



Coupling dendroecological and remote sensing techniques to assess the biophysical traits of *Juniperus virginiana* and *Pinus ponderosa* within the Semi-Arid grasslands of the Nebraska Sandhills

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ARTICLE INFO

Keywords:

Tree rings
Dendrochronology
Remote sensing
Vegetation indices
Woody encroachment
Eastern redcedar
Ponderosa pine

ABSTRACT

Woody species encroachment is occurring within the semi-arid grasslands of the Nebraska Sandhills U.S., primarily driven by native *Juniperus virginiana* and *Pinus ponderosa*, altering ecosystems and the services they provide. Effective, low cost, and cross-scale monitoring of woody species growth and performance is necessary for integrated grassland and forest management in the face of climate variability and change. In this study, we sought to establish a relationship between remote sensing-derived vegetation indices (VIs), tree dendrochronological (raw and standardized tree ring width) measurements, and the abiotic environment [(precipitation, temperature, Palmer Drought Severity Index (PDSI), and soil water content (0–300 cm depth)], over a 30-year period (1984–2013), to assess the performance of encroaching woody *J. virginiana* and *P. ponderosa* within the Nebraska Sandhills. We also investigated whether VIs can be used as an effective alternative tool to replace or complement ground measurements. Our results indicate that precipitation, temperature, and PDSI were significant ($p < 0.05$) predictors of *J. virginiana* and *P. ponderosa* growth based on dendrochronological measurements and VIs, while soil water content from 40 to 300 cm depth was a significant predictor of *J. virginiana* performance. Out of the six VIs that were investigated, four were significant predictors of tree ring growth. R^2 values between grassland VIs and growing season climate were greater than those of *J. virginiana* or *P. ponderosa*, while grassland performance was decoupled from soil water content. Additionally, climatic conditions in the previous year were significant determinants of current year growth of tree species but did not affect current year grassland performance. This study provides evidence for the efficacy of remote sensing-based VIs in monitoring interannual variation in the growth of woody species, while determining abiotic factors impacting the growth of grassland vegetation, *J. virginiana*, and *P. ponderosa* in the Nebraska Sandhills.

1. Introduction

Over the past century, grassland ecosystems have experienced a displacement of herbaceous vegetation in favor of woody species (Archer et al., 2017). This directional shift, known as woody species encroachment (WSE), occurs globally at a rate of 0.1 to 2.3% cover change per year (Barger et al., 2011). Woody invasive species, both native and non-native, may outcompete herbaceous vegetation for resources (e.g., water, nutrients, and radiation), resulting in rapid transitions from grasslands and savannas to wooded areas in the absence of

effective mitigation and/or natural disturbance (Msanne et al., 2017). Consequently, areas impacted by WSE tend to experience shifts in ecosystems and the services they provide, including declines in species richness and diversity (Ratajczak et al., 2012; Sala and Maestre, 2014; Mazis et al., 2021); reductions in net primary productivity and forage availability with subsequent impacts on livestock rearing communities (Twidwell et al., 2013); ecohydrological alterations leading to reduced soil water and runoff (Awada et al., 2012; Kishawi et al., 2023); shifts in microbial communities (Fowler, 2021) and biogeochemical cycles (Hibbard et al., 2001); and the emergence of respiratory problems in

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<https://doi.org/10.1016/j.foreco.2023.121184>

Received 13 March 2023; Received in revised form 5 June 2023; Accepted 6 June 2023

Available online 21 June 2023

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humans in response to pollen (Leis et al., 2017). Several drivers have been posited to explain global WSE, including fire regime shifts, increasing atmospheric CO₂ concentrations, nitrogen deposition, and intensive livestock grazing (Archer 1994, Harr et al., 2014, Archer et al., 2017, García Criado et al., 2020).

In the semi-arid grasslands of the Nebraska Sandhills, the largest C₄-dominated grass dune-stabilized region in the western hemisphere (50,000 km²; Bleed and Flowerday 1998), C₃ coniferous *Juniperus virginiana* (eastern redcedar) and *Pinus ponderosa* (ponderosa pine) have emerged as primary drivers displacing C₄ grasslands vegetation (Eggemeier et al., 2006). *Juniperus virginiana* is spreading throughout the Great Plains and into the Nebraska Sandhills, while *P. ponderosa* is expanding into grasslands beyond its historic grassland-woodland ecotones (Eggemeier et al., 2006). While native to the region, the encroachment of both species carries the potential to disrupt services vital to economic and ecological resilience. In the Sandhills, where water availability is a limiting factor and prolonged periods of drought are not uncommon (Awada et al., 2012), the drought resistance strategies of *J. virginiana* and *P. ponderosa*, together with their deep root systems (Eggemeier et al., 2006; 2009, Bihmidine et al., 2010) and response to increasing CO₂ levels in the atmosphere, confer a competitive advantage to trees over native C₄-dominated grasslands within the region (Battipaglia et al., 2020). Additionally, *J. virginiana*, and to a lesser extent *P. ponderosa*, exhibit plasticity in their water uptake strategies, absorbing moisture from alternating soil depths during the year depending on water availability and accessibility, whereas grasses primarily absorb water from the upper soil profile, and have been shown to go dormant under August drought (Eggemeier et al., 2006; 2009). Aus Der Au et al., (2018), using dendroecological techniques, concluded that while *J. virginiana* and *P. ponderosa* significantly respond to precipitation and temperature throughout the year, present intra- and inter-annual prevailing weather variation do not appear to limit their growth and performance. This suggests that *J. virginiana* and *P. ponderosa* growth may be decoupled from that of the native grasses.

In this study, we aimed to establish a relationship between satellite-based remote sensing Vegetation Indices (VIs) and dendroecological techniques to assess the performance of encroaching *J. virginiana* and *P. ponderosa* in mature monoculture even-aged stands over a 30-year period (1984–2013) in the semi-arid grasslands of the Nebraska Sandhills. We hypothesized that environmental stresses that impact photosynthetic capacity and foliage growth also impact annual tree ring growth, which can be detected using remote sensing techniques due to anticipated changes in plant reflectance properties under stresses (e.g., drought). We further hypothesize that the impact of stresses on *J. virginiana* and *P. ponderosa* performance are decoupled from that of herbaceous grasslands vegetation due to differences in physiology, response to stress, and access to water in the soil profile, which may exacerbate the problem of WSE. Specifically, we first derived VIs from Landsat 5 (1984–2011) and Landsat 7 (2012–2013) satellite imagery over stands of *J. virginiana*, *P. ponderosa*, and adjacent grasslands; we then regressed VIs against dendrochronologies and climatic variables. To determine if tree performance was decoupled from that of grasslands, we investigated the relationship between VIs derived over adjacent open grassland areas and tree VIs and dendrochronologies. Results from this study will aid in the development of fast, accurate, scalable, and labor-saving tools to remotely assess the performance of invasive woody species in the Nebraska Sandhills and other regions in the Great Plains, and in improving surveillance and monitoring capabilities of grassland vegetation in the context of WSE, adaptive management, and climate change.

2. Materials and methods

2.1. Site characteristics

The study was conducted at the Nebraska National Forest (NNF),

located within the semi-arid Sandhills in Thomas County, Nebraska, U.S. (41°50'45" N, 100°20'06" W). The NNF was established in 1902, and as of the date of publication, is the largest hand-planted forest in North America. The NNF is primarily composed of *P. ponderosa* and *J. virginiana* stands that were planted in the 1930's and 1940's (Eggemeier et al., 2009). Within the NNF, six monoculture even-aged stands dominated by *P. ponderosa* (n = 3) or *J. virginiana* (n = 3) were selected. All sites were mature high density stands, with a basal area of 36.6–51.5 m² ha⁻¹ (566–933 trees ha⁻¹) for *P. ponderosa*, and 28.4–36.3 m² ha⁻¹ (1,700–2,233 trees ha⁻¹) for *J. virginiana*, as determined by three replicated 100 m² plots that were measured within each of the six stands. The forest understory was mainly litter covered or bare ground (>50%) with interspersed C₃ grasses, forbs, and cacti (Mazis et al., 2021). Three additional open (i.e., absent of trees) grassland sites located within 1 km of the western boundaries of the forested area of the NNF were also selected for the study (Fig. 1). These grassland sites served as a control, and are dominated by C₄ grasses, along with a mixture of C₃ grasses, shrubs, and cacti. Grassland sites were lightly grazed by cattle throughout the study period. More details on species composition and management practices can be found in Mazis et al., (2021).

2.2. Climate

Monthly precipitation and temperature data for Thomas County, Nebraska were acquired from the NOAA National Centers for Environmental Information: Climate at a Glance timeseries (NOAA, 2022), and aggregated into annual values (Fig. 2A). Although micro-meteorological data were available from nearby local weather stations, we decided to use NOAA's datasets, which offer an extensive time series of compiled and complete climate records. We analyzed annual and growing season (May–September) precipitation and maximum monthly temperatures (obtained by averaging daily maximum temperature values for each month). Monthly Palmer Drought Severity Index (PDSI) data were acquired via NOAA for the North-Central climate division in Nebraska. PDSI quantifies drought by considering precipitation, temperature, and soil characteristics, with index values ranging from −10 (extreme drought) to +10 (very wet).

2.3. Soil water

Soils at the NNF and surrounding areas are Valentine fine sands (Bleed and Flowerday, 1998). Soil water was measured monthly from March 2005–December 2013 at all studied sites, apart from one *P. ponderosa* stand where data collection began in May 2006. Access tubes were installed at each site, and measurements were obtained using a TRIME-TDR (IMKO GmbH, Germany) probe that was inserted into each tube. As described by Mazis et al., (2021), the probe measures water content (%) from soil surface to 300 cm depth in 20 cm increments. The incremental depth readings were averaged to assess soil water content at 0–40, 40–100, and 100–300 cm depths.

2.4. Tree rings

Tree cores from two *P. ponderosa* and two *J. virginiana* stands were collected; details on the core sampling procedures can be found in Aus Der Au et al., (2018). Briefly, a total of 30 north and south-facing cores from 15 trees were collected from each of two stands of *P. ponderosa* and *J. virginiana*, from dominant trees located within 50 m of the stand center point, totaling 120 cores collected from 60 trees. Cores were acquired using a three-threaded auger placed at a height of 1.3 m perpendicular to the vertical stem of the tree. The cores were dried, placed into a microtome holder, and shaved methodically until all rings were visible. A Leica Wild M32 microscope (Leica, Germany) was used to measure tree ring widths to the nearest 0.01 mm and measurements were recorded in TSAPWin (Time Series Analysis and Presentation,

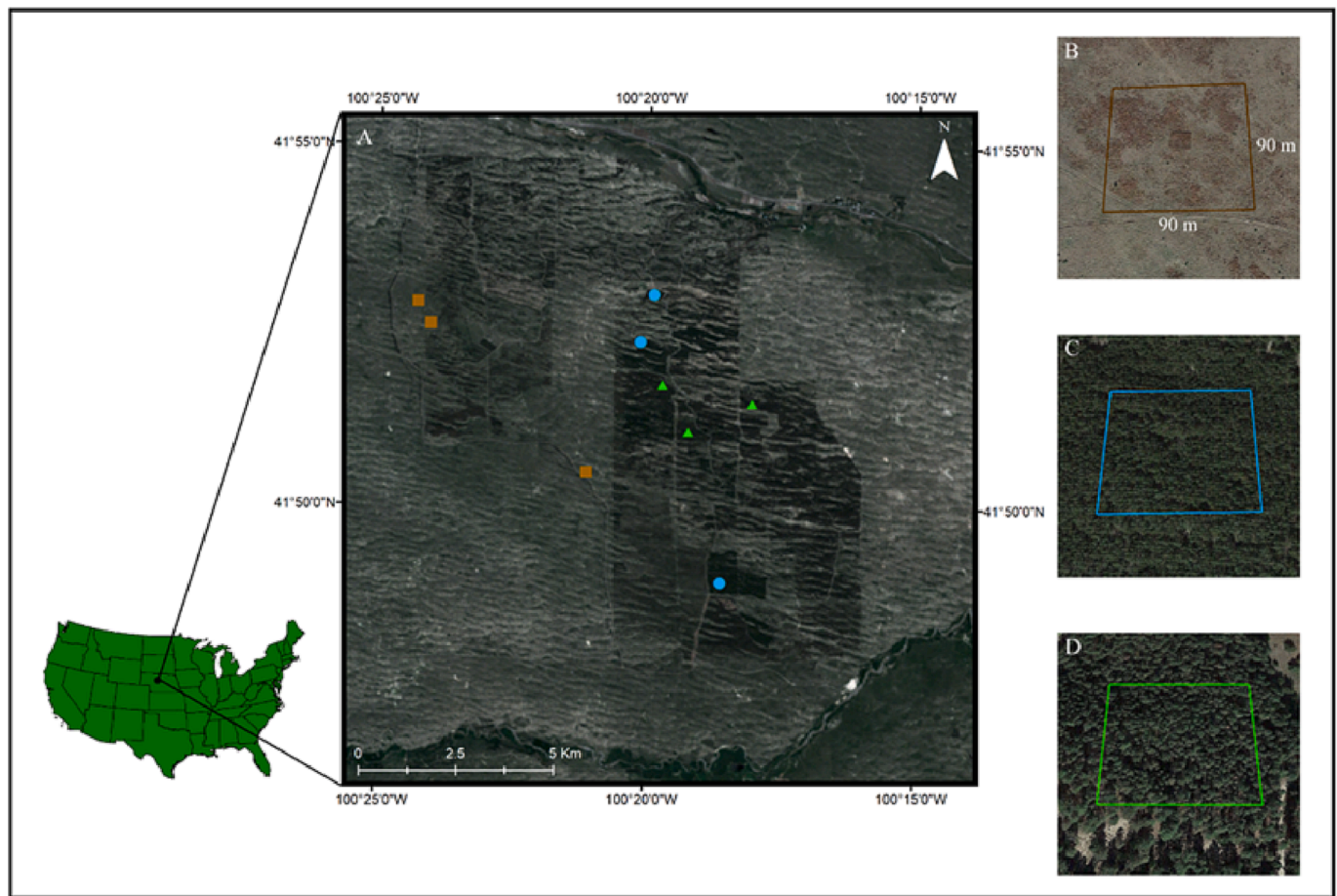


Fig. 1. Study sites at the Nebraska National Forest (NNF). Grassland sites are represented by brown squares, *Juniperus virginiana* stands by blue circles, and *Pinus ponderosa* stands with green triangles (A). Example grassland (B), *J. virginiana* (C), and *P. ponderosa* (D) sites (respectively) with Maximum Value Composite (MVC) pixel windows (8,100 m²) overlaid.

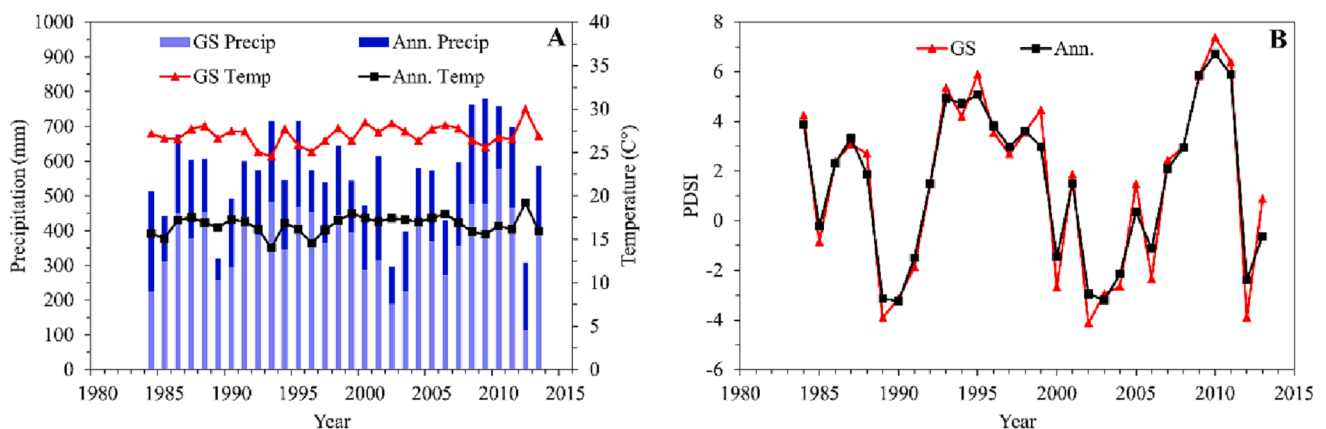


Fig. 2. Growing season (GS) and annual (Ann.) cumulative precipitation (Precip), average temperatures (Temp) (A), and Palmer Drought Severity Index (PDSI) values (B), from 1984 to 2013, National Oceanic and Atmospheric Administration (NOAA).

Frank Rinn, Heidelberg, Germany). The north and south-facing cores were crossdated for each tree and for each stand, and missing rings were added manually. Crossdating accuracy was verified using the program COFECHA. Tree ring widths were standardized with the “Detrender” package (Campelo, 2012) in the program RStudio using a 30-year spline, 0.66 split ratio, and 0.5p-value. Ring width standardization removes growth effects related to the age and size of individual trees.

2.5. Remote sensing and vegetation indices

Satellite image-based VIs were used to assess *J. virginiana* and *P. ponderosa* performance. Historical, multispectral Landsat imagery was used for this study due to its long historical record of image data, moderate spatial resolution (30 m), and public availability at no cost. Several prior studies have demonstrated the value of using Landsat imagery for similar dendrochronology research (Wang et al., 2017,

Bumann et al., 2019, Erasmí et al., 2021). Historical image data from 1984 to 2013 were acquired by from two Landsat sensors including the Landsat 5 Thematic Mapper (TM) sensor, which was launched in 1984 and decommissioned in 2012, and the Landsat 7 Enhanced Thematic Mapper (ETM+) sensor, which was used to complete the last two years (2012 and 2013) of the historical record. Both Landsat satellites have optical sensors that detect reflected electromagnetic energy in equivalent bands from visible, near-infrared (NIR), and shortwave infrared (SWIR) wavelengths (Landsat 4-7 Collection 1 (C1) Surface Reflectance (LEDAPS) Product Guide, 2020).

Collection 1/Tier 1 surface reflectance Landsat images were acquired from Google Earth Engine's (GEE) cloud-based analysis platform. Tier 1 images are those featuring the highest geographic accuracy, while surface reflectance products have been processed to limit atmospheric effects and are preferred for time series analysis. Within GEE, Landsat collections were filtered to include only imagery from the May to September growing season of each year. Imagery outside of this date range may include snow, dormant and/or browning vegetation. The collections were further filtered to include only images acquired over path 31/row 31, the Landsat image scene that contains the entirety of the study area. Cloud masking was applied to eliminate pixels with a high probability of cloud cover or cloud shadow.

Images were processed within GEE to derive VIs from surface reflectance data. We calculated six VIs (Table 1), including the commonly-used Normalized Difference Vegetation Index (NDVI; Rouse et al., 1974), Enhanced Vegetation Index (EVI & EVI2; Liu and Huete, 1995), and Land Surface Water Index (LSWI; Xiao et al., 2004), as well as lesser-investigated indices [i.e., Green Chlorophyll Index (GCI; Gitelson et al., 2003) and Green-Red Vegetation Index (GRVI; Tucker, 1979)] that have shown prior success in evergreen tree monitoring (Huete, 2012, Muraoka et al., 2013, Xue and Su, 2017). We produced Maximum Value Composite (MVC) images for each VI per study year. MVC operates by reducing a collection of images to a single image where every pixel is assigned the highest VI value from the collection on an annual time-frame. This technique reduces the impact of residual cloud cover and provides a relatively cloud-free image that represents peak greenness (i.e., time of annual maximum productivity), which is ideal for interannual comparisons of vegetative performance (Erasmí et al., 2021). All MVC images were downloaded from GEE in a WGS 84, UTM Zone 14 coordinate system. The annual MVC VI images were then layer-stacked in the spatial analysis program ENVI. A 3 × 3-pixel window (90 m × 90 m) was placed around each site location center point, and the arithmetic mean of the pixel values within each window was determined for each VI year⁻¹.

Table 1
Derived vegetation indices (VIs) that were used in this study.

Index	Equation	Reference
Normalized Difference Vegetation Index (NDVI)	$= \frac{NIR - Red}{NIR + Red}$	(Rouse et al., 1974)
Enhanced Vegetation Index (EVI)	$= 2.5 * \left(\frac{NIR - Red}{NIR + 6 * Red - 7.5 * Blue + 1} \right)$	(Liu and Huete, 1995)
Enhanced Vegetation Index 2 (EVI2)	$= 2.5 * \left(\frac{NIR - Red}{NIR + 2.4 * Red + 1} \right)$	(Jiang et al., 2008)
Green Chlorophyll Index (GCI)	$= \left(\frac{NIR}{Green} \right) - 1$	(Gitelson et al., 2003)
Green-Red Vegetation Index (GRVI)	$= \frac{Green - Red}{Green + Red}$	(Tucker, 1979)
Land Surface Water Index (LSWI)	$= \frac{NIR - SWIR}{NIR + SWIR}$	(Xiao et al., 2004)

2.6. Analysis

Linear Regression analyses were conducted in RStudio (version 1.4.1717) using the package “ggpmisc” (Aphalo, 2017), an extension of the “ggplot2” (Wickam, 2016) package, to assess the impact of climatic factors on tree ring growth and the efficacy of VIs to characterize the interannual growth of *J. virginiana* and *P. ponderosa*. We performed a series of regressions between VIs recorded over tree and grassland sites, tree ring widths, and growing season climate and soil water content. Least Absolute Shrinkage and Selection Operator (LASSO; Tibshirani, 1996) regressions were conducted to determine which variables impact growth in the context of a global model where all independent variables are considered simultaneously. Because climatic and soil water variables are often intercorrelated, it may be difficult to establish specific factors influencing growth. The LASSO analysis applies a shrinkage factor (lambda) to minimize variable coefficients. Variable coefficients reduced to zero are eliminated from the model. In this case, LASSO provides an advantage during variable selection compared to commonly used stepwise regression methods. We conducted LASSO analysis in RStudio using the “glmnet” package (Friedman et al., 2010). Lambda was defined as one standard error from the minimum mean squared error (MSE). Each vegetation category was analyzed separately, with grasslands/forest stands set as a fixed effect to account for variability between site locations. VIs acted as response variables for all sites for the period of 1984–2013, while raw and standardized ring widths were additional response variables for tree stands. Each dependent variable was analyzed separately. For the period spanning 2005–2013, both climatic and soil water factors were considered independent variables. Growing season and one-year lagged annual temporal scales were considered for climatic variables, along with growing season soil water content.

3. Results

3.1. Environmental conditions

During the 30-year study period from 1984 to 2013, average annual precipitation was 566 mm and ranged between 296 and 781 mm, with growing season (May–September) cumulative precipitation accounting for 65% of annual totals (Fig. 2A). Annual average maximum temperature was 16.7 °C and ranged between 14.1 and 19.2 °C, and annual values of PDSI ranged from −3.2 to 6.7 and averaged 1.48 (Fig. 2B). Negative PDSI values, which are indicative of drought conditions (Palmer, 1965), occurred in 37% of years during the study period. Years with severe drought were characterized by PDSI values lower than −3.0 (Palmer, 1965), and were observed in 1989, 1990, 2002, and 2012.

Soil water content (%) down to 3 m depth was significantly higher in grasslands than *P. ponderosa* and *J. virginiana* stands during the study period (Fig. 3; 2005–2013). Annual soil water content increased with soil depth in grassland sites, averaging 9.8, 14.4, and 16.3%, for 0–40, 40–100, and 100–300 cm, respectively. On the other hand, soil water content varied little with soil depth under *P. ponderosa* and *J. virginiana* stands, averaging 10.3 and 7.2% over the 0–300 cm soil profile, respectively.

3.2. Tree ring growth

Mean raw ring widths during the 30-year study period averaged 0.87 ± 0.06 mm yr⁻¹ for *P. ponderosa* and 0.73 ± 0.04 mm yr⁻¹ for *J. virginiana* (Fig. 4A). Most trees were planted in the 1940's and 1950's and were therefore mature by 1984; nonetheless, standardization was performed to remove any remaining growth trends affecting interannual variability, resulting in an average standardized growth rate of 1.0 ± 0.06 mm yr⁻¹ for *P. ponderosa* and 1.0 ± 0.04 mm year⁻¹ for *J. virginiana* (Fig. 4B). We regressed raw ring width measurements against those of standardized widths; since the two measurements were significantly

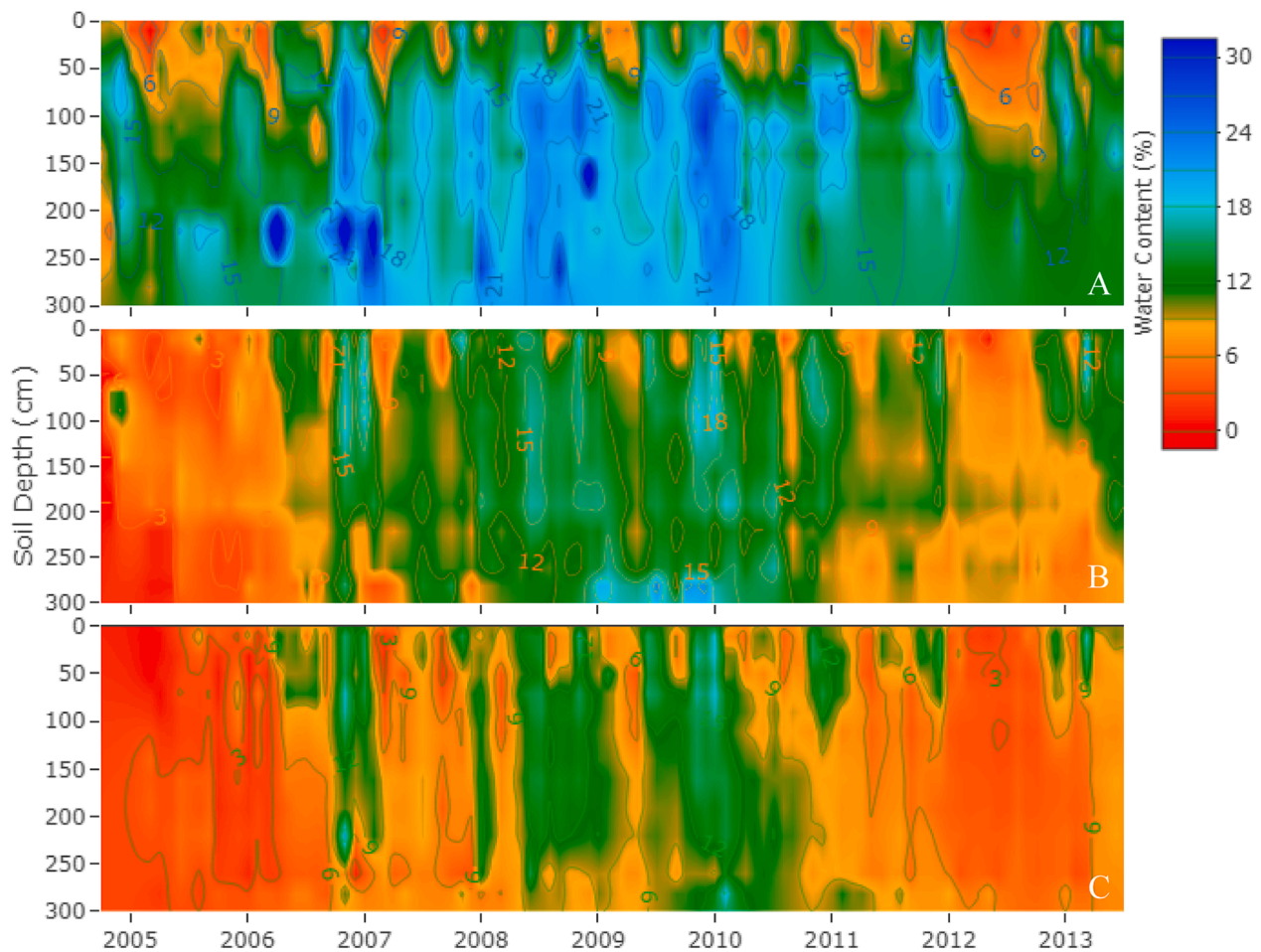


Fig. 3. Average monthly soil water content (%) up to 300 cm depth, for grasslands (A), *Pinus ponderosa* (B), and *Juniperus virginiana* (C) sites at the Nebraska National Forest, Halsey, NE, from March 2005–December 2013.

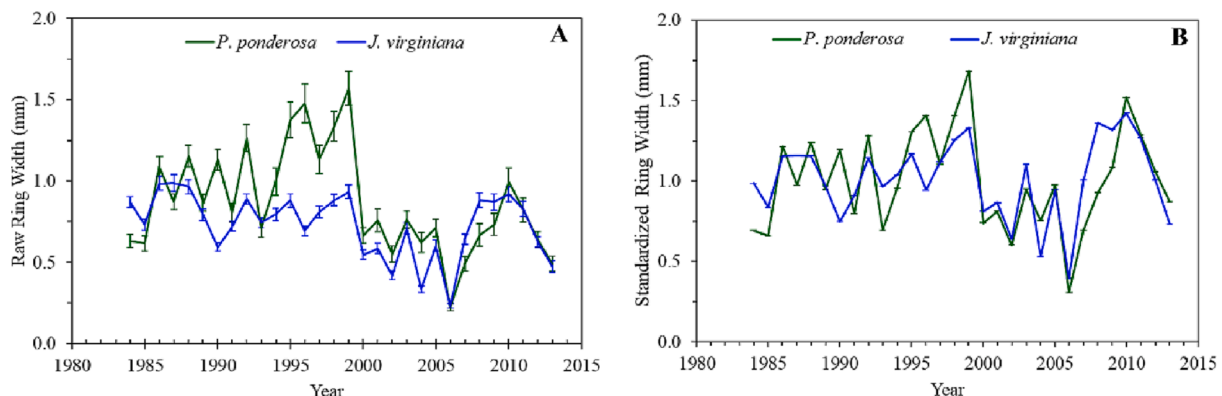


Fig. 4. Raw (A) and standardized (B) tree ring width chronologies from 1984 to 2013, with standard error bars (\pm), for *Pinus ponderosa* and *Juniperus virginiana* stands in the semi-arid grasslands of the Nebraska Sandhills, Nebraska National Forest, Halsey, NE.

correlated (Fig. S1, $p < 0.001$) and resulted in similar findings, and for the purpose of this study (i.e., focusing on abiotic factors), we present results from the standardized tree ring analysis in the main segment of the manuscript, while those from the raw ring data analysis can be found in the supplemental (S) materials.

Raw and standardized tree ring growth varied during the study period, with peak growth observed in 1999 and 2010, while a significant decline in annual tree ring growth was recorded in 2002, 2004, 2006,

and 2013 (Fig. 4). *Pinus ponderosa* growth peaked in 1999 after an eight-year period of moist conditions (PDSI > 0), while *J. virginiana* growth peaked in 2010, which corresponded to the highest PDSI value recorded during the study. Interannual growth variations of the two species followed a similar pattern with the exception of 1990, 1996, and 1997, when *P. ponderosa* and *J. virginiana* exhibited contrasting growth trends. Tree ring widths were significantly ($p < 0.05$) correlated with growing season precipitation, temperature, and PDSI in both tree species (Fig. 5

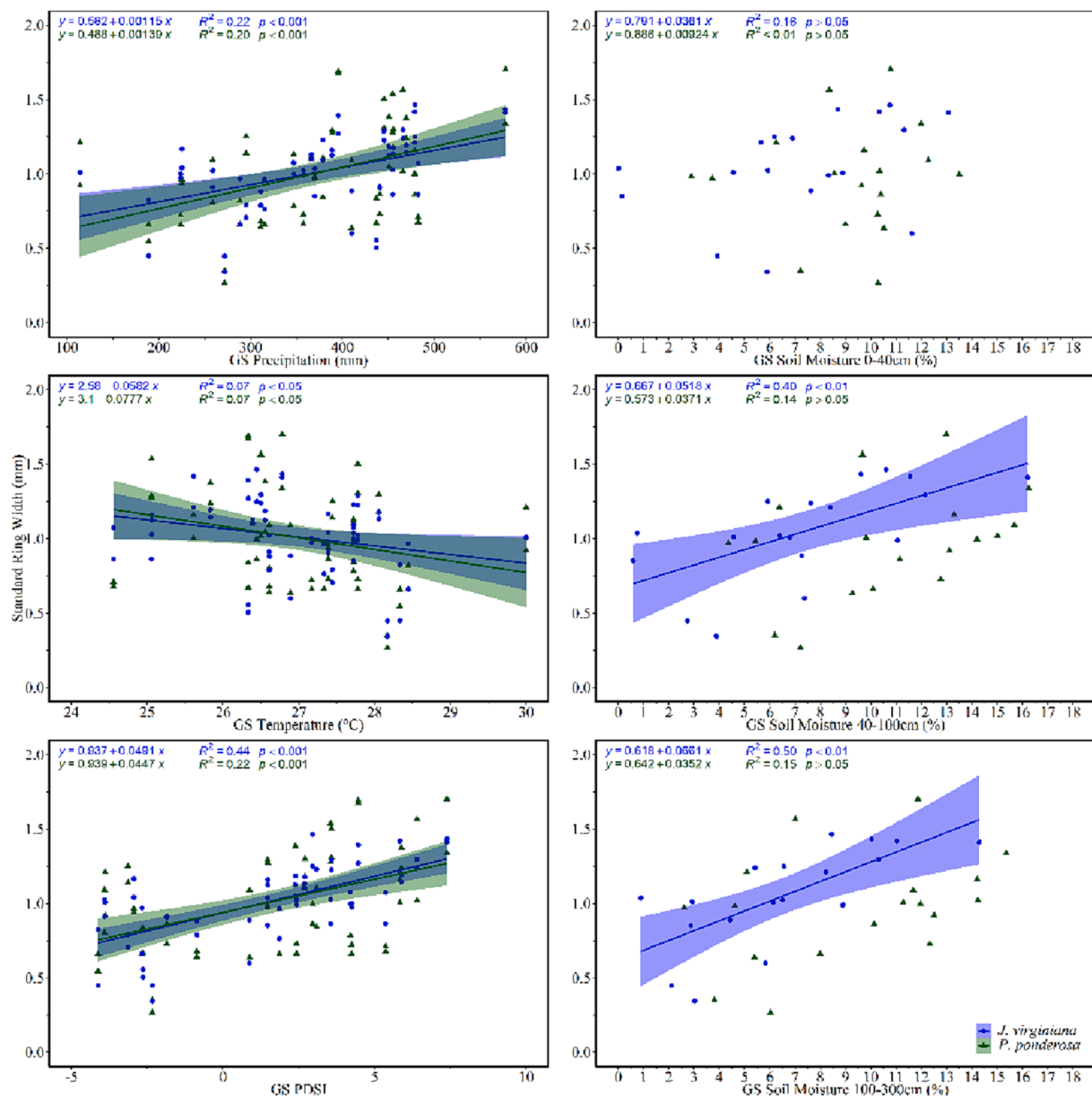


Fig. 5. Standardized tree ring widths of *Pinus ponderosa* and *Juniperus virginiana*, as a function of growing season (GS) precipitation, temperature, and PDSI (1984–2013) and soil water content (2005–2013), at the Nebraska National Forest, Halsey, NE.

& Fig. S2). Higher growing season precipitation and PDSI were associated with increased growth rates (wider than average tree rings), while higher growing season maximum temperature seemed to have a negative effect on annual tree ring growth. PDSI was the best correlated climatic predictor for annual tree ring growth, particularly when regressed against standardized ring width values, for both *J. virginiana* ($R^2 = 0.44$, $p < 0.001$) and *P. ponderosa* ($R^2 = 0.22$, $p < 0.001$).

Average monthly soil water content from 0 to 300 cm depth was available from 2005 to 2013 (Fig. 3). During this period, *J. virginiana* tree ring growth was not impacted by soil water content in the upper soil profile (0–40 cm), whereas growth was significantly ($p < 0.05$) and positively related to growing season soil water content at depths of 40–100 and 100–300 cm (Fig. 5). The strongest relationship was reported for *J. virginiana* raw tree ring growth and water content below 100 cm in the soil profile ($p < 0.001$, $R^2 = 0.54$). *Pinus ponderosa* tree ring growth was not significantly related to growing season water content in the 0–300 cm soil profile.

3.3. Remote sensing and vegetation indices

Electromagnetic reflectance properties were related to vegetative biophysical traits through the calculation of various VIs using multispectral Landsat satellite imagery. Six VIs were calculated from the multispectral data to determine which indices best characterize inter-annual variations in foliage reflectance characteristics in response to abiotic factors (Table 2). All six VIs were significantly correlated ($p < 0.01$) with measured climatic parameters in grassland sites. Stronger relationships were found between grassland VIs and precipitation and PDSI than with temperature. Of the suite of VIs calculated for *P. ponderosa* sites, NDVI, GCI, and GRVI showed a significant relationship with PDSI ($p < 0.01$) while only GCI and GRVI responded significantly to precipitation ($p < 0.05$). None of the calculated VIs correlated with temperature for *P. ponderosa*. *Juniperus virginiana* VIs exhibited significant responses to precipitation and PDSI ($p < 0.05$), while only LSWI significantly correlated with temperature ($p < 0.05$).

Table 2

Correlations between vegetation indices (VIs) and growing season (May–Sept.) climatic variables for each vegetation type with coefficient of determination (R^2) and significance (p). ***, **, *, ns for significance at < 0.001 , < 0.01 , < 0.05 , and non-significant, respectively.

Climate	VI	Grassland		<i>P. ponderosa</i>		<i>J. virginiana</i>	
		R^2	p	R^2	p	R^2	p
Precipitation	NDVI	0.45	***	0.03	ns	0.18	***
	EVI	0.31	***	0.01	ns	0.07	**
	EVI2	0.36	***	0.01	ns	0.07	*
	GCI	0.44	***	0.05	*	0.20	***
	GRVI	0.40	***	0.11	**	0.24	***
Max Temperature	LSWI	0.33	***	0.00	ns	0.30	***
	NDVI	0.24	***	0.00	ns	0.01	ns
	EVI	0.09	**	0.00	ns	0.01	ns
	EVI2	0.11	**	0.01	ns	0.00	ns
	GCI	0.23	***	0.00	ns	0.04	ns
Average PDSI	GRVI	0.20	***	0.03	ns	0.02	ns
	LSWI	0.12	**	0.01	ns	0.08	**
	NDVI	0.32	***	0.11	**	0.26	***
	EVI	0.22	***	0.04	ns	0.08	**
	EVI2	0.25	***	0.03	ns	0.08	**
	GCI	0.35	***	0.14	***	0.30	***
	GRVI	0.24	***	0.16	***	0.22	***
	LSWI	0.25	***	0.02	ns	0.28	***

3.4. Vegetation indices as proxies for interannual vegetation growth

Regression analyses between VIs and annual tree ring growth were performed to assess the efficacy of using remote sensing and vegetation optical properties as a meaningful tool to determine the performance of *P. ponderosa* and *J. virginiana* (Fig. 6 & Fig. S3, Table S1). Of the calculated VIs, NDVI, GCI, GRVI and LSWI were significantly ($p < 0.05$) and positively related to raw (Fig. S3) and standardized (Fig. 6) tree ring growth in *P. ponderosa* and *J. virginiana*. On the other hand, EVI and EVI2 were only significantly correlated with tree ring growth of *J. virginiana*.

To determine if grassland performance is coupled with that of *P. ponderosa* and *J. virginiana* stands and can be used as a proxy in cases where homogenous image pixels over smaller forested areas cannot be obtained due to low spatial resolution imagery, we regressed VIs of grasslands with tree rings (Table 3, Fig. S4). Grassland NDVI, GCI, and GRVI were significantly ($p < 0.05$) correlated with *P. ponderosa* ring widths. Stronger relationships were found between grassland VIs and *J. virginiana* tree ring widths than *P. ponderosa* ring widths. All calculated VIs were significantly ($p < 0.05$) correlated with tree ring growth of *J. virginiana* except for EVI and raw ring widths of *J. virginiana*.

To investigate the use of VIs as a proxy for vegetation growth, as well as assess if biophysical responses of herbaceous vegetation is coupled with woody vegetation in response to abiotic parameters, we selected NDVI as a proxy indicator. We first present the interannual variability in grassland NDVI compared to forested stands (Fig. 7). Grassland NDVI exhibited a more severe response to drought. For example, from 2011 to 2012 growing season precipitation dropped from 465.8 mm to 114.3 mm, and mean grassland NDVI declined from 0.56 to 0.45 (19.6% decline), while over the same period mean *J. virginiana* NDVI decreased from 0.63 to 0.61 (3.2% decline), and mean *P. ponderosa* NDVI increased slightly. We regressed NDVI against climate and soil water variables for each vegetation cover type (Fig. 8). Growing season precipitation was significantly correlated with grassland NDVI ($p < 0.001$, $R^2 = 0.45$), and to a lesser extent with *J. virginiana* NDVI ($p < 0.001$, $R^2 = 0.18$), while no significant relationship was found for *P. ponderosa*. Increase in growing season temperature negatively impacted grassland NDVI ($p < 0.001$, $R^2 = 0.24$), while no significant relationship was found between temperature and NDVI over forested sites. Growing season PDSI was found to significantly impact NDVI in all vegetation types. No significant relationship was found between soil water and NDVI in grassland or

P. ponderosa sites, while *J. virginiana* NDVI was significantly correlated with soil water from 0 to 40 cm depth ($p < 0.001$, $R^2 = 0.46$), 40–100 cm depth ($p < 0.001$, $R^2 = 0.39$), and 100–300 cm depth ($p < 0.05$, $R^2 = 0.20$). These responses demonstrate the potential for woody species to outperform herbaceous vegetation in drought periods, as *J. virginiana* and *P. ponderosa* appear more resilient to interannual fluctuations in precipitation and temperature. Furthermore, NDVI was shown to be a significant predictor of tree ring growth in both species (Fig. 6 & Fig. S3). NDVI derived over adjacent grasslands was significantly correlated with tree chronologies and NDVI (Figs. 6, 7B, & Fig. S3) of *J. virginiana* and *P. ponderosa*, suggesting that the interannual performance of the three species may be linked by similar factors.

LASSO analysis was performed to further investigate coupling between species (Table 4, Table S3). LASSO is a regression analysis method that selects for a sparse model by setting the coefficients of less impactful variables to zero, allowing for unbiased parameter selection. NDVI was a dependent response variable for all species, and raw and standardized ring chronologies were included as additional response variables for *P. ponderosa* and *J. virginiana*. In addition to growing season precipitation, temperature, PDSI, and soil water content (0–40, 40–100, 100–300 cm depth), we also included previous-year (lagged) annual precipitation, temperature, and PDSI as additional independent variables to assess the potential for prior-year climate to effect current-year vegetative performance. Our results indicate that only current-year climatic variables were selected for grassland sites, while lagged precipitation and PDSI were selected for *P. ponderosa*, and lagged temperature and PDSI were selected for *J. virginiana*. Soil water content at depths of 0–40 cm and 100–300 cm were additionally selected for *J. virginiana*. These results further demonstrate differences in factors affecting growth between woody and herbaceous species in the region.

4. Discussion

4.1. Tree ring growth and the abiotic environment

The goal of this study was to investigate the use of remote sensing as an alternative, efficient, and scalable tool to assess the performance of encroaching woody species *P. ponderosa* and *J. virginiana* in the semi-arid grasslands of the Nebraska Sandhills. We used tree ring chronologies (1984 to 2013, 30 years) to first examine the response of the two species to interannual variability in abiotic environmental conditions (i. e., precipitation, temperature, PDSI, and soil water content), and then regressed these chronologies against VIs derived from remote sensing imagery to demonstrate the validity of the method.

Annual tree ring growth generally followed interannual variability in the abiotic environment. For example, in 2000 and 2006 below average precipitation along with above average temperatures resulted in below average standardized ring growth of both studied species (Fig. 2A & 4A). In 2000 and 2006, PDSI values were indicative of drought conditions and resulted in low tree ring growth, while in 1999 and 2005 when PDSI was > 0 , indicative of an absence of drought, standardized ring widths of both tree species exhibited average to above average tree ring growth. Regression analysis confirmed that tree rings widths of both tree species were positively correlated to growing season precipitation and PDSI, and negatively correlated with growing season temperature. PDSI was the best predictor of tree ring growth for both species, suggesting that the combined effects of precipitation and temperature strongly influence tree growth (Awada et al., 2012, Grossiord et al., 2020), and that the drought avoidance and tolerance strategies exhibited by *P. ponderosa* and *J. virginiana*, respectively, together with their ability to access deep soil water (Eggemeier et al., 2009), enabled a degree of resilience to annual climatic fluctuations (Bihmidine et al., 2010), particularly in water-limited environments such as the Nebraska Sandhills (Awada et al., 2012). Our results are in agreement with Aus Der Au et al., (2018), who reported similar results for *P. ponderosa* and *J. virginiana*, as well as others that have investigated the effects of climate on tree ring growth in

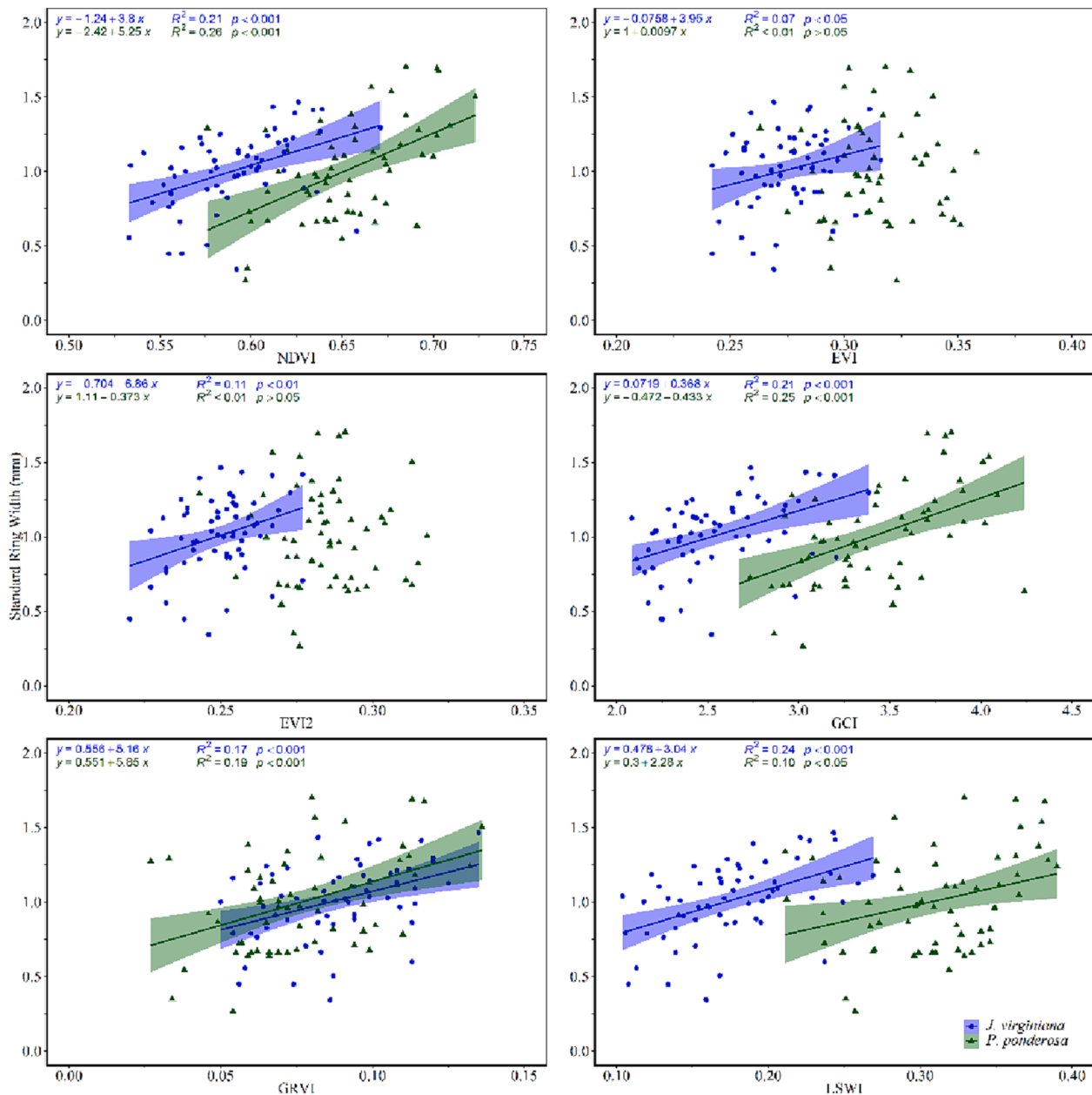


Fig. 6. Standardized (B) tree ring widths of *Pinus ponderosa* and *Juniperus virginiana*, as a function of the Normalized Difference Vegetation Index (NDVI), Enhanced Vegetation Index (EVI), Enhanced Vegetation Index 2 (EVI2), Green Chlorophyll Index (GCI), and Land Surface Water Index (LSWI) (1984–2013), at the Nebraska National Forest, Halsey, NE.

temperate regions (e.g., Fritts 1974, Cregg et al., 1988, Anderson-Teixeira et al., 2022).

To further understand the role of water availability, we regressed tree ring chronologies of *P. ponderosa* and *J. virginiana* against available data on soil water content (0–300 cm) during the growing season from 2005 to 2013. We found strong and significant positive relationships between soil water content, and tree ring widths of *J. virginiana* at depths exceeding 40 cm. Soil water content was lower in *J. virginiana* sites than *P. ponderosa* sites, likely due to higher stand densities (within the NNF) and water interception rates of *J. virginiana* relative to *P. ponderosa* (Awada et al., 2012, Caterina et al., 2013). Furthermore, *J. virginiana* – and to a lesser extent, *P. ponderosa* – exhibits plasticity in soil water uptake strategies, absorbing water from alternating soil depths throughout the growing season (Eggemeier et al., 2009), which explains the relationship between water content beneath the upper soil profile and *J. virginiana* ring growth, particularly when precipitation is limited.

No significant relationship was found between soil water content and raw or standardized ring widths for *P. ponderosa*. An explanation for the difference in ring growth response to soil water content between *P. ponderosa* and *J. virginiana* may be due to divergent stomatal regulation strategies between Pinaceae and Cupressaceae families, whereby anisohydric Cupressaceae maintains stomatal conductance at much lower water potentials compared to isohydric Pinaceae, resulting in a decoupling of growth to growing season evaporative demand in Pinaceae species, particularly during moderate to severe droughts (Voelker et al., 2018). This is further supported by Eggemeier et al. (2006), who found that stomatal conductance is maintained in *J. virginiana* during greater increases in vapor pressure deficit compared to *P. ponderosa*, suggesting that *P. ponderosa* growth may be inhibited by increasing evaporative demand irrespective of soil water content.

Table 3

Results of correlations between standardized tree ring chronologies of forested stands and vegetation indices (VIs) derived from grassland sites with coefficient of determination (R^2) and significance (p). ***, **, *, ns for significance at < 0.001 , < 0.01 , < 0.05 , and non-significant, respectively.

Species	VI	Ring Width (standardized)	
		R^2	p
<i>P. Ponderosa</i>	NDVI	0.11	**
	EVI	0.02	ns
	EVI2	0.03	ns
	GCI	0.16	**
	GRVI	0.08	*
	LSWI	0.05	ns
<i>J. virginiana</i>	NDVI	0.19	***
	EVI	0.07	*
	EVI2	0.11	*
	GCI	0.26	***
	GRVI	0.08	*
	LSWI	0.14	**

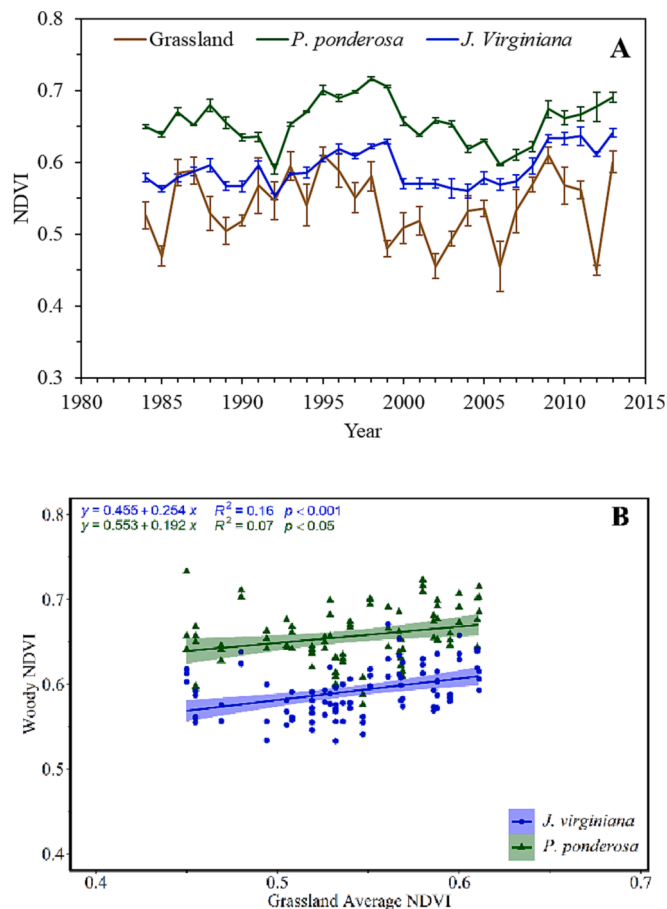


Fig. 7. Normalized Difference Vegetation Index (NDVI) from 1984 to 2013 averaged for native open grassland, *Pinus ponderosa*, and *Juniperus virginiana* with standard error bars (\pm) (A), and NDVI of *P. ponderosa* and *J. virginiana* as a function of NDVI averaged over open grasslands (B) in the semi-arid grasslands of the Nebraska Sandhills, Nebraska National Forest, Halsey, NE.

4.2. Vegetation indices as proxies for tree growth

To determine whether growth responses to environmental stresses that were detected via tree ring chronologies can also be observed through VIs using remote sensing techniques, we regressed VIs derived over *P. ponderosa* and *J. virginiana* stands with growing season

precipitation, temperature, and PDSI. While VIs have been used for decades measuring the vegetative performance of numerous species (Xue and Su 2017, Zeng et al., 2022), evergreen species present additional challenges to researchers due to their phenological characteristic of retaining foliage for several years compared to deciduous species, resulting in difficulties in evaluating the effects of current-year abiotic variations via leaf reflectance properties due to autocorrelation (Bernier et al., 2011). To account for this challenge, we selected a variety of indices that have shown prior success in evaluating coniferous evergreen performance (GCI, GRVI), as well as commonly used indices with a strong record in the literature for application across a swath of vegetative functional groups (NDVI, EVI, EVI2, LSWI). We found that VIs and tree ring increments exhibited similar responses to climatic variability. When significant, relationships between VIs and increasing precipitation and PDSI were positive, while relationships between VIs and increasing temperatures were negative. Consistent with our dendrochronological regressions, relationships between VIs and climate were stronger for *J. virginiana* than for *P. ponderosa*, likely owing to differences in stomatal regulation between the two species (Voelker et al., 2018).

Chlorophyll indices, such as GCI, have been successful in measuring evergreen GPP, phenological traits, and Light Use Efficiency (LUE) across multiple spatial scales (Wu et al., 2012, Zeng et al., 2022). GRVI, similar to GCI in that it includes a Green band in its equation, can detect subtle disturbances to vegetation (Motohka et al., 2010), and is more sensitive to photosynthetic capacity in evergreen conifers than NDVI or EVI (Nagai et al., 2012). Both GCI and GRVI exhibited significant responses to variations in precipitation and PDSI and were significantly correlated with tree ring chronologies of both *P. ponderosa* and *J. virginiana*, demonstrating their potential use for studying evergreen conifer species. LSWI, an index with a particularly inconsistent nomenclature (Ji et al., 2011), is sensitive to leaf water content within evergreen conifers (Xiao et al., 2004) and other plant functional groups, and as a result is responsive to water availability via precipitation and soil water content (Wagle et al., 2014). While LSWI was significantly correlated to tree ring chronologies in both species, it appears to be more responsive to climatic variations affecting *J. virginiana* than *P. ponderosa*. Additionally, LSWI values were higher for *P. ponderosa* than *J. virginiana* stands, perhaps owing to the difference in genetic, physiology and drought adaptive strategies of the two species, wherein *P. ponderosa* retains water by closing stomata in drought conditions to avoid cavitation (Bihmidine et al., 2010). NDVI, EVI, and EVI2 have an extensive record of application in vegetation research, with NDVI the more susceptible of the three to atmospheric and soil effects that are accounted for in the EVI and EVI2 calculations, while EVI2 forgoes the blue band that is included in the EVI equation (Jiang et al., 2008). EVI and EVI2 were the least effective indices in characterizing foliage performance in response to climatic variations for both tree species and were insignificant proxies for ring growth in *P. ponderosa*. Based on these results, we confirm our hypothesis that environmental stressors impacting tree ring growth also affect foliage growth, which can be detected using remote sensing techniques. EVI and EVI2 were especially poor indicators for these species, while NDVI, GCI, GRVI, and LSWI are more likely to be effective proxies depending on the species and parameters of interest. This study builds upon previous research in establishing a relationship between remote sensing-derived VIs and tree ring measurements (He and Shao 2006, Bumann et al., 2019, Erasmí et al., 2021), and the significant relationships found in this study may enable real-time cross-scale monitoring of encroaching woody species in the Sandhills with a much lower cost of labor than would be possible using only physical data collection techniques.

4.3. Comparisons between invasive tree and grassland performance in response to the abiotic environment

Comparisons between performance of grasslands and wooded areas in response to abiotic factors were investigated utilizing NDVI.

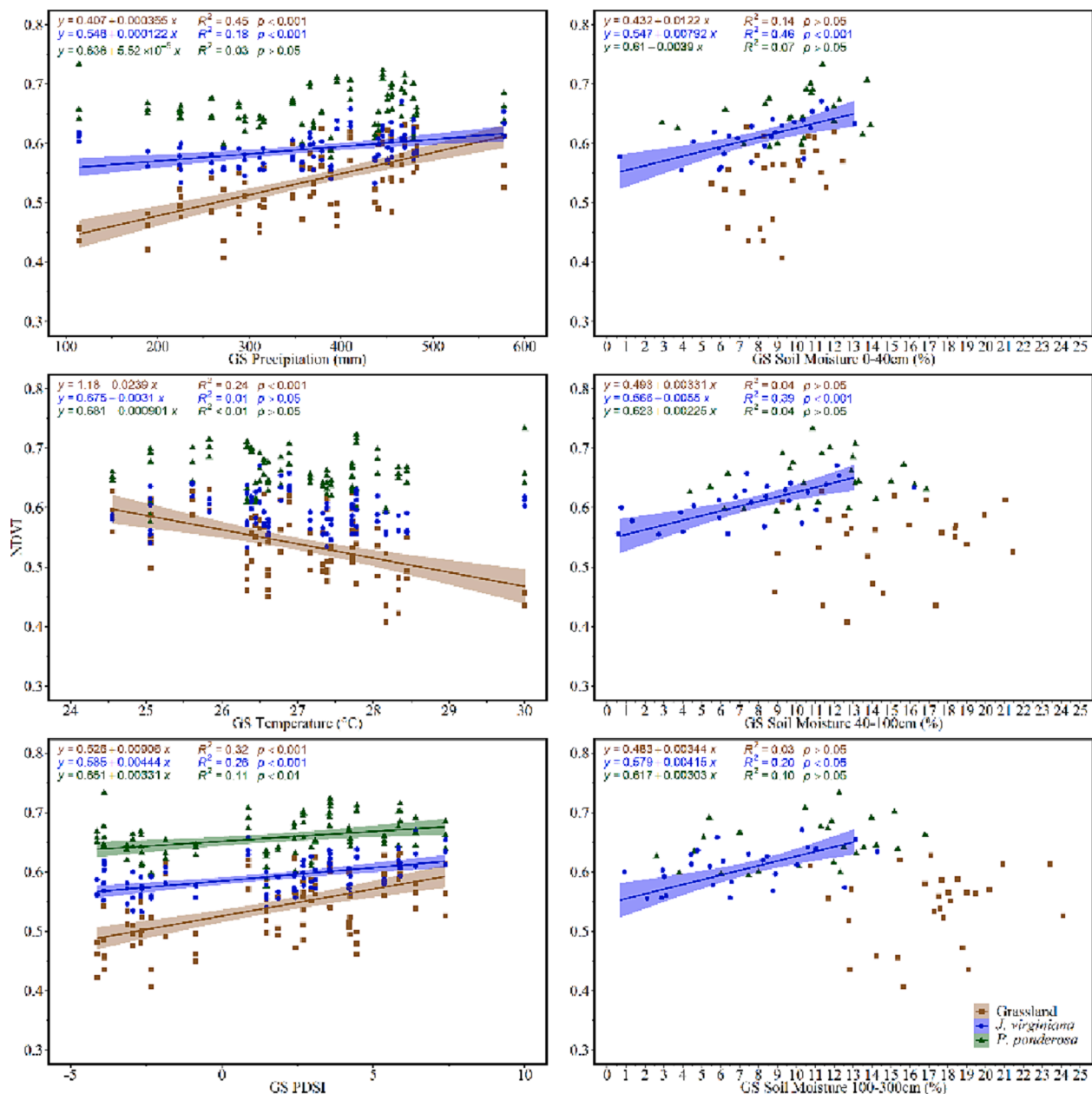


Fig. 8. Regressions between Normalized Difference Vegetation Index (NDVI) of grasslands, *Pinus ponderosa* and *Juniperus virginiana* with growing season (GS) precipitation, temperature, and PDSI (1984–2013) and soil water content (2005–2013) in the semi-arid grasslands of the Nebraska Sandhills, Nebraska National Forest, Halsey, NE.

Grassland NDVI varied significantly more on an annual basis than that of *P. ponderosa* or *J. virginiana* (Fig. 7A), particularly in years with low precipitation (e.g., 2012). Eggemeyer et al., (2009), found that herbaceous species in the Sandhills were dependent on current precipitation events and water in the top soil (0–50 cm), and were forced into senescence as a result of drought conditions, while *P. ponderosa* and *J. virginiana* maintained water status. The drought resistance strategies of coniferous species (Hacke and Sperry 2001, Hacke et al., 2015), in addition to deeper rooting depths and plasticity in water absorption strategies shared by both tree species enable a degree of decoupling from current year climatic variations that are not shared by native grassland species (Eggemeyer et al., 2006; 2009). Additionally, LASSO analysis – which has been used in previous studies of remote sensing-based assessments of vegetation change in response to climate (Wang et al., 2021) – selected only current year climatic variables for grassland NDVI, while 1-year lagged climatic variables were selected for *J. virginiana* and

P. ponderosa, further emphasizing ecophysiological differences between species functional groups. While Guretzky et al. (2016) found positive correlations between 3-year lagged growing season precipitation and warm season grass species basal cover in the NNF, responses to current year climatic variations are more likely to be observed through foliage reflectance properties (i.e., NDVI) as grasses brown and senesce that may not be observable in measures of basal coverage. Although grassland performance was found to be more steeply affected by current year climate, and unaffected by soil water content and previous year climate, grassland NDVI was nonetheless a significant, albeit weak, predictor of *P. ponderosa* and *J. virginiana* tree ring growth and NDVI (Figs. 6, 7B, & Fig. S3). It is possible that trees located in the densely planted NNF are under a greater degree of stress due to intraspecific competition that forces a greater degree of dependency on current year climatic events than might exist in unplanted or sparser forests. All species groups in this study responded significantly to current year climatic events, therefore

Table 4

Results of Least Absolute Shrinkage and Selection Operator (LASSO) regressions. Response variables were the Normalized Difference Vegetation Index (NDVI) for grassland sites, and NDVI along with standardized ring chronologies for tree sites. Independent variables included growing season precipitation, temperature, and PDSI, along with previous year (lagged) precipitation, temperature, and PDSI from 1984 to 2013, in addition to growing season soil water content (SW) stratified by depth (0–40 cm, 40–100 cm, and 100–300 cm) from 2005 to 2013. A check mark indicates a variable was selected as contributing to annual variation of a given response variable.

LASSO Climate and Soil Water Content (%)					
Abiotic variables	Grassland	<i>P. ponderosa</i>		<i>J. virginiana</i>	
	NDVI	NDVI	Ring Width	NDVI	Ring Width
Precipitation: Lagged		✓			
Precipitation: GS	✓	✓	✓	✓	
Temperature: Lagged				✓	
Temperature: GS	✓			✓	
PDSI: Lagged		✓		✓	
PDSI: GS	✓	✓	✓	✓	✓
SW 0 – 40 GS				✓	
SW 40 – 100 GS					
SW 100 – 300 GS					✓

we cannot fully accept our hypothesis that grassland performance is decoupled from that of woody species in the Sandhills. However, there is evidence to suggest differences in the degree of response between species.

5. Conclusion

Woody species encroachment is occurring globally in grassland and savannah communities (Archer, 1994, Barger et al., 2011) altering ecosystems and the services they provide (Ratajczak et al., 2012). In the semi-arid grasslands of the Nebraska Sandhills, encroaching woody *C3 J. virginiana* and *P. ponderosa* are displacing native *C4*-dominated grasslands. In this study, we sought to investigate whether remote sensing techniques could be used as efficient and cost-effective methods to determine the performance of coniferous encroaching woody species, by establishing a relationship between VIs derived from remote sensing techniques and dendrochronological measurements.

Our results showed that both VIs and tree ring growth of *P. ponderosa* and *J. virginiana* responded similarly to interannual variability in the abiotic environment. We found significant, positive correlations between VIs (particularly NDVI, GCI, GRVI, and LSWI) and tree ring growth using linear regressions, demonstrating efficacy for the use of VIs as proxies for the interannual performance and growth of both studied tree species. We further demonstrated that the performance of grassland sites was coupled more strongly to current year climatic trends than that of *P. ponderosa* or *J. virginiana*, while *J. virginiana* exhibited a significant response to variations in soil water content that was not found for grassland or *P. ponderosa* sites. While VIs derived over grassland areas can be predictors of tree ring growth for *P. ponderosa* and *J. virginiana*, the reliance on current year precipitation and temperature for grassland growth and drought resistance properties of both tree species indicates a degree of decoupling in performance between woody and herbaceous species in the Sandhills region that may increase in the future due to climate change.

Our results indicate the potential to predict the performance and growth of invading woody species and adjacent grasslands based on current year climatic fluctuations using remote sensing techniques. These results will enable cross-scale monitoring methods that may be used to attenuate future encroachment as global climate change persists, leading to increasing temperatures and decreasing precipitation that we predict will hasten the spread of woody encroachment while hampering the performance of native herbaceous species.

CRedit authorship contribution statement

R. Allen: Investigation, Methodology, Visualization, Writing – original draft. **A. Mazis:** Methodology, Visualization, Writing – review & editing. **B. Wardlow:** Conceptualization, Methodology, Writing – review & editing. **P. Cherubini:** Conceptualization, Methodology, Writing – review & editing. **J. Hiller:** Investigation, Data curation, Writing – review & editing. **D. Wedin:** Writing – review & editing. **T. Awada:** Conceptualization, Methodology, Funding acquisition, Resources, Project administration, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgement

Funding for this project was provided by the McIntire Stennis Forestry Funds – USDA (1017953). We would like to thank the U.S. Forest Service for the Access to the Nebraska National Forest at Halsey.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.121184>.

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