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Woody Encroachment of a Riparian Corridor in a Tallgrass Prairie: Dendrochronological Evidence from Kansas

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The density of forested cover in grassland regions has been increasing globally during the past several decades. Although there is some evidence to suggest that climate change is playing a role in this woody encroachment, there is a lack of consensus on both the causes and consequences of this land cover change. To examine the role of climate on tree establishment and growth at a very large spatial scale, we used dendrochronological techniques coupled with spatial analyses of the effects of climate drivers on biotic responses such as establishment and growth. We sampled ring widths of selected large trees and collected establishment dates of trees for four deciduous tree species in the riparian zone of a 119 ha experimental watershed at the Kansas Konza Prairie Biological Station, near the current prairie–forest boundary of North America. Annual tree-ring width is positively correlated with the Palmer Drought Severity Index and growing season precipitation, although winter climate variables also affect deciduous tree growth. A pulse in tree establishment occurred shortly after a shift in management in the 1980s, including bison grazing and biennial burning treatments. Spatial patterns of woody vegetation expansion in this watershed indicate that recruitment is increasing at higher elevations in the riparian corridor.

Keywords: dendrochronology, Flint Hills, PDSI, riparian zone, woody expansion.

The boundaries between grass and tree biomes have intrigued landscape ecologists for decades. Forests and grasslands have radically different ecosystem properties, such as carbon storage, albedo, and net primary productivity (Knapp *et al.* 2008; Barger *et al.* 2011). Yet, the dynamics of the boundaries including future cover have been difficult to predict. As the global phenomenon of woody expansion continues, single-factor explanations such as changes in fire (Heisler Briggs, and Knapp 2003), grazing, land use (Archer, Schimel, and Holland 1995), and atmospheric carbon dioxide concentrations (Bond and Midgley 2012) have been insufficient. A more nuanced approach to spatial scale could help clarify the relative roles of climate variables in determining the dynamics of grasses and trees.

Relatively coarse climate variables such as mean annual temperature (MAT) and mean annual precipitation (MAP) explain broad patterns of forest and grass cover on both global (Staver, Archibald, and Levin 2011) and continental scales (Sankaran *et al.* 2005). Briefly, sufficient precipitation (approximately 1,000 mm MAP) is needed to support woody vegetation, but grassy biomes cover large areas of Earth that are mesic enough to support closed forests (Bond 2008). In those places, disturbances such as fires and grazers are invoked to explain this apparent mismatch between climate and vegetation cover.

Disturbances such as fire and grazing are important determinants of land cover at local scales (Grimm 1984; Heisler, Briggs, and Knapp 2003). Higher disturbance frequency or severity seems to favor grass- land cover and reduce forest cover. Grazing and fire together could have interactive effects that are more complicated than either factor alone (Staver *et al.* 2009). Disturbance can, in fact, shift ecosystems between alternative stable states within a single climate. For example, under moderate annual rainfall conditions (1,000 to 2,500 mm) with mild seasonality (less than 7 months), tree cover is bimodal, and only fire differentiates between savanna and forest (Staver, Archibald, and Levin 2011). In addition, although flood events might affect tree establishment, especially in relation to seedling uprootment, little to no flooding has occurred in this watershed in recent decades.

There is also empirical evidence for a possible role of climate at local scales of tree establishment. A dendroecological study in Minnesota demonstrated that bur oak trees (*Quercus macrocarpa*) established during drought episodes, not wet times, in a savanna (Ziegler *et al.* 2008)

and more broadly across the region (Shu- man *et al.* 2009). Spatial patterns of woody cover from aerial photographs at Konza Prairie Biological Station near the prairie–forest boundary in Kansas indicate gradual expansion of woody areas since 1939 (Knight, Briggs, and Nellis 1994; Briggs *et al.* 2005), but potential drivers of this pattern are unclear. A better understanding of the mechanisms behind woody expansion is especially important given that tallgrass prairie is a unique and rare ecosystem type (Samson and Knopf 1994).

Here, the authors studied the history of woody cover in a single watershed in a tallgrass prairie biome through dendrochronological techniques to evaluate woody expansion. The authors sampled at both high temporal (annual) and spatial (sub-10 m scale) resolution. They had two objectives: (1) to determine the timing and spatial pattern of tree establishment in a single experimental watershed of King’s Creek at Konza Prairie Biological Station, and (2) to test the relative strength of climatic drivers on facilitating tree establishment and growth, particularly exploring if the biotic response to climatic drivers varies with spatial position along the stream channel.

Methods and Materials

Study Area

This study took place along the riparian corridor (Figure 1) of King’s Creek in an experimental watershed called N2B at Konza Prairie Biological Station (KPBS) in Kansas. This is a well-studied long-term ecological research (LTER) site located in the Flint Hills ecoregion, the largest continuous tract of unplowed native tallgrass prairie in North America (Samson and Knopf 1994). Prior to its use as a research station, the area was held by private land- owners who used the land for grazing cattle. In 1981, with the establishment of the LTER, the 3,487 ha area was divided into sections that have been subjected to experimental treatments including the grazing of cattle, bison, or both, and controlled burning at different seasons, but usually March through May. The N2B watershed is burned biennially and grazed by a herd of approximately 300 bison. Parent material in the Flint Hills is nearly horizontal, stream-dissected, interbedded Permian limestones and shales overlain by discontinuous Quaternary alluvium (Macpherson 1996).

Climate for the northeast region of Kansas (Kansas Climate Division Three) is characteristic of midcontinental or continental areas (Fay *et al.* 2011) with hot summers and cold winters.

Average monthly temperatures range from -3°C in January to 27°C in July for 1983 through 2009, with a mean annual temperature of 13°C (Craine *et al.* 2011). When compared with data from 1949 through 1979, average annual temperatures have increased 0.51°C throughout the region, with the largest increases occurring January to March ($>1.67^{\circ}\text{C}$; National Climate Data Center [NCDC] 2012). Average annual precipitation was 927 mm (1983–2009), and ranged from 21 mm (January) to 134 mm (June). During the biologically active growing period (May–September), precipitation averaged 114 mm. Precipitation regimes have also shifted when compared to 1950 through 1979, with average annual precipitation increasing 53 mm, although May to September precipitation values only increased moderately (1.25 mm) over the same period. Although precipitation amounts vary considerably throughout the year regionally, drought conditions are also periodically present. A good measure of drought conditions at local scales is the Palmer Drought Severity Index (PDSI). The PDSI measures deviations of monthly moisture conditions from normal conditions, indicates the intensity of long-term drought patterns, and is calculated based on precipitation, temperature, and local available water content values (Palmer 1965).

Vegetation in the Flint Hills tallgrass prairie is dominated by C4 grasses (especially big bluestem [*Andropogon gerardii*], Indian grass [*Sorghastrum nutans*], and little bluestem [*Schizachyrium scoparium*]), but both hardwood (bur oak, hackberry [*Celtis occidentalis*], white ash [*Fraxinus americana*], American sycamore [*Platanus occidentalis*]) and coniferous (eastern redcedar [*Juniperus virginiana*]) trees exist, typically in or near dissected riparian corridors and lowlands. A MAP of 900 mm is mesic enough to support forest or savannah vegetation; however, historic fires, droughts, and grazing play important roles in maintaining the area as grassland (Briggs *et al.* 1997).

The largest stream system draining KPBS is King's Creek and its tributaries, which are medium to low in gradient (>30 to 100 m/km), dendritic in pattern, and ephemeral or intermittent, having sustained flows only in the spring season or after rainfall events, especially in headwater regions. Mean monthly discharge from King's Creek is 0.01 m³/s in September and 0.23 m³/s in May (Mast and Turk 1999). The King's Creek watershed is a Hydrologic Benchmark Network station used by the U.S. Geological Survey as a reference watershed because it is minimally affected by human activities (Mast and Turk 1999). Because of its reference status, King's Creek was fitted with a concrete weir so that water discharge could be sampled accurately.

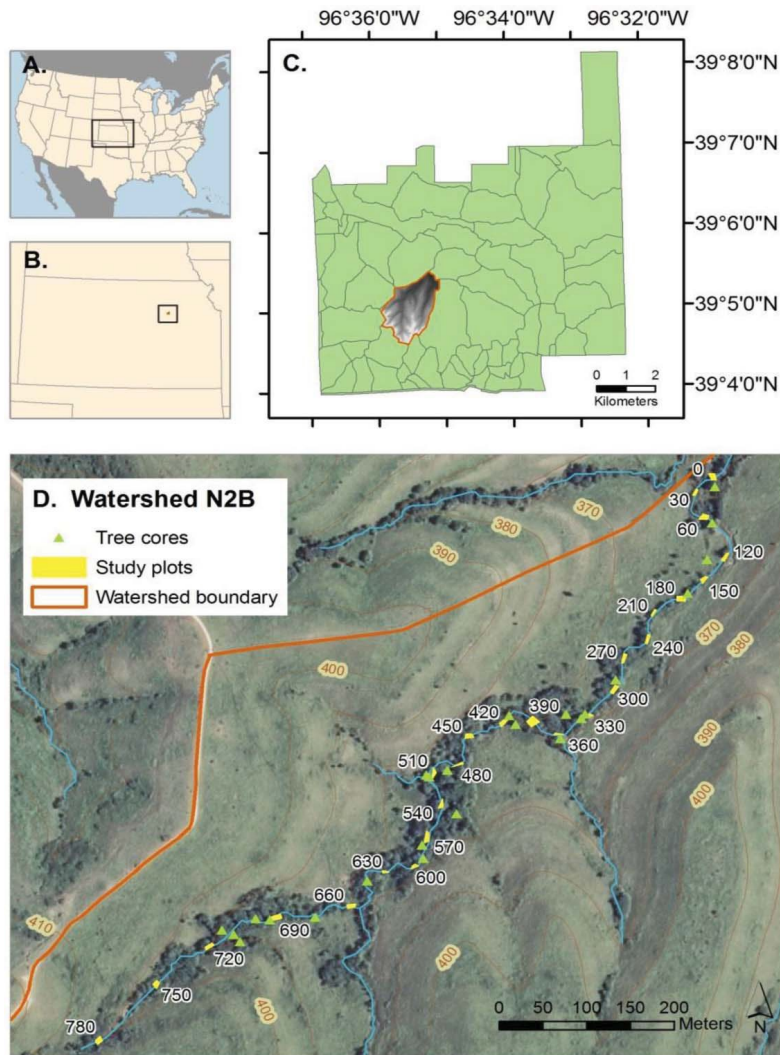


Figure 1 Location of study area within (A) the United States, (B) the state of Kansas, (C) Konza Prairie Biological Station highlighting the N2B watershed, and (D) the study area within the N2B experimental watershed. (Color figure available online.)

Riparian Corridor Tree Plots and Increment Cores

Twenty-six plots measuring 10 × 10 m were sampled for woody vegetation along 4 km of a recently cleared riparian corridor in the N2B watershed of Konza Prairie (Figure 1) from January to March 2011. The riparian corridor had been cleared of woody vegetation within 10 m of each side of the stream channel as part of an unrelated experiment in late fall 2010. The remaining stumps were sanded to conduct annual ring counts. Other data including trunk diameters, tree positions relative to the channel, and tree species were also documented systematically. All stumps within each plot were sampled, resulting in a total sample size of 155 tree stumps.

The largest trees in the riparian corridor were girdled beginning in September 2010 as part of the same woody removal study. Increment cores measuring 5 mm in diameter were collected from the girdled trees ($n = 20$) along the length of the channel. All of these trees were deciduous species: hackberry, white ash, American sycamore, and bur oak. These cores were collected following the method of Fritts and Swetnam (1989) with a Hagl f increment borer, and then were dried at 60 C for twenty-four hours. Once dried, the cores were mounted into Jorgensen wood clamps, then sanded using incrementally finer grit sandpapers (up to 600 grits) until annual rings could be counted. Sanded and polished cores were then scanned using a 1,200 dpi Epson flatbed scanner. These images were imported into Cybis Coorecoder 7.4 (2012) and Cybis CDendro 7.7 (2012) software for counting and measuring of rings. Heavy and negative exponent detrending (curve-fitting algorithm) of raw ring width data was also performed in CDendro to remove age-related growth trends (Zhang *et al.* 2012).

Climate data from the northeast region of Kansas (1895–2010) was acquired from the NCDC (2012), which included monthly values for temperature and precipitation (minimum, maximum, mean), as well as PDSI values.

Statistical Analyses of Plot and Core Data

Stepwise multiple linear regression analysis with forward and backward elimination was used to determine which variables were predictors of mean ring width (Table 1). Variables were allowed to enter and stay in the model at the significance level of $p < 0.05$. Before the regression analyses, residuals of predictor variables were tested for normality as measured by the Anderson–Darling test. Variables with residuals violating the assumption of normality were transformed prior to the stepwise regression. All statistical analyses were carried out in SAS 9.2. An α value of 0.05 was used to determine statistical significance.

Table 1 *Parameters used in the stepwise multiple regression to predict mean ring widths for sampled trees in the N2B watershed of Konza Prairie Biological Station*

		Description	Units	Source
	Precipitation variables		mm	National Climatic Data Center
	Mo Precip	Total monthly precipitation		
	AnPrecip	Total annual precipitation		
	PrcpMJJ_7yr	7-year moving average of mean precipitation for May, June, July		
	Temperature variables		C°	National Climatic Data Center
	Mo Tmean	Mean monthly temperature		
	AnAvTemp	Mean annual temperature		
	TempMJJ_7yr	7-year moving average of mean temperature for May, June, July		
	PDSI variables		Indexes	National Climatic Data Center
	Mo Tmean	Mean monthly PDSI		
	AnAvTemp	Mean annual PDSI		
	TempMJJ_7yr	7-year moving average of mean PDSI for May, June, July		

Note: PDSI D Palmer Drought Severity Index.

Results

The overall age of trees as measured from stumps in the N2B watershed is relatively young. The oldest stump of a tree sampled had established in 1880, being approximately 130 years old. The mean age of trees was 75 ± 8 years. There were large numbers of trees established in the late 1970s to early 1980s, with more than half (56 percent) of all plots having mean establishment dates within that range (Figure 2A). For individual trees within the plots, mean tree age is positively correlated with stump diameter (Figure 2B). There is a strong positive linear correlation between mean ages of trees in each plot and elevation of plots, such that as elevation increases, the mean tree age decreases (Figure 2C). This has resulted in a trend since the late 1960s of increased establishment of trees at increasingly higher elevations in the watershed, as woody species move up-channel. There was a sharp rise in both plot elevation and establishment rate around 1981, the year that the Konza Prairie LTER site was established. Tree frequency per plot and distance from the weir are not related.

Annual ring widths from the twenty largest trees in the riparian corridor could be predicted

by four climate variables (overall model $r^2 = 0.311$, $p < 0.0001$; see Table 2). Most of the variation in ring width is predicted by the seven-year average May–June–July temperatures, with warmer temperatures leading to increased growth. Three other variables were significant at the $p < 0.05$ level: August PDSI, December mean temperature, and February precipitation.

The increment cores show that a majority of the oldest trees in the riparian corridor established near the midpoint of the watershed in terms of elevation and distance to the weir (Figure 3). Although the instrumental climate record does not extend far enough back to test if climate forcing could have caused this distribution, it is possible that moisture availability played a role in this spatial pattern. Additionally, there was a large temporal gap from 1910 to 1940 when no large trees were established in the study area.

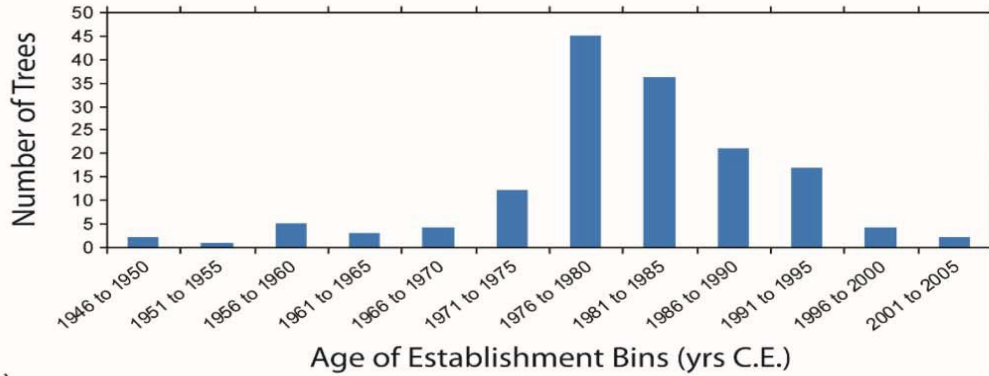
Both climate and management variables are temporally correlated with tree establishment in the N2B watershed (Figure 4). Moisture availability is partially controlling tree growth and establishment, with periods of negative PDSI exhibiting lower establishment rates. An establishment pulse occurred when controlled burning practices were initiated in 1981, although the fire return interval prior to that is largely unknown. The placement of a bison herd at Konza Prairie Biological Station in 1988 with access to the N2B watershed might have slightly diminished frequency of tree establishment.

Discussion

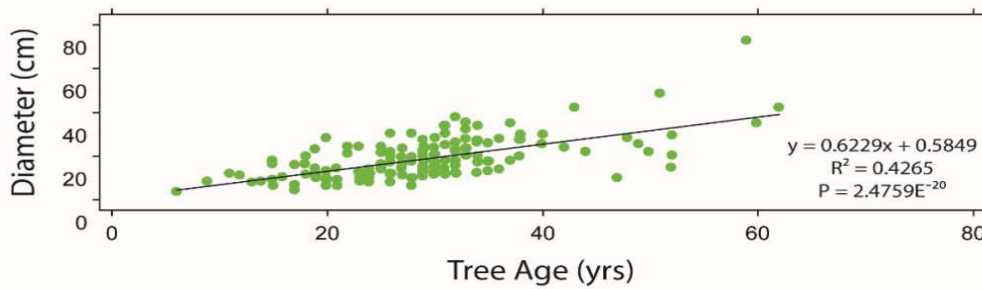
The number of trees in the riparian corridor in the N2B watershed has been significantly increasing since the late 1800s, with the rate of tree establishment increasing since the 1970s (Figure 2). The large-scale spatial pattern of this tree establishment suggests a time-transgressive pattern with trees establishing up the channel over time. Time-transgressive spatial patterns can have synchronous drivers, as demonstrated by Williams *et al.* (2010) with regional drying and rapid-response ecotone shifts, and there is evidence for synchronous drivers in this case with a strong correlation between tree growth and moist conditions as well. The strongest predictor variable for ring width was the seven-year average May–June–July temperature (Table 2). Other dendrochronological studies have suggested that higher growing season temperatures (May–June–July) promote tree growth in forests (Kelly *et al.* 2002;

Garcia-Suarez, Butler, and Baillie 2009). It was found that this relationship is also supported in the more arid grassland system of Konza Prairie.

(a)



(b)



(c)

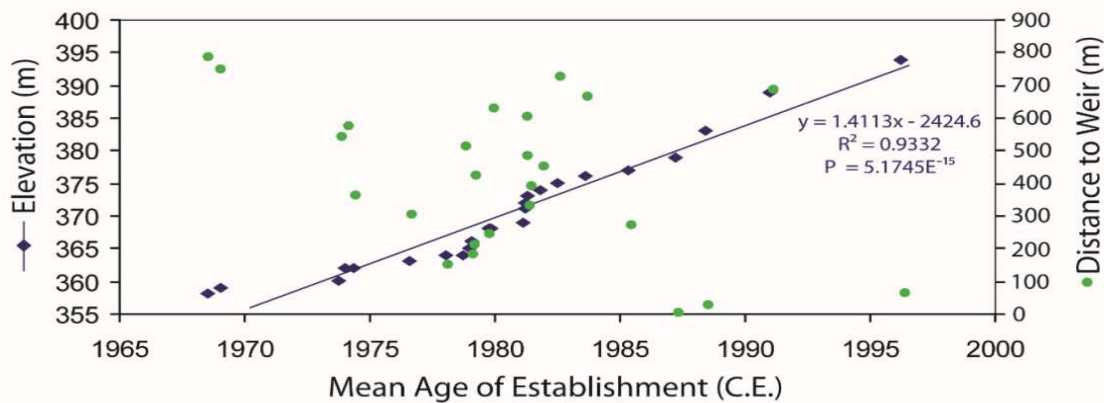


Figure 2 Spatial and temporal patterns of tree establishment along the King's Creek channel of the N2B watershed from the twenty-six study plots: (A) Number of trees establishing in time bins during the twentieth century. (B) Diameter of trees as measured from stumps <30 cm above the soil surface. (C) Mean age of establishment within a plot. Note that distance to weir for each plot can be seen in Figure 2C. (Color figure available online.)

Table 2 *Model fit and parameter estimates for the stepwise multiple regression predicting mean ring widths for sampled trees in the N2B watershed of Konza Prairie Biological Station*

(A)Model		n	r²	F value	p level
Results		110	0.311	11.96	<.0001
(B) Parameter	Units	B	SE of B	p level	Partial r²
May, June, July 7-year mean temperature	C°	-0.124	0.031	<.0001	0.2148
August PDSI		0.018	0.0007	0.0265	0.0351
December mean temperature	C°	-0.013	0.007	0.0312	0.032
February precipitation	mm	-0.002	0.0008	0.0366	0.0291

Note: PDSI = Palmer Drought Severity Index.

Three other climate variables affected tree growth, suggesting multiple interactions among climate and aspects of tree physiology. Increases in August PDSI were correlated to increases in ring width, which indicates that higher moisture availability during the hot- test month of the year positively influences tree growth. Positive relationships between moisture and tree growth have been found in many other dendro- chronological studies (Jonsson and Nilsson 2009). Our results differ from those at the bur oak savanna in Minnesota where drier, not wetter, times promoted tree establishment due to interactions among grass, fuel load, and fire frequency (Ziegler *et al.* 2008).

There are several possible explanations behind the role of winter climate variables (i.e., not during the growing season) in influencing tree growth. Increases in February precipitation were correlated to increases in ring width (Table 2), suggesting that precipitation in early spring (likely snow) promotes tree growth. This indicates a potential lag effect of moisture attenuated by temperature, such that winter moisture is still important for early spring growth through infiltration and soil water recharge. Increases in December mean temperature were also correlated to increases in ring width. Although initially counterintuitive, this result points to temperature requirements for cold-hardy deciduous trees to initiate cold-hardening, bud formation, and eventual leaf formation and flowering. That is, a deciduous cold-hardy tree has several biotic responses to temperature shifts, such as when cold- hardening is initiated by temperatures approaching freezing. Increases in ring width correlated to increases in December temperatures can be explained by the overarching need for a cold-hardy tree to reach temperatures capable of

initiating cold-hardening but mild enough to prevent necrosis caused by extremely low temperatures affecting the ability of sugars in the cells to protect them from freezing and causing cell wall damage. Overall, these results are similar to other studies involving climate variables and tree-ring growth in that ring width is most affected by rainfall, PDSI, and maximum temperatures in the late spring and early summer (Garcia-Suarez, Butler, and Baillie 2009), but additionally suggest that nongrowing season climate variables might influence deciduous tree growth as well.

Potential reasons for a lack of establishment during the period from about 1910 to 1940 include drought conditions, increased fire frequency, grazing, or human alteration (logging and clearing), although with the limited historical data available for this watershed it is difficult to evaluate these factors quantitatively. It is plausible, however, that because the average PDSI index value was -0.5 for this thirty-year period, that tree establishment and growth could have been inhibited due to drought-induced weakening and susceptibility to stress (mildew infections, insect attacks, etc.), which can lead to mortality (Andersson, Milberg, and Bergman 2011). Moreover, this period includes the most severe drought recorded in the United States, which might have killed the already stunted (by below-average moisture conditions) early-stage trees established at this time.

The main spatial pattern of woody expansion for this study area is increasing establishment occurring along the riparian corridor at higher elevations and longitudinal distance from the weir. This confirms previous studies (Knight, Briggs, and Nellis 1994; Briggs *et al.* 2005) but also pinpoints the past few decades as an especially dynamic time. There is evidence for this woody expansion being driven by both climatic (precipitation and temperature variables) and anthropogenic factors (prescribed fire and grazing regimes set by managers). The role of additional anthropogenic factors such as increased atmospheric carbon dioxide in stimulating tree growth (Bond and Midgley 2012) was not addressed in this study, but could likely contribute to recruitment. It is largely unknown if this conversion from tallgrass prairie to wooded grassland is reversible. Temporal studies of this conversion in other areas suggest potential irreversibility of a shift from grass cover to tree cover (Briggs *et al.* 1997; Elliott 2012). In this watershed near the current prairie–forest boundary, this might also be an irreversible shift in land cover with profound ecosystem

consequences.

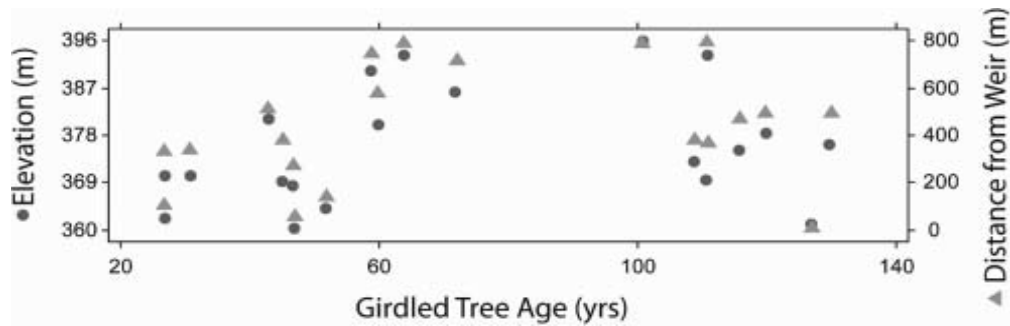


Figure 3 Relationship between age of the twenty largest trees in the riparian corridor, elevation, and up-channel distance.

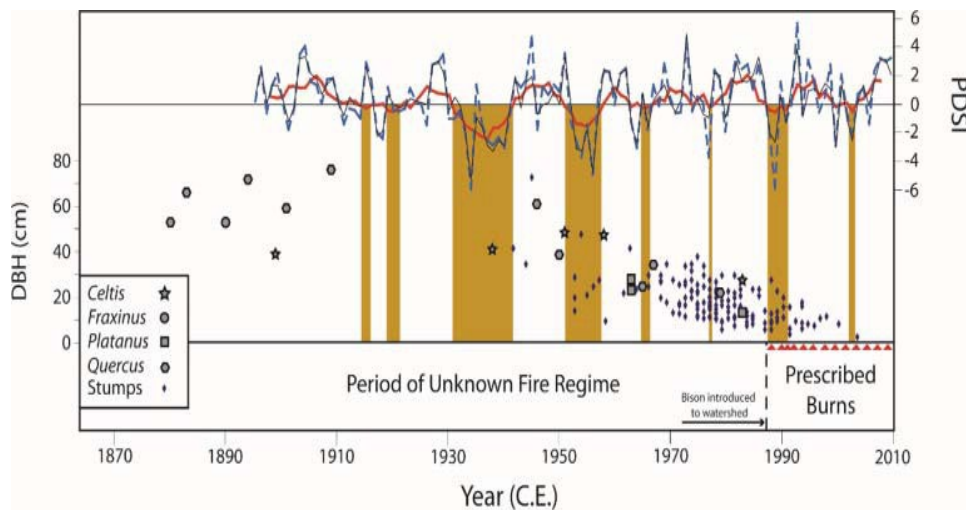


Figure 4 Tree diameter at breast height (dbh) for girdled trees and diameter at the base for tree stumps with approximate establishment year. The Palmer Drought Severity Index (PDSI) is calculated from the instrumental record and indicates relative moisture availability, with values below zero indicating below-average moisture availability classified as drought periods. Annual PDSI values are shown in black, May–June–July PDSI moving average values are shown in blue, and seven-year average PDSI values are shown in red. Known fires in the N2B watershed are indicated with red triangles, either prescribed or unprescribed burns. Native bison (*Bos bison*) were allowed access to the watershed in 1988. Brown bands indicate significant drought events. (Color figure available online.)

Conclusions

Several species of deciduous trees have expanded in spatial extent along a riparian corridor in a bison- grazed, biannually burned experimental watershed in a tallgrass prairie. These

results are congruent with several other studies ranging from global to local scales, which have documented an increase in woody cover in grassland regions (Briggs *et al.* 2005; Barger *et al.* 2011). Even in this very large-scale study of a single riparian corridor, woody expansion was at least partially explained by climate variables such as soil moisture availability in winter months, temperature, and precipitation in our study area. There is also qualitative evidence, such as the timing of notable management events, that land use change involving grazing or burning affected the timing of tree establishment in this watershed. Future work could refine the relationships among growth, climate, and moisture sources through analyses of stable oxygen isotopes in tree-ring cellulose (Nippert *et al.* 2010). Another important line of inquiry would be to determine the timing and seasonal envelope of flowering, growth, and dormancy for these deciduous tree species, to better parameterize the independent climate variables that explain tree physiology and annual tree-ring growth.

It is likely that future woody expansion will continue in the N2B watershed, as has been logged by this study, given that the conditions that dictate this phenomenon continue, with the caveat that due to the riparian treatment (clearing the 10 m margin of the riparian corridor), there will be seral species succession in the absence of the previous (removed) trees. This situation could prove interesting to study with fire and grazing regimes already in place at N2B, further helping to disentangle the roles of climate and disturbances on tallgrass prairie woody expansion in Kansas and elsewhere.

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