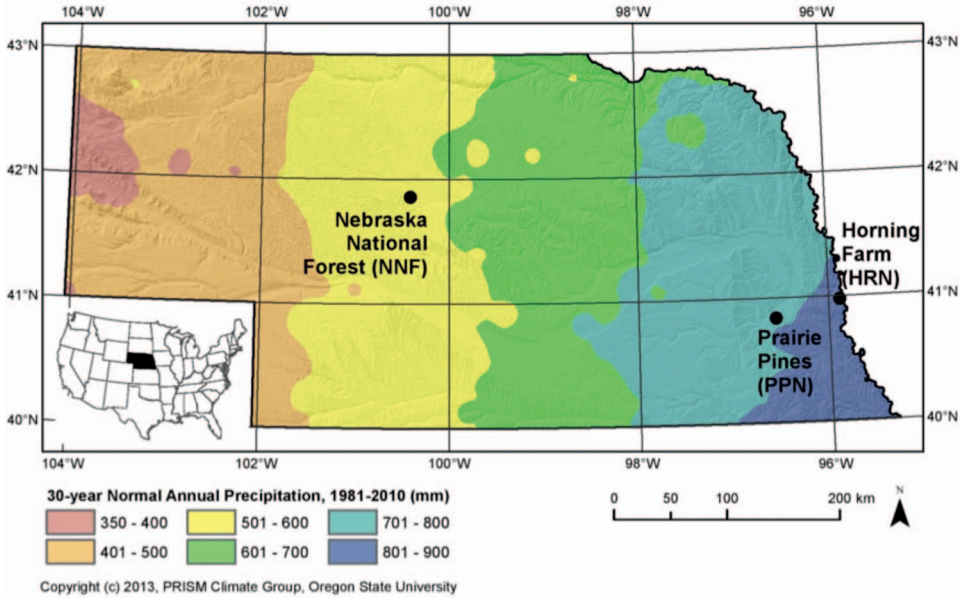


FIG. 1.—The three site locations in Nebraska: HRN and PPN (Eastern NE) and NNF (Western NE)

ratios of O and C are influenced by both the biotic and abiotic environment (Stuiver and Braziunas, 1987; Beyers *et al.*, 1992; Saurer *et al.*, 1995; Niemelä *et al.*, 1997; Leffler and Evans, 1999), and have been used to reconstruct past plant physiological processes related to water availability (Battipaglia *et al.*, 2010, 2014).

In this study we hypothesized the decline in precipitation from east to west in Nebraska (NE) affects the growth and performance of *J. virginiana* and *P. ponderosa* trees and increases their vulnerability to drought. Also, we predicted *P. ponderosa* will be more susceptible to precipitation decline than *J. virginiana* due to their different drought resistance strategies and increase in stand density exasperates the ability of both species to respond to intra- and inter-annual variability in site microclimate, especially in Western NE where water is a limiting factor for growth. To address this, we used dendroecological (*i.e.*, the study of tree rings) and stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) to examine the growth, performance, and water use efficiency of the trees, and assess the species acclimation strategies across density and precipitation regimes in NE. Our findings should improve our understanding of the ecology of these two species and help develop predictive models to determine future expansion and performance scenarios with the climate change anticipated for the region.

METHODS

Study sites.—Two locations in Eastern NE and one location in Western NE were selected (Fig. 1) to investigate the impacts of long-term precipitation gradient and stand density on the performance and growth of the two species *J. virginiana* and *P. ponderosa*. In Eastern NE we chose Horning Farm (HRN) and Prairie Pines (PPN) where the long-term average precipitation is 850 and 730 mm and the average annual temperature 10.4 and 10.7°C, respectively. HRN and PPN are two experimental farms owned by the University of Nebraska

and where original stands of *J. virginiana* and *P. ponderosa* have expanded since they were first planted around 1970. At HRN, located in Cass County, NE (354 m altitude, lat. 40°58'51"N, long. 95°52'30"W), a total of 89 samples were collected from the dense *P. ponderosa* and *J. virginiana* stands. The soils are Marshall silty loam (fine-silty, mixed, superactive, mesic Typic Hapludolls; USDA, 2017). At PPN, situated in Lancaster County, NE (375 m altitude, lat. 40°50'37"N, long. 96°33'51"W), a total of 78 samples were collected from sparse open stands. The predominant soils on this site are Aksarben silty loam (fine, smectitic, mesic Typic Argiudolls; USDA, 2017). Smooth brome (*Bromus inermis* Leyss.) dominates the understory on both sites, with less biomass in the understory of dense stands.

The Western NE location is around 350 km NW of HRN and PPN, at the Nebraska National Forest (NNF, >25,000 ha, 825 m altitude, lat. 41°51'45"N, long. 100°22'06"W). At NNF the average annual precipitation is 570 mm and the mean annual temperature 8.4°C. The forest was established around 1902 on grasslands and was hand planted for the next few decades with several coniferous species, including stands of *J. virginiana* and *P. ponderosa*. The two species later encroached into adjacent open grasslands. The soils at NNF are Valentine fine sand (mixed, mesic, Typis Ustipsamments; Lewis and Kuzila, 1998). A total of 240 samples were collected from nine plots at NNF that differed in stand densities: sparse: <5 stems per 10 m²; mid: 5–10 stems per 10 m²; dense: >10 stems per 10 m². One mid-density stand was an inter-mixture of *J. virginiana* and *P. ponderosa*. The understory at the sparse stands of *P. ponderosa* and *J. virginiana* consisted of perennial grassland community dominated with C₄ species. At the mid stand density, the understory was composed of the same species but with less grass biomass. At dense stands, understory vegetation was absent, with the exception of few individuals of cacti and some species of moss.

Sampling.—A total of 428 cores from 214 trees—with a north- and south-facing core per tree—were collected using standard methods and procedures. Since the stands within each density category were more or less even-aged, only dominant trees were selected. In the Western NE a total of 130 trees were cored (90 *P. ponderosa* and 40 *J. virginiana*), and in the Eastern NE 84 trees (54 *P. ponderosa* and 30 *J. virginiana*). Cores of 0.5 cm in diameter were taken with a three-threaded auger (Haglof Inc., Sweden). The cores were sampled at a height of 1.3 m perpendicularly to the growing axis of the tree. Each core was removed from the borer by an extractor with barbs, labelled and dried. Cores were then fixed into the holder of a microtome and layer after layer approximately 10 µm thick was cut away until the core had a plane surface over its whole extent and the tree rings became clearly visible (Gärtner *et al.*, 2015).

Ring-width measurement.—Tree-ring widths were measured under a Leica Wild M32 binocular microscope (Leica, Germany) to the nearest 0.01 mm with a linear table LINTAB (Frank Rinn, Heidelberg, Germany). The data were recorded, presented and analysed in TSAPWin (Time Series Analysis and Presentation, Frank Rinn, Heidelberg, Germany). After visually crossdating each tree northern and southern core, each sample plot was visually crossdated in TSAPWin (Stokes and Smiley, 1968). The different tree species were crossdated separately. Missing rings were inserted manually to complete the chronology. The visually crossdated data were imported to the program COFECHA for statistical analysis to check the crossdating accuracy (Grissino-Mayer, 2001). Additionally, the *Gleichläufigkeit* (Glk), a measure of the year-to-year agreement between the interval trends of two chronologies based upon the sign of agreement, usually expressed as a percentage of cases of agreement (Eckstein and Bauch, 1969), and the cross dating index (CDI), the combination of the Glk with the *t*-value of the chronology were then determined (Rinn, 2003).

TABLE 1.—Detailed information on the location of the meteorological stations

Location	Station	Altitude [m]	Latitude	Longitude	Timespan
NNF	Halsey 2 W	825	41°54′00″N	100°19′00″W	1900–1989
	Dunning 6 NW	842	41°53′60″N	100°09′00″W	1990–2016
	Bessey Nebraska USR0000NBES	897	41°53′51″N	100°18′39″W	1987–2015
The stations Halsey 2 W and Bessey Nebraska are in NNF, between 2 and 10 km North of the NNF sites, the station Dunning 6 NW 15 km to 18 km Northeast of NNF sites. NNF climate stations Halsey 2 W and Bessey Nebraska are within 0.6 km of each other, whereas the Dunning 6 NW station is 13.5 km to the East (http://hprcc.unl.edu/)					
PPN	Lincoln Agronomy Farm	366	40°51′00″N	96°37′00″W	1921–1954
	Lincoln University Power Plant	354	40°49′23″N	96°42′09″W	1955–1972
	Lincoln Airport	365	40°51′02″N	96°44′51″W	1973–2016
The stations are between 4 km and 16 km from PPN (Lincoln University Farm: 14.5 km, Lincoln Agronomy Farm: 4.5 km, Lincoln University Power Plant: 12 km, Lincoln Airport: 15.5 km.). Distances between the stations ranged between 2 km and 12 km (http://hprcc.unl.edu/)					
HRN	Glenwood 3 SW	299	41°00′34″N	95°46′25″W	1900–2008
	Glenwood	323	41°03′06″N	95°44′57″W	2008–2016
The station Glenwood 3 SW is 9.2 km East of the HRN sites, whereas station Glenwood is 13.2 km Northeast of the HRN sites. The station Glenwood 3 SW is 5 km north of station Glenwood (High Plains Regional Climate Center, University of Nebraska–Lincoln; http://hprcc.unl.edu/)					

Meteorological data.—Detailed information about the meteorological stations from which air temperature and precipitation data were taken are given in Table 1 and Figure 2. The Palmer Drought Index (PDI) values used to calculate correlations between climate data and tree-ring widths (Fig. 3) were obtained from the National Oceanic and Atmospheric Administration (NOAA, 2017). Precipitation and temperature data were obtained from local weather stations (High Plains Regional Climate Center, University of Nebraska–Lincoln).

Data analysis.—All raw ring-width measurements were standardised with the program ARSTAN (Cook and Holmes, 1986) using a 30 y smoothing spline and a variance stabilisation to remove the trees age trend (Cook and Holmes, 1986). Correlations of the tree-ring widths with monthly data of temperature, precipitation and the PDI for each sample plot were calculated using Spearman rank correlations. Temperatures and precipitation of the previous year were included in the analysis. The statistical significances of these climatic factors were tested on a monthly basis and in seasonal combination. To identify which monthly temperature and precipitation amounts influenced tree growth the most, a Stepwise Linear Regression Modelling (SLRM) was applied. We used a forward-backward approach (Cook and Pederson, 2011) and evaluated various models using the Akaike Information Criterion (AIC).

Stable C and O isotopes and Water Use Efficiency.—The combined analyses of isotope ratios of carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) in tree rings provide a mean to assess long-term ecophysiological strategy associated with the site microclimate (Sullivan *et al.*, 2017), with insights onto the relationship between stomatal conductance (g_s) and CO_2 assimilation rate

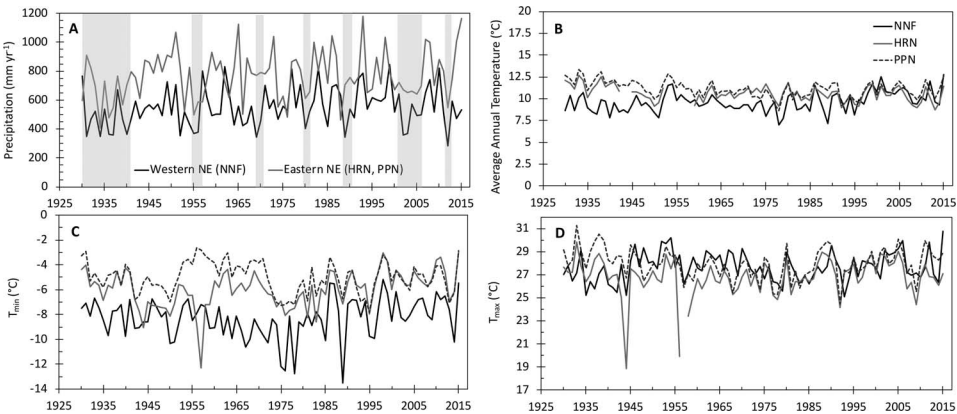


FIG. 2.—Cumulative precipitation in Eastern and Western NE, grey bars indicate years with extreme droughts ($PDI \leq -4$) (A); Annual average temperatures (B); minimum January temperatures (C); and maximum July temperatures (D) in Eastern NE (HRN, PPN) and Western (NNF)

(A) as impacted by the environment (Lévesque, 2014). Specifically, intercellular CO_2 (ci) and water use efficiency (WUE) can be derived from $\delta^{13}C$ in tree rings, due to the linear relationship between ci/ca (intercellular/air CO_2) and $\delta^{13}C$ (Farquhar *et al.*, 1982). Relative humidity (RH) can be derived from $\delta^{18}O$, with the assumption that vapor pressure in the intercellular space is an important parameter that affects g_s . By combining the $\delta^{13}C$ and $\delta^{18}O$ analysis, we can address the limitation of whether CO_2 assimilation rate or photosynthesis is mostly impacted by stomatal or carboxylation limitation. For example a reduction in ci and increase in $\delta^{13}C$ can be interpreted either as reduction in g_s or increase in photosynthesis at a constant g_s (Scheidegger *et al.*, 2000). The $\delta^{18}O$ ratio on the other hand, is dependent on the meteoric source of water, transpirational demands, biochemical fractionation, and organic matter (Battipaglia *et al.*, 2014). Its enrichment is dependent on

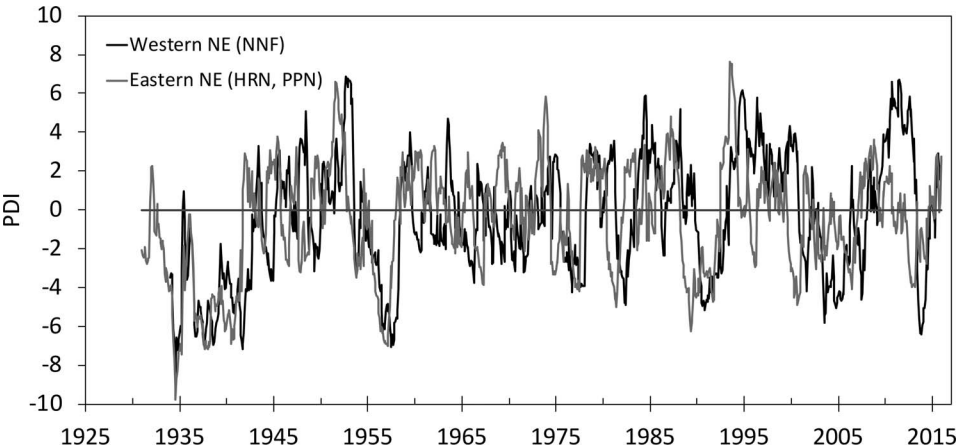


FIG. 3.—Palmer Drought Index (PDI) in Eastern NE (HRN, PPN) and Western (NNF)

vapor pressure deficit (VPD), whereby an increase in VPD or a decrease in RH causes an increase in enrichment (Saurer *et al.*, 1997, Battipaglia *et al.*, 2014). Both isotopes therefore are mediated by changes in g_s at the leaf level associated with soil-water variability and evaporative demands, and their combined measurement can be used to assess acclimation strategies to environmental constraints.

The stable $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ ratios in *P. ponderosa* tree-ring wood, at two sparse and two dense plots in Western NE, one dense plot at HRN and one sparse plot at PPN, of three individual trees per plot were analysed. The 20 years prior to the date of sampling were investigated with annual resolution. The C and O isotope content of *J. virginiana* could not be analysed because there was not enough material available in the wood samples. The samples of *P. ponderosa* were split with a blade cutter and milled in a centrifugal mill (ZM 1000, Retsch, Germany). The extraction of holocellulose was performed as described by Green (1963). The C and O isotope composition was determined on 0.9 mg holocellulose for each sample. For $\delta^{13}\text{C}$ measurements, the samples were combusted to CO_2 at 1080°C using a EURO EA elemental analyzer (EuroVector, Milan, Italy) and analyzed by isotope ratio mass spectrometry (Delta V Advantage Mass Spectrometer, Thermo Scientific, Bremen, Germany). For $\delta^{18}\text{O}$ measurements, the samples were pyrolyzed to CO at 1400°C using a high-temperature oxygen analyzer (HEKAtech, Wegberg, Germany), and the resulting gas was then analyzed with the same mass spectrometer. The results were compared against the primary reference material or standards, the Vienna Pee Dee Belemnite (VPDB) for C, and the Vienna Standard Mean Ocean Water (VSMOW) for O (Matthews and Hayes, 1978). The accuracy was better than 0.1‰ for $\delta^{13}\text{C}$ values and $\pm 0.3\text{‰}$ for $\delta^{18}\text{O}$ values.

The ^{13}C data were corrected to take into account the decrease in ^{13}C in atmospheric CO_2 caused by fossil fuel burning in the last century (Suess Effect; Keeling *et al.*, 1989). The conceptual model of Scheidegger *et al.* (2000) was applied to link stable isotopes with stomatal conductance and photosynthetic capacity, and examine the relations between climate and stable isotopes. Correlations between climate, PDI and calculated isotopes were investigated. In addition, the WUE was calculated from C isotope ratio ($\delta^{13}\text{C}$) as described by Farquhar *et al.* (1982).

RESULTS

Ring-width chronologies.—The patterns of the ring-width chronologies at NNF varied significantly more with stand density than those at PPN and HRN (Fig. 4). Trees at the two Eastern sites (PPN and HRN), on the other hand, had significantly wider rings (average ring width $415.06 \pm 29.49 \mu\text{m}$) than those at the Western sites (average ring width $243.47 \pm 7.86 \mu\text{m}$), probably because they are younger in age, and grow under both higher precipitation regime and soil nutrients. The age of *P. ponderosa* at NNF ranged from 40 to 80 y, and of *J. virginiana* from 24 to 76 y. Trees at PPN and HRN in the East were significantly younger ranging in age from 42 to 46 y for *P. ponderosa*, and 32 to 42 y for *J. virginiana*.

The stands at NNF in the West followed the same pattern: the higher the density of the plot, the more similar and the less variable the chronologies were. When the ring widths of *P. ponderosa* in sparse, mid and dense stands were compared, sparse density stands varied the most (Glk 58; CDI 23), followed by mid (Glk 69***; CDI 39), and then dense stands (Glk 82***; CDI 87) which varied the least.

The tree rings of the oldest *J. virginiana* (Glk 68**; CDI 20) also exhibited less variability than younger trees (Glk 54; CDI 19), but had a quite similar growth pattern. In general the growth of *J. virginiana* was not as affected by stand density as *P. ponderosa*, and *J. virginiana* in sparse and mid density stands were more sensitive to climate than in dense stands. The

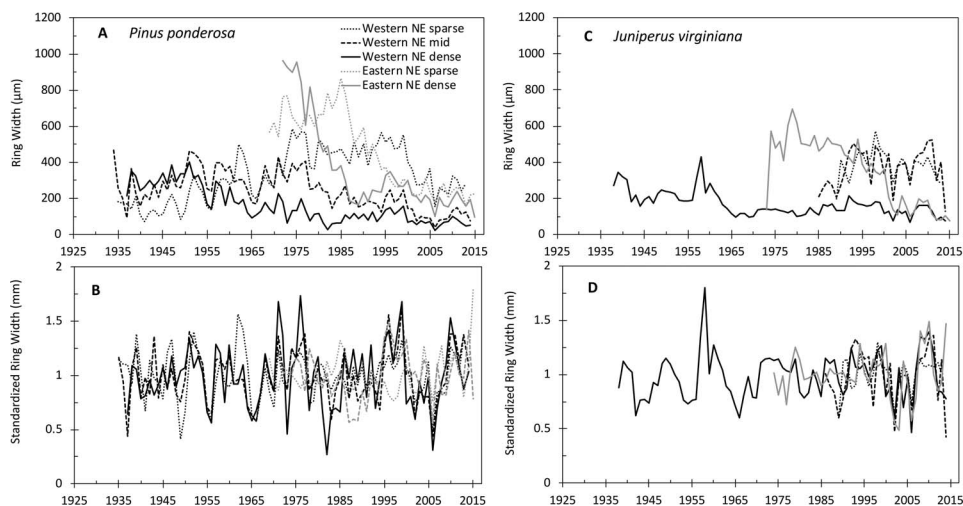


FIG. 4.—Tree ring widths and Standardized ring widths for *P. ponderosa* (A, B), and *J. virginiana* (C, D) in sparse, mid and dense stands in Eastern and Western NE

chronologies of the two species in Western NE were comparable in all stands, but at mid density sites and at one dense site the tree rings of *J. virginiana* were wider than those of *P. ponderosa*. The chronologies of the two species in Eastern NE were within the same range for all stand densities, but in the first years after establishment, the *P. ponderosa* trees at the sparse sites (Glk 90***, CDI 88) were more responsive over a longer time period than those at the dense sites. The growth sensitivity of the trees declined more rapidly at dense than at sparse sites (Fig. 4).

Climatic correlation.—To correlate climate variables with ring-widths, all raw ring-width measurements were standardised. Correlations were conducted over the whole life span of the trees with data for single months combined to reflect the climate during the growing season (Table 2). In Western NE the precipitation between April and August of the current year correlated positively and significantly with *P. ponderosa* ring widths, with the most significant values at dense sites ($P < 0.001$). For *J. virginiana*, significant values were only reported between January and June at mid and dense sites. Ring widths at dense sites were also positively correlated with the precipitation from July to December of the previous year. In Eastern NE, *P. ponderosa* ring widths at dense sites were not significantly correlated with precipitation, whereas at sparse sites, the growing season of the previous and current year, as well as current winter precipitation were significantly correlated with ring widths. The tree-ring widths of *J. virginiana* correlated positively with precipitation from April to June and September to October of the previous year but correlated negatively with current year precipitation from January to March. Additionally, ring widths were positively correlated with precipitation in November and December of the current year.

Overall, precipitation during the growing season was positively correlated with standardized tree-ring widths in the Western NE. In Eastern NE no clear correlation patterns were detectable. The influence of previous year precipitation was generally lower than that of the precipitation of the current year. Tree growth correlated mostly positively with precipitation but mostly negatively with temperature.

TABLE 2.—Stand level standardized tree ring widths correlations with precipitation (p) and temperature (t): “p” and “t” stand for previous year, and “P” and “T” for the present year. Only statistically significant correlations are shown at levels: $P < 0.05^*$, $P < 0.01^{**}$, $P < 0.001^{***}$

Precipitation			Temperature		
Months	Density	Correlation	Months	Density	Correlation
Western NE <i>P. ponderosa</i>			Western NE <i>P. ponderosa</i>		
pND	sparse	−0.258*	tApril	sparse	−0.392***
PAMJ	sparse	0.317*	tApril	mid	−0.428***
PAMJ	mid	0.267**	tApril	mid	−0.373***
PAMJ	dense	0.384***	tApril	dense	−0.231*
PAMJ	dense	0.285**	tApril	dense	−0.258*
PJA	sparse	0.416**	tJuly	sparse	−0.362*
PJA	sparse	0.148**	tJuly	mid	−0.271*
PJA	mid	0.328**	tSeptember	mid	−0.257*
PJA	dense	0.292**	tSeptember	mid	−0.233*
PND	sparse	−0.362*	tSeptember	dense	−0.245*
PND	sparse	−0.227*	TApril	sparse	−0.368*
PND	mid	−0.303*	TMay	dense	−0.231*
			TJuly	dense	−0.27*
Western NE <i>J. virginiana</i>			Western NE <i>J. virginiana</i>		
pJA	dense	0.267*	TJune	dense	−0.337*
pSO	dense	0.270*	TJuly	dense	−0.517***
pND	dense	0.258*	TJuly	dense	−0.297**
PJFM	dense	0.248*	TSeptember	sparse	0.436*
PAMJ	mid	0.417*			
PAMJ	dense	0.492***	Eastern NE <i>P. ponderosa</i>		
PAMJ	dense	0.37***	TJanuary	dense	−0.334*
PAMJ	dense	0.292*	TOctober	dense	0.399**
Eastern NE <i>P. ponderosa</i>			tJune	sparse	0.331*
pAMJ	sparse	0.301*	tSeptember	sparse	0.279*
PAMJ	sparse	0.453**	tDecember	sparse	0.301*
PND	sparse	0.494***	tDecember	sparse	0.312*
			TMay	sparse	0.395**
Eastern NE <i>J. virginiana</i>			TJune	sparse	0.337*
pAMJ	dense	0.421**	TJune	sparse	0.393**
pSO	dense	0.337*	TDecember	sparse	0.566***
pSO	dense	0.474**			
PJFM	dense	−0.313*	Eastern NE <i>J. virginiana</i>		
PSO	dense	0.397*	tJanuary	dense	−0.347*
PND	dense	0.683***	tApril	dense	−0.426**
			tJuly	dense	−0.427**
			tJuly	dense	−0.434*
			TJuly	dense	−0.327*

Combining the months for temperature in the same way we did for precipitation revealed few significant correlations (Table 2), therefore, correlation analyses were conducted on a monthly basis to better represent the impact of temperature on tree-ring growth. In Western NE the ring widths of *P. ponderosa* were negatively correlated with temperature in April, July, and September (up to $r = -0.428$; $P < 0.001$), independently of stand density. For the

current year, only three significant values were found, but the correlation was not as high with the previous year. For *J. virginiana*, significant negative correlations between standardized tree ring widths and temperatures were only observed for June and July (up to $r = -0.517$; $P < 0.001$), and one positive correlation was recorded for September of the current year at a sparse site ($r = 0.436$; $P < 0.05$). For *P. ponderosa* in Eastern NE, only the January temperature was negatively correlated with ring widths ($r = -0.334$; $P < 0.05$), whereas temperatures in June, September, and December of the previous year and of May, June, October, and December of the current year were positively correlated with ring widths (up to $r = 0.566$; $P < 0.001$). In contrast all *J. virginiana* correlations were negative and significant for: January, April, and July of the previous year and July of the current year (up to $r = -0.434$; $P < 0.05$).

Palmer Drought Index (PDI).—To investigate the combined cumulative effect of precipitation and temperature, correlations were performed between standardized ring widths and the PDI for each species (Table 3). *Pinus ponderosa* in Western NE was found to significantly correlate with PDI at one sparse and one dense site throughout the growing season, which indicates that drought stress as expressed by PDI had a significant negative impact on the species. For *J. virginiana* the correlations with PDI were high at one mid and two dense sites throughout the whole year and at another dense site from June to the end of the year (up to $r = 0.692$; $P < 0.001$). In Eastern NE correlations between tree ring widths and PDI were more ambiguous than in Western NE. Only two statistically significant values were found for *P. ponderosa* in September and December ($r = 0.314$; $P < 0.05$) and one for *J. virginiana* in January ($r = 0.309$; $P < 0.05$). Overall, trees in Western NE appear to be more affected by drought conditions than those in Eastern NE, but the site characteristics also play a significant role.

In Western NE less than half the variance in tree-ring widths was explained by climatic factors according to the results of stepwise linear regression modelling (SLRM, Table 1S). This was the case for 90% of the total sites in Western NE (where r ranged between 0.13 and 0.48, except for one dense site *J. virginiana* where $r = 0.62$). At the sites in Eastern NE, climatic conditions seem to exert the main influence on tree-ring widths, where two third of Eastern NE sites were influenced by precipitation and temperature (r ranged between 0.65 and 0.86), whereas stand density had little influence.

Water use efficiency.—Stable isotope analyses were only conducted for *P. ponderosa* as explained earlier. The water use efficiency (WUE) calculated from $\delta^{13}\text{C}$ values ranged from 100 to 125 $\mu\text{mol mol}^{-1}$ for *P. ponderosa* in the Western location (Fig. 5) and were slightly higher than those in Eastern NE, which varied from 90 to 115 $\mu\text{mol mol}^{-1}$. Stable isotopes varied little from year to year at sparse and dense sites, and this variation was not statistically significant. WUE, however, increased from 1996 to 2006 ($P < 0.01$) before it declined. The decline was not statistically significant.

We analysed the relationship between C and O isotopes ($\delta^{18}\text{O} / \delta^{13}\text{C}$), using the conceptual model of Scheidegger *et al.* (2000) to link stable isotopes with stomatal conductance and photosynthetic capacity and climate. We found that the $\delta^{18}\text{O} / \delta^{13}\text{C}$ correlations for *P. ponderosa* in sparse stands ($r = 0.536$; $P < 0.05$) and in dense stands ($r = 0.377$; not significant) in Western NE were less significant than those of in sparse stands ($r = 0.638$; $P < 0.01$) and in dense stands ($r = 0.794$; $P < 0.001$) in Eastern NE. An increase in $\delta^{18}\text{O}$ was accompanied by an increase in $\delta^{13}\text{C}$ (Fig. 6), indicating a strong stomatal control of photosynthesis (A). At *P. ponderosa* dense sites in Western NE, A and g_s were regulated or, alternatively, stomatal control was not tight. Additionally, the two highest $\delta^{18}\text{O}$ values coincided with PDI showing extreme or moderate droughts, whereas the two lowest $\delta^{18}\text{O}$

TABLE 3.—Correlations of Palmer Drought Index (PDI) with standardized ring widths. Only significant interactions are shown at levels: $P < 0.05^*$, $P < 0.01^{**}$, $P < 0.001^{***}$

PDI		
Months	Density	Correlation
Western NE <i>P. ponderosa</i>		
JAN	sparse	0.309*
JAN	dense	0.226*
FEB	dense	0.25*
MAR	dense	0.27*
APR	sparse	0.33*
APR	dense	0.309**
APR	dense	0.272*
MAY	sparse	0.406**
MAY	mid	0.283**
MAY	mid	0.259**
MAY	dense	0.342**
MAY	dense	0.304**
JUN	sparse	0.397**
JUN	dense	0.356***
JUN	dense	0.291**
JUL	sparse	0.408**
JUL	dense	0.347**
JUL	dense	0.305**
AUG	sparse	0.424**
AUG	dense	0.322**
AUG	dense	0.32**
SEP	sparse	0.342*
SEP	dense	0.277**
SEP	dense	0.249*
Western NE <i>J. virginiana</i>		
JAN	mid	0.382*
JAN	dense	0.327**
JAN	dense	0.368**
FEB	mid	0.38*
FEB	dense	0.338**
FEB	dense	0.379**
MAR	mid	0.442**
MAR	dense	0.383***
MAR	dense	0.429***
APR	mid	0.486**
APR	dense	0.414***

TABLE 3.—Continued

PDI		
Months	Density	Correlation
APR	dense	0.488***
MAY	mid	0.581***
MAY	dense	0.465***
MAY	dense	0.551***
JUN	mid	0.623***
JUN	dense	0.428**
JUN	dense	0.456***
JUN	dense	0.519***
JUL	sparse	0.414*
JUL	mid	0.692***
JUL	dense	0.489***
JUL	dense	0.525***
JUL	dense	0.542***
AUG	mid	0.662***
AUG	dense	0.521***
AUG	dense	0.474***
AUG	dense	0.468***
SEP	mid	0.63***
SEP	dense	0.513***
SEP	dense	0.424***
SEP	dense	0.413***
OCT	mid	0.642***
OCT	dense	0.498***
OCT	dense	0.392***
OCT	dense	0.373**
NOV	mid	0.674***
NOV	dense	0.498***
NOV	dense	0.387***
NOV	dense	0.358**
DEC	mid	0.606***
DEC	dense	0.477***
DEC	dense	0.349**
DEC	dense	0.283**
Eastern NE <i>P. ponderosa</i>		
SEP	sparse	0.305*
DEC	sparse	0.314*
Eastern NE <i>J. virginiana</i>		
JAN	dense	0.309*

values occurred in years when no droughts were recorded. When considering the PDI, the calculated climate correlations for $\delta^{13}\text{C}$ resulted in significant correlations from January to May ($P < 0.01$) for Western NE independent of stand density (data not shown), but no significant values were found for Eastern NE. The correlations between $\delta^{18}\text{O}$ and climate

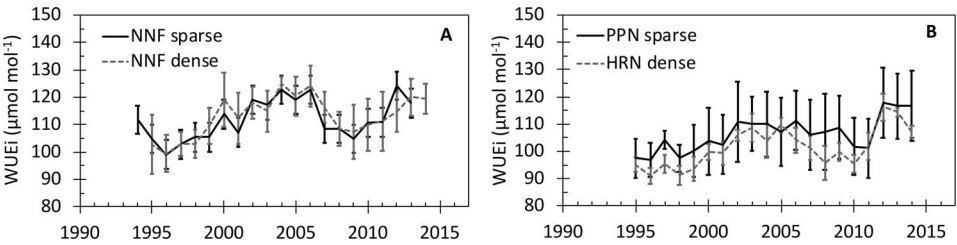


FIG. 5.—Water use efficiency (WUEi) of annual tree rings in sparse and dense stands of *P. ponderosa* in Eastern and Western NE

were only significant for precipitation at sparse and dense sites in Western NE and at sparse sites in Eastern NE ($P < 0.01$; data not shown).

DISCUSSION

Ring-width chronologies.—Tree ring width patterns in Western NE generally differed from those in Eastern NE, although at all locations several synchronous negative peaks occurred, induced by extreme dry years (Fig. 4). In Western NE, *P. ponderosa* ring widths were strongly influenced by stand density which was not the case for *J. virginiana*. This can be attributed to different acclimation and physiological adjustments of the two species. For example, *J. virginiana* in the Sandhills has been shown to maintain photosynthetic activity and stomatal function under wider range of water stress conditions than *P. ponderosa* (Eggemeyer *et al.*, 2009; Bihmidine *et al.*, 2010) and maintain A and g_s under increasing stand density and decreasing nutrient availability (Msanne *et al.*, 2017). The growth patterns of trees at sparse stands varied more individually than at mid and dense stands and the chronologies correlated less with each other (Fig. 4). Unlike open stands resources are often limited and competition is high in dense stands (Stiell, 1970), which could explain why the ring-width

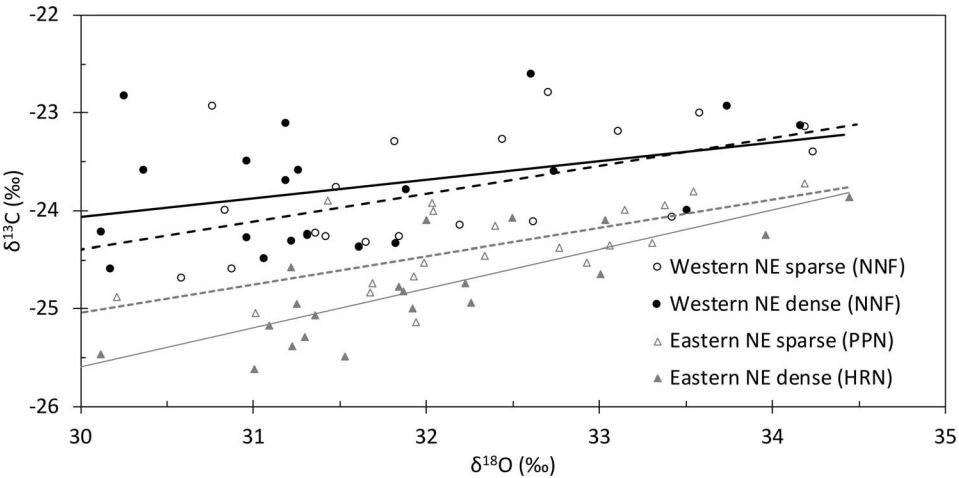


FIG. 6.— $\delta^{18}\text{O}$ / $\delta^{13}\text{C}$ relationship in annual tree rings of sparse and dense stands of *P. ponderosa* in Eastern and Western NE

patterns in dense stands vary less than at other stand densities (Sands and Mulligan, 1990). These findings across sites highlight the importance of microhabitat conditions to the performance of trees (McDowell *et al.*, 2003; Msanne *et al.*, 2017), which in this case are characterised by different temperature, light, wind, precipitation, competition levels, access to ground water, and soil characteristics (*e.g.*, higher water holding capacity and nutrient levels in silty loam soils in the East than in sandy soils in the West). Water availability and access to water were shown to be critical for both species to succeed, which was evident in the tree-ring width patterns for both species independent of stand density and location. In extremely dry years, for instance, 2006 (*see* Fig. 2A), tree rings of *P. ponderosa* were much narrower. Similar results were found for most of the *J. virginiana* stands in Western NE. In semi-arid environments, soil-water content has been shown to be one of the most important factors affecting tree-ring widths (*e.g.*, Cherubini *et al.* 2003). Where the soil moisture was high, growth was faster and wider rings were built (Sands and Mulligan, 1990). Since soil moisture is closely related to drought, it is not surprising that most of the very narrow rings corresponded with drier years.

Climatic correlations.—Climatic conditions in Western NE are characterised by snowmelt in March, followed by a relatively wet period during spring and early summer (April through June), when around 70% of the precipitation occurs (Eggemeyer *et al.*, 2006). Extensive drought periods regularly occur in July and August and moderate droughts in September and October. Precipitation from November to February falls mostly as snow. For both species a small number of low significant correlations between precipitation and the ring widths of the previous year were found (Table 2). In the current year, precipitation positively influenced tree-ring widths during the initial period of the growing season from April to June especially at mid and dense sites. Both species were found to rely on and compete with native grasses for water in the top-soil profile during spring and early summer when moisture is available (Eggemeyer *et al.*, 2009). The precipitation during the dry season, July and August, also showed a positive influence on ring widths, which would be enhanced by the ability of both species to shift their water uptake deeper in the soil profile (Eggemeyer *et al.*, 2009; Awada *et al.*, 2013). Climate correlations in Western NE showed the growth of *P. ponderosa* was greatly influenced by precipitation regardless of the stand density. In contrast the tree-ring growth of *J. virginiana* correlated more with microclimate at sites with high stand density. One of the limiting factors for tree-ring growth is water availability as cambial activity is reduced when water is limited. Changes in water availability has been found to occur after thinning, which results in less competition for resources, according to stand density reduction experiments (Di Matteo *et al.* 2010). The tree-ring patterns in this case are similar to those in periods of wetter than normal and showed larger tree rings (Westoby, 1984; McDowell *et al.*, 2003; Murrell, 2009). The response of *J. virginiana* in our study supports the findings of other studies that increasing stand density, result in less soil moisture availability and trees in this case become more dependent on precipitation and groundwater (*e.g.*, Awada *et al.*, 2013; Msanne *et al.*, 2017).

Regardless of stand density, site location and, therefore microhabitat conditions, we found that increases in temperatures during winter to generally be positively correlated with the ring widths of both species, while temperature extremes during the growing season were negatively correlated. According to Fritts (1976), the temperatures in September and October of the previous year have a strong influence on tree-ring growth. Above-average temperatures and a small number of frost days in these months lead to enhanced growth. Additionally, if temperatures in winter and spring are higher than average and water is available, cambial activity is initiated earlier in the year and leads to the formation of wider

rings. In contrast droughts during the growing season influence tree growth negatively as shown by the negative correlations between temperature and ring width from April to July (Fritts, 1976; Woodhouse *et al.*, 2001). This is supported by the correlations between ring growth and the PDI as well (Table 3). The most significant correlations with the PDI were found in trees in Western NE. Eastern NE trees were less limited by droughts, even though temperatures were slightly higher, but this was compensated for by the overall higher precipitation levels in the East (Wilhite and Hubbard, 1998). 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. This explains why drought during the growing season has a very negative impact on tree growth (Wilhite and Hubbard, 1998; Eggenmeyer *et al.*, 2006, 2009).

The precipitation levels and available soil moisture, as determined by the PDI, were limiting factors for tree growth in Western NE, as the stepwise linear regression modelling (SLRM) also confirmed. In Western NE additional factors that we have not evaluated in this study, such as soil texture (sandy vs. silty loam), aspect, slope, shading, grazing, access to groundwater, and low nutrient soil availability (Msanne *et al.*, 2017) can also be limiting factors (Sands and Mulligan, 1990; Oberhuber *et al.*, 1998), which might explain why temperature and precipitation have therefore less explanatory power. However, water availability and the markedly different ecohydrology on dunes, as well as interdunal valleys, may explain the correlation patterns best (Gosselin *et al.*, 1999, 2006).

Water use efficiency and isotope ratios.—The relationship between WUE and carbon isotope fractionation during photosynthesis is well-established (Farquhar *et al.*, 1989). The $\delta^{18}\text{O}/\delta^{13}\text{C}$ relationship is determined by both g_s and A , which are influenced by environmental and plant-internal factors. Changes in $\delta^{18}\text{O}$ of soil water may influence the relationship as well (Scheidegger *et al.*, 2000). The isotopic ratio at the drier Western location was characterised by lower g_s , and therefore higher $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ enrichment in leaf and organic matter, and WUE. $\delta^{13}\text{C}$ and therefore WUE has been found to increase during periods of low precipitation or water stress in several studies as Rubisco discrimination decreases leading to tissues enrichment, whereas $\delta^{18}\text{O}$ responds to the prevailing humidity and soil water conditions, as well as temperature (Saurer *et al.*, 1995, 1997; Gosselin, 1999, 2006; Bégin *et al.*, 2015). By analysing both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, the photosynthesis-related and water-related influences on trees stable isotope composition can be more easily separated. We found $\delta^{13}\text{C}$ and WUE to be higher in Western NE than in Eastern NE almost every year (Fig. 5), probably due to the sensitivity of *P. ponderosa* stomata to vapor pressure deficits and drought (Bihmidine *et al.*, 2010). The decline in precipitation across the gradient from East to West seems to make WUE more independent of stand density (Scheidegger *et al.*, 2000). These findings were also supported by the $\delta^{18}\text{O}$ results, which revealed no significant differences between sites (Scheidegger *et al.*, 2000). The values of $\delta^{18}\text{O}$ were higher in summer rainfall than in deep, long-stored groundwater (Allison and Hughes, 1983). This indicates trees at sparse sites do not absorb as much water from groundwater as trees at dense sites do, as Saurer *et al.* (1997) and Eggenmeyer *et al.* (2009) also found. They showed trees have an impact on water availability in soils and that in turn feedback on the spatial pattern of absorbing water. The trees in the Western NE have sufficient plasticity to take water from different soil depths according to groundwater availability (at around 7 m in our study), which allows them to survive and to recover from drought stress (Scheidegger *et al.*, 2000; Eggenmeyer *et al.*, 2006, 2009). This also explains the small differences between the Western and Eastern NE $\delta^{18}\text{O}$ values. The dependence of $\delta^{13}\text{C}$ on climate was tested, resulting in significant values ($P < 0.05$) in Western NE, but not in Eastern NE because more

$\delta^{13}\text{C}$ is incorporated in the tissues at drier sites and is more strongly influenced by climate than $\delta^{13}\text{C}$ at more humid sites (Saurer *et al.*, 1995). Trees in Western NE thus are affected more by droughts than trees in Eastern NE, also confirmed by the correlation between climate, tree-ring widths and the PDI. For $\delta^{18}\text{O}$, significant values resulted for precipitation, independent of density and sampling region. The highest $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values tended to coincide with extremely dry years, as the PDI data showed which further supports our findings.

CONCLUSIONS

The *P. ponderosa* and *J. virginiana* in our study showed an acclimation to changing climate and water resources. We found, as hypothesised, the stand density of *J. virginiana* and *P. ponderosa* in the invaded grassland ecosystems strongly affects tree-ring growth. The results have shown that the higher the stand density, the narrower the rings and the less variable the chronologies were. Tree-ring widths correlated highly with precipitation, but the responses at the drier site in Western Sandhills grasslands were more pronounced than those in Eastern NE. That said, we have limited evidence that current variability in the east and the moisture-limited Sandhills will cause a permanent decline in growth of either species. The drought response strategies of the two species, characterized by an avoidance strategy in *P. ponderosa*, and tolerance strategy in *J. virginiana* have permitted them to successfully grow and spread, once established and have access to deep soil moisture. Even with extreme drought events, in high stand densities, both species avoided intra-specific competition by taking up water from different depths or by enhancing their WUE. However, if temperatures continue to rise, and if precipitation and groundwater levels decline and drought increases in frequency and severity, the future distribution and spread of the species might be impacted, with *P. ponderosa* being more susceptible to precipitation decline and increase of vapor pressure deficit than *J. virginiana* due to the different drought resistance strategy.

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