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Annual rings of perennial forbs and mature oaks show similar effects of climate but inconsistent responses to fire in the North American prairie –forest ecotone

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Abstract: For the prairie – forest ecotone of central North America, research of the effects of climate and fire on the annual growth of non-woody plant types is currently needed to compliment dendrochronological research used for predicting the stability of this ecotone in the future. Using cores of *Quercus stellata* and collars of taproots of *Asclepias viridis* from central Oklahoma, as well as cores from *Quercus macrocarpa* and *Lespedeza capitata* collars in central Minnesota, we aimed to distinguish the response towards annual precipitation and temperature, as well as fire regime, between these co-existing plant types through patterns in annual ring growth. The effect of spring fire on the annual growth increment was only consistently significant for one of the forbs, with a positive relationship. The strong negative effect of summer temperature was consistent between forbs and *Q. stellata*, while the positive effect of either growing season precipitation was consistent between plant types. Furthermore, we found stronger patch specific annual ring patterns in forbs in comparison with trees when patches are separated based on unique fire histories. Overall, such efforts could be used in further studies to better predict growth rates of dominant plant types in landscapes susceptible to significant environmental change.

Keywords: Annual rings, *Asclepias viridis*, climate, dendrochronology, fire, forbs, herb-chronology, *Lespedeza capitata*, prairie – forest ecotone, *Quercus stellata*, *Quercus macrocarpa*

Introduction

The prairie - forest ecotone of central North America is responsive to environmental changes, leading to dramatic shifts of vegetation boundaries (Umbanhowar *et al.* 2006; Camill *et al.* 2003). Differential responses by the two dominant vegetation types to climate have led from a closed woodland to a more open savanna under prolonged aridity, whereas woodland expansion has resulted during wetter periods (Umbanhowar *et al.* 2006; Camill *et al.* 2003; Bartlein & Whitlock 1993; Baker *et al.* 2002). Periodic fire also plays a key role in the shifting boundaries between grassland and woodlands in this and other regions (Scholes & Archer 1997; Hoagland 2000; Peterson & Reich 2001). Fire deters woodland expansion, thereby favoring graminoids and forbs (McPherson 1997; Peterson & Reich 2001; Peterson, Reich & Wrage 2007). The belowground regenerative buds of geophytic grassland plants enable resprouting after fire (Rogers & Hartnett 2001). With predominantly above ground buds, fire effects on trees are contingent on its life history stage (Sankaran, Ratnam & Hanan 2004). Juvenile stages often suffer large mortality or stem topkill rates from fire (Peterson & Reich 2001; Hoffman & Solbrig 2003), while more mature trees have regenerative buds that grow predominantly above the flame zone (Bond *et al.* 2003), and have thicker fire tolerant bark (Rowe 1983), are less affected.

Besides the role of fire and climate on the more long-term composition of the prairie-forest ecotone, the differential response of coexisting species to fire and climate is likely to be mediated by different patterns of annual growth of different plant types. Annual growth of the grassland component of this ecotone is highly influenced by the year to year fluctuation of climatic conditions as well as the occurrence of fire, much of which is the result of the effects these environmental conditions have on the competitive environment between different grassland functional groups (Turner & Knapp 1996; Bond & Parr 2010). Historical summer season fires are thought to facilitate the competitive balance between these two functional types, temporarily eliminating warm season grasses at the peak of their relative resource use-use efficiency and promoting secondary flush of growth for forbs in the ameliorated light conditions (Howe 1995). Spring fire also facilitates forb presence in grasslands by eliminating litter and ameliorating growth when forbs emerge (Brockway *et al.* 2002). In addition, North American grassland annual net primary production is largely affected by annual precipitation (Knapp *et al.* 2006), whereas the annual growth of forb species may be less affected by short-term arid conditions

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79 compared to grasses due to their deeper roots and access to water deep into the soil column
80 (Mariotte *et al.* 2013), though evidence for this mechanism is mixed (Nippert & Knapp 2007;
81 Fay *et al.* 2002). With respect to woody plants, species specific drought –induced mortality and
82 increasing density of non-oak species from fire suppression are dramatically changing forest
83 structure and thus fire regime, further leading to considerable shifts in composition in this
84 ecotone (Peterson & Reich 2001; Nowacki & Abrams 2008; DeSantis, Hallgren & Stahle 2011;
85 DeSantis *et al.* 2010).

86 With a predicted future regional expanse of longevity and intensity of drought periods,
87 erosion and flooding from more interspersed heavier rainfall events, doubling to quadrupling of
88 the amount of days with an excess of 37 °C high temperature in different regions (Christensen *et al.*
89 2007; Teskey *et al.* 2015) and continued disruption of historical fire regimes (Curtis 1959;
90 Nuzzo 1986; Allen & Palmer 2011), a better understanding of how climate, fire affects the
91 annual growth of different coexisting plant types is needed to understand successional dynamics
92 of the U.S. prairie – forest ecotone in the future. Measurements of annual plant growth rates,
93 such as those obtained by the use of dendrochronology, serve as important metrics to help
94 understand how woody species respond to such environmental conditions. In addition, an
95 emerging discipline named ‘Herb-chronology’ (Dietz & Ullmann 1998) uses the annual rings
96 that occur in the perennial tap root of geophytic forbs as a measure for plant growth response to
97 climatic (Dietz & von Arx 2005; Liu & Zhang 2010; von Arx *et al.* 2012; Franklin *et al.* 2013;
98 Olano *et al.* 2013) and site-related ecological conditions (Dietz & Ullmann 1998; Dee & Palmer
99 2016). Thus, we aim to compare the ability of herbaceous root rings to detect climatic and/or fire
100 history which may differentially impact growth relative to the ability of growth rings in trees to
101 detect the very same environmental conditions. Such a comparison may help us understand how
102 these two life forms are likely to respond to a future changing environment.

103 The eastern Great Plains of North America provides a fitting environment to answer the
104 following questions: **1.** By using fire management as a means of disturbance, what is the relative
105 sensitivity towards year-to-year site-specific growth conditions between the annual rings of
106 herbaceous and neighboring mature overstory tree species? **2.** How does the effect of annual
107 temperature and precipitation differ between the secondary growth of these coexisting life-
108 forms? **3.** How do these climatic variables interact with fire to impact annual ring variation in
109 both plant types? We predict that annual rings within geophytic forb species will carry higher

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patch fidelity (higher mean annual ring pairwise correlations amongst individuals within the same burn unit rather than among different units) in comparison with neighboring trees since fire could relatively positively affect the growth of the former in greater capacity by removing competitor aboveground biomass, but also in some cases with dormant season burns, helps to ameliorate aboveground growth conditions (Howe 1995; Brockway et al. 2002). On the other hand, mature overstory woody species of this region will be more responsive to changes in interannual climate and will show less patch fidelity due to their overwintering buds being above the effects of the flame (Rowe 1983) and tight coupling between annual growth decline, mortality, and climatic response (Wyckoff & Bowers 2010; Leblanc & Stahle 2015).

Materials and methods

Study locations

We selected two study sites representing different parts of the prairie-forest ecotone, but nonetheless had a varied and well-documented fire history: The Tallgrass Prairie Preserve (TP) of Oklahoma and the Cedar Creek Ecosystem Science Reserve (CC) of Minnesota. The TP consists of approximately 15,800 hectares owned and managed by The Nature Conservancy and is located Osage County, Oklahoma. It consists primarily of a mixture of tallgrass prairie interspersed with open woodland (Allen et al. 2009). The tallgrass prairie of this region is dominated by C4 grasses but contains a high diversity of forbs (Turner and Knapp 1996). Generally, tallgrass prairie occurs on fine-textured soils derived from shale and limestone (Powell & Lowry 1980). The dominant woodland type is known as Crosstimbers, and is dominated by two fire adapted oak species, *Quercus stellata* Münchh., *Quercus marilandica* Wangenh., The Crosstimbers of TP are open woodlands located on shallower and rockier soils in comparison to most tallgrass prairie, with a soil that is coarse-textured and derived from sandstone (Powell & Lowry 1980). Fire was a historic component of this landscape, with an average return interval of 2.5 years (Allen & Palmer 2011). Since 1991, prescribed fire has been used to manage prairie and crosstimber vegetation as well as resident Bison (*Bison bison*) populations. The regional climate is continental with annual precipitation averaging 94 cm. Annual precipitation is strongly bimodal with March-June and September-October representing two peaks of rain occurrence. Monthly average temperatures (2001- 2015) range between 4°C and 33°C through the duration of the growing season (beginning of March – end of September).

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Outside of this growing season time period the average annual minimum temperature is -5 °C occurring in January, with the average maximum temperature being 33 °C occurring during the growing season in July. The average potential evapotranspiration (short-crop) for July (2001 – 2015) is 18.5 cm where it is highest, compared to a low of 10.2 cm for March in the growing season. The last freeze occurring in early April and the first freeze occurring in late October on average.

The Cedar Creek Ecosystem Science Reserve (CC) is located in Atoka and Isanti Counties of southeast Minnesota. CC is a 2200 hectare long-term ecological research site owned and operated by The Nature Conservancy and the University of Minnesota. The primary components of the oak savannas within CC are the fire adapted *Quercus macrocarpa* Michx. and *Quercus ellipsoidalis* E.J. Hill. As with the TP, the grasslands in CC are dominated by C4 grasses and have a high forb diversity (Cochrane & Iltis 2000). Most of the soil types at CC are derived from a glacial outwash sandplain, with tallgrass prairie and oak savannas occurring on the nitrogen-poor uplands (Cavender-Bares & Reich 2012). CC has a continental climate with an average annual precipitation of 77 cm with just over 70% of this total occurring between the months of May and October (Reich *et al.* 2001). Monthly average temperatures (2001- 2015) range between -9 °C and 23°C through the duration of the growing season (beginning of March – end of September). Outside of this growing season time period the average annual minimum temperature is -30 °C occurring in January, with the average maximum temperature being 39 °C occurring during the growing season in July. The average potential evapotranspiration (short-crop) for July (2001 – 2015) is 19.6 cm where it is highest, compared to a low of 3.4 cm for March in the growing season. On average, the last freeze occurs in early May with the first freeze usually occurring in early October.

Focal species

One herbaceous forb species and one tree species were sampled from each of these two study locations, totaling four species for the overall study. For TP, the forb *Asclepias viridis* (Walter) A. Gray was sampled along with the tree *Quercus stellata*. *A. viridis* is a geophytic forb belonging to the Apocynaceae, and is frequent and conspicuous in the TP. Its root system is an underground stem containing a pith with a semi-ring porous annual ring structure. On average *A. viridis* has 2 – 4 aboveground shoots that are fairly prostrate and no longer than 50cm long. TP

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represents the western end of the geographic range of *A. viridis*. *Q. stellata* is one of the main components of the Cross Timbers. *Q. stellata* is a member of the white oak tribe with a height typically between 10 – 15 meters, has semi-ring porous structure.

The two species studied in CC were *Lespedeza capitata* Michx. and *Quercus macrocarpa* *L. capitata* (Fabaceae) is a taprooted geophyte with multiple aboveground shoots that may reach 1.5m. *L. capitata* has a semi-ring porous annual ring structure and is fairly abundant in the prairie of CC, existing in scattered subpopulations. For CC, *L. capitata* is close to its northern limits but can be found as far west as western North Dakota. *Q. macrocarpa* is an abundant component of the oak savanna, another member of the white oaks, has semi-ring porous wood structure, and can grow up to 40 meters tall. Similar to *Q. stellata*, *Q. macrocarpa* can live on average to between 200 – 300 years old. *Q. macrocarpa* can be found as far north as southern Manitoba and as far west as central Montana.

Field and laboratory methods

For TP, we chose 4 different patches (AKA burn units) with different histories of prescribed burns (for the period of 2009-2014) which had adjacent tallgrass prairie and stands of Crosstimbers. The four patches that were chosen did not experience summer burns during this time period, only dormant (usually end of winter or very early spring) season burns, corresponding with the very early emergence of *A. viridis* shoots (personal observation). In addition, three of the four patches experienced 2 – 3 burns during the period under consideration while the fourth unit experienced 5 in the same timeframe.

We used 3 adjacent patches (burn units) at CC, all with largely different fire histories from the period of 2008 – 2015, one of which stood apart from the other two in its burn frequency as it was only burned 3 times in the years considered while the other two units burned 5 – 6 times on alternate years. Each patch was located in the southeast portion of CC, with a large makeup of tallgrass prairie and oak savanna. As with TP, fire occurrence was not beyond mid-May in years of a burn.

In mid-July 2015, 20 *A. viridis* and 20 *Q. stellata* were sampled from each of the four patches at TP. *A. viridis* was sampled along 100m transects that were parallel to the prairie – forest ecotone at each patch. *Q. stellata* were sampled along the forest edge of the same ecotone, the same 100m distance as the *A. viridis* transects. *Q. stellata* that grew on medium to high

slopes or relatively rockier microsites were chosen to avoid complacent series, as is a common practice in dendrochronology (Speer 2010). Individuals between 30 – 110 cm in dbh (diameter at breast height) were chosen since they represented likely mature specimens without large age growth decline (Stahle & Hehr 1984). For both species, 2015 was not included in analysis since growth was still active at time of sampling. In mid-October of 2015, 20 *L. capitata* and 20 *Q. macrocarpa* at CC were sampled following the same protocol as in the TP. By this time both species had senesced and thus 2015 was used in analysis. Sampling of *Q. macrocarpa* (between 30 – 110 cm in dbh as well) to avoid complacent series was difficult in this environment since there were little changes in site topography.

Forbs were excavated whole but only the first 5 cm of the root just below the root crown (root to shoot transitional zone) was saved for further analysis. This root zone is commonly used in herb-chronology and is used to track the individual since its first year of growth through the annual rings (Dietz & Ullman 1998). Root samples were then stored in jars containing 75% ethanol for transport to the laboratory. Laboratory methods for the geophyte roots consisted of using a sledge microtome to cut approximately 20-30 μm thin sections of each root collar that were then stained with a mixture of Safranin and Astra Blue to enhance ring borders with lignified tissue staining red and parenchyma staining purplish-blue (Schweingruber, Borner & Schulze 2011).

Trees were cored with an increment borer, depending on DBH, coring only ensued until it was perceived that the last 30 or 40 years of annual growth was captured. Cores were stored in straws that were slit open to facilitate ventilation and prevent fungus growth. One section per individual was then immediately photographed and saved for future image analysis using ImageJ (Abramoff et al. 2004). Tree cores were sanded by using sequential finer grained sandpaper to enhance ring borders, and then measured by using a Velmex (Velmex Inc. 2009) with J2X software (Voor Tech Consulting 2008).

Analytical Methods

Ring widths for the forbs were measured using the measurement tool in ImageJ (Abramoff et al. 2004). Ring width for each corresponding year was the average of the lengths of 4 radii to account for the variance in width about the circumference of each ring. For tree rings, ring width measurements using J2X were stored as .rwi files. Raw ring widths of both the forbs

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and trees were imported into R version 3.2.0 (R Core Team 2015), for eventual use of the diagnostic tools within the dplR package (Bunn *et al.* 2016). For forb species, mean pairwise correlations within species for each burn unit (and also amongst all units) were calculated using Microsoft Excel and double checked using the interseries.cor function in dplR.

Given the differences forbs and trees with respect to the length of the time series, several steps must be taken before calculating mean pairwise correlations. Since for both tree species the average series length was close to 35 – 45 years we chose not to use any special age detrending methods. In addition, we did not consider age detrending because our eventual analysis would be using standardized ring widths per individual for only the years which overlap with the years considered for neighboring forb chronologies (also standardized per individual), which on average was less than the last 10 years. For the tree species in our study in particular, using dplR, raw ring widths were first subdivided into 16 year segments and their mean correlations with the same 16 year segments of all other tree series in the patch were checked for their correlation coefficients using the corr.rwl.seg function. Problem segments are flagged if they drop below the 0.50 correlation coefficient level. As the standard method for troubleshooting problem series with tree cores, we used ccf.series.rwl function, where the mean correlation coefficients are shown if series with many problem segments are shifted up or down in a few years to help aide in fixing any possible cross-dating error. After these problems were fixed, mean correlations for trees within or among all burn units were calculated using the interseries.cor function. A maximum of three series with its pairwise correlations considerably below 0.50 were dropped from analysis per unit since these were likely cross-dating errors that could not be fixed, likely attributable to false or missing rings.

The preceding methods were not possible for forb species since the time series are not long enough for these diagnostic tools based on 16 year overlapping segments. In addition, it is unknown at this point if forb series may be cross-dated in a similar manner to trees. There is likely a strong ecological signal that may vary immensely between individuals, rendering cross-dating, as it done for trees with their reliable consistent response to annual climate, likely not possible for herb-chronology. Nonetheless, using correlation matrices, we found a few forb series with overall low mean pairwise-correlation and decided to not remove them as to preserve any ecological signal found in this study, though the possibility of false/missing rings contributing to these low mean pairwise correlations may exist.

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For correlation with climatic variables, we used raw ring widths for each of the four species that were standardized per individual according to that individual's chronology within the years of 2009 – 2014 for TP species and 2011 – 2015 for CC species. This standardization procedure was done by taking an individual's average ring width for the whole chronology and for each year subtracting this average from the corresponding ring width and dividing by the standard deviation to get a final standardized value for each year in each individual chronology. Total precipitation and average daily maximum temperature were combined respectively into two seasonal categories. For both sites, a current year's March through June was used for spring and June – September for summer. We did not consider further splitting these correlative analyses into early/late seasons or individual months since our herbaceous species reached a maximum of a decade old, thus any effort would introduce an overabundance of correlative tests for a relatively small amount of responses (years) compared to more traditional tree ring analyses. We also apply this reasoning towards only including maximum temperatures for each season rather than minimum or average temperatures since we wanted to avoid the overabundance of correlative tests for a smaller sample size and chose maximum temperatures it may represent the greatest stress on water availability and thus, growth. During exploratory analysis, winter and fall climatic variables proved to have no discernable effect on ring widths and thus were left out of further analyses. We only used overlapping growth years between forbs and trees in consideration of these correlations, 2009 – 2014 for TP and 2011 – 2015 for CC. To test for fire effects, we used ANOVA for individual species each year to find a difference in mean ring width between individuals from burned and unburned patches. For climate and fire interactive effects, we could only visually monitor the patterns between hot/cold, dry/wet years in conjunction with the results of the ANOVA fire effects since in individual years the amount of patches burned compared to unburned was highly unbalanced, thereby jeopardizing possible results obtained from any traditional linear modeling. All above analyses were done in SPSS (IBM Corp. 2012). In addition, we also correlated ring widths with values of the Palmer Drought Severity Index (PDSI) for the overlapping years. We specifically chose PDSI to better represent previous year's effect on the current year's annual ring as well as the influence of evapotranspiration (ET). Use of PDSI in this manner would help avoid the potential issue mentioned above with an overabundance of correlative tests when considering the short chronologies of forbs, as well as the expected collinearity of ET with seasonal temperature and precipitation.

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To test the ability of whether or not annual rings in forbs carry a stronger patch specific signal (based on fire history in this study) than adjacent trees, which we predict carry a stronger consistency of signal among patches based on the fact that trees are likely more responsive to climate, we used permutation tests. Using these tests, we want to investigate the notion that the highest mean pairwise correlation can only be found when the correlation is done on individuals all originating from the same patch, AKA “patch fidelity”. In other words, we refer to the term patch fidelity to imply how strongly interannual growth patterns are tied to a patch. To statistically back our permutation tests, we compared all 10,000 permutations to Ω_x , which we define as the “fidelity test statistic”. Ω_1 is a value chosen *a priori* with the following formula:

$$\Omega_1 = r_{\text{within}} - r_{\text{amongst}} \quad \text{Eq. 1}$$

This formula was used for all four species individually and represents the difference between the mean correlation (r) of within patch pairwise correlations and among patch correlations observed in the field in each separate species case (Table 1). In addition, we wanted to know whether or not forbs showed a stronger patch fidelity in comparison to trees if both plant types indeed show their own patch fidelity. To do this we used the following fidelity test statistic formula, Ω_2 , which is chosen *a priori* based on observed differences patch fidelity in the field (Table 1):

$$\Omega_2 = [r_{\text{within (forb)}} - r_{\text{amongst (forb)}}] - [r_{\text{within (tree)}} - r_{\text{amongst (tree)}}] \quad \text{Eq. 2}$$

Using each forb or tree’s standardized ring widths (2009 – 2014 for TP and 2011 – 2015 for CC), we employed 10,000 iterations of shuffling individuals of the target species into random patches to test for the ability of either plant type to maintain an average intra-patch mean pairwise correlation that was comparable to what was found in the field. In all permutations, we used a one-tailed test to compare our permutations to the associated fidelity test statistic. If 97.5% or more of the permutations generated a value that was lower than the fidelity test statistic then we can conclude evidence of patch fidelity or, in the case of the relative patch fidelity strength permutation, whether or not forbs show higher patch fidelity than coexisting trees.

In addition, species fidelity was tested by using the same permutation test procedure for testing patch fidelity. Species fidelity is the ability of a species to maintain higher mean pairwise correlations compared to when assignment of individuals to a species is random. The fidelity

test statistic, Ω_3 , used in this instance was once again based on the actual observed differences in the field (Table 1):

$$\Omega_3 = r_{forb} - r_{tree} \tag{Eq. 3}$$

The permutation process for this analysis was done in separate tests for species specific to either TP or CC, where we would randomly shuffle individuals into an arbitrary species identity. All permutation tests were programed and done in R version 3.2.0 (R Core Team 2015).

Results

TP Results

From the TP, a total of 70 *Q. stellata* were used in analysis between the 4 patches along with a total of 56 *A. viridis* between all of the 4 patches. 10 of the original 80 tree series were dropped from the analysis because they had they had strong age growth decline in the latter years and were hard to distinguish one ring from another, thus precluding reliable cross dating. 24 of the original 80 *A. viridis* were excluded from analysis because of degradation or possessing fewer than three rings. The average age of *A. viridis* was ten years old, amounting 2004 – 2014 as the overlap years for analysis for the TP between forbs and trees. Figure 1A and 1B show the overall chronologies for the *A. viridis* and *Q. stellata* of the TP. A few series of *Q. stellata* are as old as the late 1920's while most series cover only the last 4-5 decades. *Q. stellata* had several marker years: 1981, 1984, 1996, and 2006. *A. viridis* had one series as old as 2003, with most being only as old as 2007. For the chronology as a whole, a notable sharp ring width decline exists for *A. viridis* in 2011 with the strongest increase occurring in 2013. The marker years described above (2003 and beyond) could most likely be tied to climate as evidenced by ring width correlations with annual temperature and precipitation outlined below.

Intra-patch (within) and inter-patch (among) mean yearly pairwise correlations for TP species are found in Figure 2A and 2C respectively. As a basis for comparison, moderate (0.3 – 0.5) to high (0.6 – 1.0) mean pairwise correlations can be inferred as a moderate to a highly conserved signals respectively within the annual ring patterns shared amongst individuals tested within or amongst patches, while lower (0.0 - 0.2) likely indicate a lack of a shared signal between individuals in their annual ring patterns. Overall, *Q. stellata* had high mean pairwise

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correlations consistently within and among patches while *A. viridis* could be classified as having moderately conserved annual ring patterns amongst individuals within and among patches. *A. viridis* also had comparatively more variation in their mean pairwise correlations both within and amongst patches. While the difference between the mean pairwise correlations within patches and among patches was positive for both species, the difference was slightly higher for *A. viridis*.

Table 1 shows the results from the permutation tests, with statistical support both site and species fidelity for both forbs and trees for TP. Each randomization test had p values < 0.025 , corresponding to a one tail test testing that 97.5% of the permutations fell below the test statistic chosen for each test. Comparatively, *A. viridis* was close to passing our cutoff of rejecting the null ($p \leq 0.025$) for demonstrating a stronger patch fidelity over trees based on our one tail test but was just under the mark (Table 1). More specifically, 9,612 out of the 10,000 permutations generated a lower difference between the average within patch correlations for forbs over within patch correlations for trees.

Overall, climatic correlations with standardized ring widths only using overlapping years of growth between trees and forbs, were fairly strong for summer season maximum daily temperature while spring temperature was slightly weaker but still negatively related to rings widths across both species (Table 2, Figure 3 for TP). The ring widths for both *A. viridis* and *Q. stellata* were both significantly positively correlated with total summer precipitation with *Q. stellata* having a much stronger correlation coefficient (Table 2, Figure 3). Fire was not strongly related to annual ring increment of either TP species, with both species only having a significant effect of fire in either 2009 or 2010, which was positive in both cases (Table 2, Figure 3). Comparatively, the effect of fire was much weaker for *Q. stellata* than it was for *A. viridis* in the year which fire was significant (Table 2). Possible interactive effects between fire, climate, and annual ring widths can be seen in Figure 3, though fire had a weak main effect. Figure 3A, shows that relatively cooler years with a spring burn are associated with the highest average ring widths for *A. viridis*, though in 2013 and 2014 this difference is not significant between unburned and burned patches. *Q. stellata* shows a positive effect of summer precipitation on ring width, with burned patches experiencing larger ring widths, though in most cases this is not significant (Figure 3B). Overall, the lack of simultaneous burned and unburned treatments in the overly hot and dry years of 2011 and 2012 severely hurts the chance to monitor interaction effects between fire and climate more efficiently for TP species.

Figure 5A shows associations with the Palmer Drought Index (PDSI) for TP, only *Q. stellata* had significant correlations with PDSI, with the strongest being current year’s summer and the previous spring.

CC Results

For 20 out of the 60 series of *Q. macrocarpa*, rings were difficult to cross-date due to indiscernible ring borders in the last decade, resulting in these 20 series being dropped from the following analyses. Over the last few decades, marker years for *Q. macrocarpa* were only in 1988 and 2009 for their relatively steep declines in width compared to surrounding years. Thus, for the 20 series which had to be dropped, using the marker year of 1988 still did not produce reliable cross-dating for these series since the last decade had rings indistinguishable from each other, including the other marker year of 2009. A total of 59 *L. capitata* were used in the final analysis, with only one being dropped because it possessed less than three rings. Figure 1C and 1D shows the chronologies for *L. capitata* and *Q. macrocarpa* from CC. A few series of *Q. macrocarpa* are as old as the 1890’s. *L. capitata* had a chronology as old as 2005, with a notable drastic increase in its RWI for 2011. The average age of *L. capitata* was six years old, amounting 2008 – 2015 as the overlap years for analysis for CC between forbs and trees.

The intra- and inter-patch mean pairwise correlations for *Q. macrocarpa* and *L. capitata* for CC are shown in Figure 2B and 2C respectively. Both plant types had mean inter-patch pairwise correlations that were quite low (between 0.0 and 0.2). For *Q. macrocarpa*, other than burn unit 104 with a high intra-patch mean correlation, intra-patch correlations were substantially low being close to zero while the intra-patch correlations were fairly consistent and larger for *L. capitata*. Table 1 shows the results from the permutation tests, with statistical support both site and species fidelity for both forbs and trees for CC. *L. capitata*, had the overall largest positive difference between within and among pairwise correlations compared to the other three target species in the study including *Q. macrocarpa*. Thus, we found strong evidence of a relatively higher patch fidelity for *L. capitata* compared to *Q. macrocarpa* at CC (Table 1).

For *Q. macrocarpa* and *L. capitata* at CC, only spring and summer precipitation were consistently correlated with ring width, positively for *L. capitata* and negatively for *Q. macrocarpa* (Table 2). Summer temperature was the strongest negative correlation with ring width for *L. capitata*. Fire proved to have a consistent positive effect on *L. capitata* (except for

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2014) and no effect on *Q. macrocarpa* (Table 2 and Figure 4). Being that for this period (2011 – 2015) there was not much of range of maximum daily summer temperatures, possible interaction effects are hard to distinguish for *L. capitata* (Figure 4A). However, combining temperature with total precipitation from summer months from Figure 4B, it appears that the driest years cause the most separation between burn and unburned patches, with the large mean growth in burned patches. Figure 5B shows associations with the PDSI for CC. *L. capitata* was strongly correlated with current year's spring and summer PDSI, while *Q. macrocarpa* was only correlated with the previous summer PDSI.

Discussion

Overall, herb-chronology in tandem with dendrochronology proved to be a useful methodological approach for comparing how the two coexisting plant types respond differently to the yearly environment. We found that fire does have a relatively larger role in the annual growth of perennial forbs in comparison to coexisting mature oak species. In addition, even though we found that both forb species had a stronger patch fidelity than trees, variation in annual ring patterns of forbs were more strongly related to climate than to fire. Both forb and tree annual growth were consistently negatively linked to summer temperatures. The fire and climate interaction was only evident with forb species, with relatively cooler wetter years with a burn leading to the largest ring widths.

Spring fire and the putative role of competition on annual ring patterns in forbs

Though numerous studies describe the influence of fire on forb abundance and demography (Overbeck et al. 2007; Collins & Calabrese 2012; Lettow et al. 2014), we found only tenuous evidence for the effects of fire on the annual growth of forb species. Though we found higher pairwise correlations between individuals within the same patch based on fire history rather than among patches of different fire histories, this effect paled in comparison to the strength of negative correlations between ring widths and summer temperatures. Our predictions of spring fire having an overriding effect on annual ring width were based on the supposition that such fire would lessen suppression by litter and aboveground competition. Additionally we

supposed that annual ring growth is a dependable proxy for aboveground growth. In the following, we explain how these suppositions may have been misleading.

The extent to which belowground annual rings in forbs correlate with aboveground performance has yet to be determined. Dietz & von Arx (2005) found that annual ring width was negatively related to reproductive biomass, likely because of the amount of carbon sources needed to sustain such growth (Bazzaz *et al.* 1987) may be taken away at the expense of increased secondary growth. We assume that since root annual rings are largely made up of parenchyma and fiber cells (Pratt *et al.* 2007), larger ring width is the result of a need to accommodate storage needs from carbon surplus and high photosynthetic output (Lacointe 2000), though this has yet to be experimentally evaluated. Thus, for ring widths to be reliable indicators for the aboveground growth environment, the negative effects from shading by neighbors and litter accumulation and subsequent ameliorative effects of spring fire would both have to be substantial enough to shift the carbon balance within a plant to cause a detectable variation in ring width between years with or without a burn.

In this study, we found that only one of the forb species, *L. capitata*, responded to spring fire. The temporal occurrence of fire and how it is coupled with the emergence of *L. capitata* in comparison to *A. viridis* and the manipulation of the aboveground competitive environment could play a role in our findings. Controlled burns at TP usually occur in in early March and April, before the peak emergence times for several C4 grasses, which may play a role in the muted effects of fire for the early spring emerger *A. viridis*. In contrast, spring fires occur later in the season at CC, possibly more effectively eliminating key grass competitors as *L. capitata* itself is emerging.

Possible indirect fire effects on annual ring patterns of forbs

The effect of fire and its volatilization of nitrogen could be particularly important since ring growth of the legume *L. capitata* was consistently positively affected by fire. Nitrogen availability is significantly decreased under sites with higher frequency of burn (Blair 1997; Reich *et al.* 2001; Wan *et al.* 2001), thus, the response is usually positive for legume species cover since they are not limited by nitrogen availability in the soil in comparison to non-legume species, giving them a competitive advantage (Turner & Knapp 1996; Reich *et al.* 2001). Counteractively, fire also increases phosphorus availability after a burn (Boerner 1982). Thus,

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fire frequency may play a large positive role on the growth of *L. capitata* through the availability of nutrients. In fact, our low inter-patch correlation we found with *L. capitata* may be directly linked to this phenomenon since one patch had substantially fewer annual fires from 2011-2015 compared to the other two and by far had the smallest ring widths at the end of our study period, though we explain other possible reasons for this result below.

Conversely, *A. viridis*, did not show such low inter-patch correlation as *L. capitata*. Once such reason could be because TP, relative to CC, did not have such a dramatic difference in between its fire histories for each patch. However, *A. viridis* may be less responsive to changes in nutrient availability brought on by fire history. Thus, we cannot attribute the differences in inter-patch correlations amongst the two species to either a species or site effect. To overall better address this, similar studies in the future should consider testing multiple species which occur together at two or more study sites.

One of the most consistent responses we found for perennial forb ring growth was the correlation with climate. Primarily, both forb species in this study had significant and strong negative correlations with summer temperatures. Temperature is often negatively related to ring widths in forbs (Dietz & von Arx 2005; Liu & Zhang 2010; Franklin et al. 2013; Dee & Palmer 2016), likely because of evaporative stress negatively effecting photosynthetic rates (Frank & Inouye 1994). We found suggestions of a possible fire/climate interaction since the largest ring widths consistently occurred in cooler/wetter years with a burn for both forb species. Below, we discuss the ramifications of this possible interaction even though the lack of a balanced study design compromises our ability to reach firm conclusions.

Fire within this region of the U.S. has well-documented effects on soil water and temperature that may last months after its occurrence. Removal of litter during a spring burn may increase albedo and raise upper soil temperatures significantly over sites that are not burned to period of up to 3 months after fire (Ewing & Engle 1988; Bremer & Ham 1999; Vermeire *et al.* 2005). In addition, up to 25% percent higher greater cumulative evapotranspiration three months following fire has been observed in burned sites compared to unburned (Vermeire *et al.* 2005). For herbaceous species with a majority of root biomass in the upper soil strata, relatively hot years with fire could cause evaporative stress (Nippert, Fay & Knapp 2007)., possibly leading to less carbon assimilation and reduced ring widths (Lacointe 2000).

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Though one limitation to our study was the lack of both burn treatments in the hot and dry years of 2011 and 2012 for TP, the possible negative effect of burning during a hot dry year may be evidenced by *A. viridis* and its smallest ring widths of the study being observed in 2011 when all patches were burned. In all other years, which were milder climatically, burn sites actually resulted in relatively larger rings than unburned sites. In addition, unburned patches in 2012, the other hot dry year, showed considerably larger ring widths than patches that were burned in 2011.

Negative response of fire in hotter years, however, was not the case for *L. capitata* as it experienced its most reduced ring width in years of relatively hotter temperatures without a burn. Roots of *L. capitata* reach farther into the soil in comparison to *A. viridis* (personal observation), thus *L. capitata* may be less sensitive to evaporative stress brought on by burning but more susceptible to litter buildup and interception that precludes soil water recharge at lower depths in longer unburned conditions in hotter/dry years (Seastedt 1985) though this could be heavily contingent upon species compositions and soil texture (Craine & Nippert 2014). Nevertheless, infrequently burned patches, such as one of our patches at CC, amounted to smaller ring widths compared to other patches, which may be the result of litter buildup and decreased water infiltration in addition to decreased phosphorus availability in these conditions (Boerner 1982). Overall, it can be suggested from our study that differences in overall physiology, anatomy, and life history could play a role in how forbs respond differently to a fire and climate interaction and its effect on the growth environment.

Tree rings and overall comparison to neighboring forbs

Besides a possible interaction between fire and the wet and cooler conditions of the summer of 2010, which may have increased soil fertility for *Q. stellata* (Certini 2005), fire was not obviously related to tree ring patterns. The lack of fire and its effect on ring increments in trees also shows with our patch fidelity tests: both study site forbs were more responsive to localized conditions as were trees. The patch fidelity of trees could be more attributable to possible changes in localized precipitation/ temperature between patches which we did not consider in our study. Admittedly, this could be the case for forb patch fidelity as well, though it is clear the fire effect is stronger in forbs in our study while climatic conditions have been closely related to tree ring growth in a number of previous studies. Furthermore, we contend that

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the possibility of direct effects of fire on tree growth are likely minor since all trees cored in our study had their regenerative buds and most of their foliar biomass well above the flame zone.

Q. stellata ring widths and their connection to climate of our region have been well studied through the early 1980's (although with longer time series, as we restricted our years of analysis to overlap with the growth of our shorter lived forbs). Stahle & Hehr (1984) found the same inverse relationships to seasonal temperatures and proportionality to summer precipitation as we did in our study, though we found a much stronger negative association with summer temperature. Though precipitation is still important, we contend that record high temperatures in summer over the timeframe of our study are likely driving evaporative stress which could become the ultimate current driver of tree growth in this region if average summer temperatures continue to rise. Furthermore, PDSI was more strongly related to tree growth than forb growth in our study, highlighting the influence of longer climatic trends on the growth of woody species while forbs seem to more sensitive to year to year climatic variation and site ecology (Dietz & von Arx 2005; Liu & Zhang 2010; Dee & Palmer 2016). On a related note however, future studies should consider more attention to the exact previous year's effect on current ring widths for forbs as long as chronologies are long enough to warrant such a correlative analysis in addition to current years and their climatic influences. In dendrochronology research, previous years climate have considerable influence on the ring increment in current years, especially as aboveground buds are forming in trees for the next season (Leblanc & Stahle 2015). However, such an endeavor would have to consider the timing of bud formation for forbs and other potentially used hemicryptophytes in future studies, which at present time is unknown for many species.

One unexpected trend was the insignificant correlation between *Q. macrocarpa* and temperature in our study. We are confident that complacent rings were likely responsible for this and unfortunately our *Q. macrocarpa* results cannot be much use for getting at our driving comparative questions regarding trees and neighboring forb growth response to fire and climate. Indeed, *Q. macrocarpa*, like *Q. stellata*, in other studies is highly correlated with PDSI (Wyckoff & Bowers 2010) and year to year variation in precipitation and temperature (Leblanc & Stahle 2015). However, individual selection of trees growing on either slopes or rocky areas was nearly impossible in the three southwest burn units of CC used in this study as the area had little topographic variability. We are confident that series were cross-dated correctly, at least for our

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time period of concern, since 1988 was almost always a good marker year which parallels previous studies with bur oak (Leblanc & Stahle 2015). Another possibility could be the increase of atmospheric CO₂ can diminish climate and tree growth relations (Voelker et al. 2014), likely owing in part to bur oak individuals appearing to be increasingly insensitive to drought at these northern latitudes (Wyckoff & Bowers 2010).

Conclusions

To our knowledge, this work is the first attempt to compare and contrast how the annual growth rings in coexisting plant types across multiple sites in an expansive prairie – forest ecotone respond to periodic disturbance and/or climate. With the predicted threat of even higher temperatures and more rainfall seasonal variability within some of the regions of this prairie – forest ecotone of North America (Christensen *et al.* 2007), along with the ongoing anthropogenic changes to the historical fire of this landscape (Curtis 1959; Nuzzo 1986; Allen & Palmer 2011), much more research will be needed to predict likely changes in the overall dynamics of this transitional zone. Since we found similarities between forb and tree ring growth towards climate but disparate responses to fire, we suggest further using herb-chronology with dendrochronology in tandem. Efforts to gain a deeper knowledge of the implications of annual growth environment on the growth of these coexisting plant types may help aid predictions for future growth response and even composition within this environmentally sensitive ecotone.

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References

Abràmoff M.D., Magalhães P.J. & Ram S.J. (2004) Image processing with ImageJ. *Biophotonics International*, **11**, 36-42.

Dee, J. D. and Palmer, M. W.

Annual rings in the U.S. prairie – forest ecotone

- Allen, M. S., Hamilton, R. G., Melcher, U., & Palmer, M. W. (2009). Lessons from the prairie: research at The Nature Conservancy's tallgrass prairie preserve. *Oklahoma Academy of Sciences*, Stillwater.
- Allen C.D., Macalady A.K., Chenchouni H., Bachelet D., McDowell N., Vennetier M., Kitzberger T., Rigling A., Breshears D.D. & Hogg E.T. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660-684.
- Allen M.S. & Palmer M.W. (2011) Fire history of a prairie/forest boundary: more than 250 years of frequent fire in a North American tallgrass prairie. *Journal of Vegetation Science*, **22**, 436-444.
- Baker R.G., Bettis E.A., Denniston R.F., Gonzalez L.A., Strickland L. & Krieg J.R. (2002) Holocene paleoenvironments in southeastern Minnesota—chasing the prairie-forest ecotone. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **177**, 103-122.
- Bartlein P.J. & Whitlock C. (1993) Paleoclimatic interpretation of the Elk Lake pollen record. *Geological Society of America Special Papers*, **276**, 275-294.
- Baum K.A. & Sharber W.V. (2012) Fire creates host plant patches for monarch butterflies. *Biology letters*, **8**, 968-971.
- Bazzaz F.A., Chiariello N.R., Coley P.D. & Pitelka L.F. (1987) Allocating resources to reproduction and defense. *BioScience*, **37**, 58-67.
- Beghin R., Cherubini P., Battipaglia G., Siegwolf R., Saurer M. & Bovio G. (2011) Tree-ring growth and stable isotopes (^{13}C and ^{15}N) detect effects of wildfires on tree physiological processes in *Pinus sylvestris* L. *Trees*, **25**, 627-636.
- Bigler C., Gavin D.G., Gunning C. & Veblen T.T. (2007) Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains. *Oikos*, **116**, 1983-1994.
- Blair J.M. (1997) Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis. *Ecology*, **78**, 2359-2368.
- Boerner R.E. (1982) Fire and nutrient cycling in temperate ecosystems. *BioScience*, **32**, 187-192.
- Bond W., Midgley G., Woodward F., Hoffman M. & Cowling R. (2003) What controls South African vegetation—climate or fire? *South African Journal of Botany*, **69**, 79-91.
- Bond W.J. & Parr C.L. (2010) Beyond the forest edge: ecology, diversity and conservation of the grassy biomes. *Biological Conservation*, **143**, 2395-2404

Dee, J. D. and Palmer, M. W.

Annual rings in the U.S. prairie – forest ecotone

- Bremer D.J. & Ham J.M. (1999) Effect of spring burning on the surface energy balance in a tallgrass prairie. *Agricultural and Forest Meteorology*, **97**, 43-54.
- Brockway D.G., Gatewood R.G. & Paris R.B. (2002) Restoring fire as an ecological process in shortgrass prairie ecosystems: initial effects of prescribed burning during the dormant and growing seasons. *Journal of Environmental Management*, **65**, 135-152.
- Bunn, A., Korpela, M., Biondi, F., Campelo, F., Mérian, P., Qeadan, F., & Zang, C. (2016) dplR: Dendrochronology Program Library in R. R package version 1.6.4
- Camill P., Umbanhowar C.E., Teed R., Geiss C.E., Aldinger J., Dvorak L., Kenning J., Limmer J. & Walkup K. (2003) Late-glacial and Holocene climatic effects on fire and vegetation dynamics at the prairie–forest ecotone in south-central Minnesota. *Journal of Ecology*, **91**, 822-836.
- Cavender-Bares J. & Reich P.B. (2012) Shocks to the system: community assembly of the oak savanna in a 40-year fire frequency experiment. *Ecology*, **93**, S52-S69.
- Certini G. (2005) Effects of fire on properties of forest soils: a review. *Oecologia*, **143**, 1-10.
- Christensen, J.H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, I. (2007) Regional climate projections. *Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds S.Solomon, D. Qin, M., Manning, Z. Chen, M. Marquis, K.B. Avery, M. Tignor & H.L.Miller), pp. 847– 940. Cambridge University Press, Cambridge, UK/New York, NY, USA.
- Clark S.L. & Hallgren S.W. (2003) Dynamics of oak (*Quercus marilandica* and *Q. stellata*) reproduction in an old-growth Cross Timbers forest. *Southeastern Naturalist*, **2**, 559-574.
- Cochrane T.S. & Iltis H.H. (2000) Atlas of the Wisconsin prairie and savanna flora. *Technical Bulletin-Department of Natural Resources, Wisconsin*.
- Collins S.L. & Calabrese L.B. (2012) Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie. *Journal of Vegetation Science*, **23**, 563-575.
- Craine J.M. & Nippert J.B. (2014) Cessation of burning dries soils long term in a tallgrass prairie. *Ecosystems*, **17**, 54-65.
- Curtis J.T. (1959) *The vegetation of Wisconsin: an ordination of plant communities*. University of Wisconsin Pres.
- Dee J.R. & Palmer M.W. (2016) Application of herb chronology: Annual fertilization and climate reveal annual ring signatures within the roots of US tallgrass prairie plants. *Botany*, **94**, 277-288.

Dee, J. D. and Palmer, M. W.

Annual rings in the U.S. prairie – forest ecotone

- DeSantis R.D., Hallgren S.W. & Stahle D.W. (2010) Historic fire regime of an upland oak forest in south-central North America. *Fire Ecology*, **6**, 45-61.
- DeSantis R.D., Hallgren S.W. & Stahle D.W. (2011) Drought and fire suppression lead to rapid forest composition change in a forest-prairie ecotone. *Forest Ecology and Management*, **261**, 1833-1840.
- Dietz H. & Ullmann I. (1998) Ecological Application of ‘Herbchronology’: Comparative Stand Age Structure Analyses of the Invasive Plant *Bunias orientalis* L. *Annals of Botany*, **82**, 471-480.
- Dietz H. & von Arx G. (2005) Climatic fluctuation causes large-scale synchronous variation in radial root increments of perennial forbs. *Ecology*, **86**, 327-333.
- Ewing A. & Engle D. (1988) Effects of late summer fire on tallgrass prairie microclimate and community composition. *American Midland Naturalist*, 212-223.
- Fay P.A., Carlisle J.D., Danner B.T., Lett M.S., McCarron J.K., Stewart C., Knapp A.K., Blair J.M. & Collins S.L. (2002) Altered rainfall patterns, gas exchange, and growth in grasses and forbs. *International Journal of Plant Sciences*, **163**, 549-557.
- Frank D.A. & Inouye R.S. (1994) Temporal variation in actual evapotranspiration of terrestrial ecosystems: patterns and ecological implications. *Journal of Biogeography*, 401-411.
- Franklin R.S. (2013) Growth response of the alpine shrub, *Linanthus pungens*, to snowpack and temperature at a rock glacier site in the eastern Sierra Nevada of California, USA. *Quaternary International*, **310**, 20-33.
- Gaire N., Koirala M., Bhujju D. & Borgaonkar H. (2014) Treeline dynamics with climate change at the central Nepal Himalaya. *Climate of the Past*, **10**, 1277-1290.
- Hengst G.E. & Dawson J.O. (1994) Bark properties and fire resistance of selected tree species from the central hardwood region of North America. *Canadian Journal of Forest Research*, **24**, 688-696.
- Higgins S.I., Bond W.J. & Trollope W.S. (2000) Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *Journal of Ecology*, **88**, 213-229.
- Hoagland B. (2000) The vegetation of Oklahoma: A classification for landscape mapping and conservation planning. *The Southwestern Naturalist*, 385-420.
- Hoffmann W.A. & Solbrig O.T. (2003) The role of topkill in the differential response of savanna woody species to fire. *Forest Ecology and management*, **180**, 273-286.
- Howe H.F. (1995) Succession and fire season in experimental prairie plantings. *Ecology*, 1917-1925.

Dee, J. D. and Palmer, M. W.

Annual rings in the U.S. prairie – forest ecotone

- IBM Corp. Released 2012. IBM SPSS Statistics for Windows, Version 19.0. Armonk, NY: IBM Corp.
- Knapp A.K., Burns C.E., Fynn R.W., Kirkman K.P., Morris C.D. & Smith M.D. (2006) Convergence and contingency in production–precipitation relationships in North American and South African C4 grasslands. *Oecologia*, **149**, 456-464.
- Lacointe A. (2000) Carbon allocation among tree organs: a review of basic processes and representation in functional-structural tree models. *Annals of Forest Science*, **57**, 521-533.
- LeBlanc D.C. & Stahle D.W. (2015) Radial growth responses of four oak species to climate in eastern and central North America. *Canadian Journal of Forest Research*, **45**, 793-804.
- Lettow M., Brudvig L., Bahlai C. & Landis D. (2014) Oak savanna management strategies and their differential effects on vegetative structure, understory light, and flowering forbs. *Forest Ecology and Management*, **329**, 89-98.
- Liu Y.B. & Zhang Q.B. (2010) Effect of climate on the growth of annual rings in the main roots of perennial forbs in an Inner Mongolian semi-arid grassland, China. *Journal of Vegetation Science*, **21**, 899-907.
- Mariotte P., Vandenberghe C., Kardol P., Hagedorn F. & Buttler A. (2013) Subordinate plant species enhance community resistance against drought in semi-natural grasslands. *Journal of Ecology*, **101**, 763-773.
- Mathisen I.E., Mikheeva A., Tutubalina O.V., Aune S. & Hofgaard A. (2014) Fifty years of tree line change in the Khibiny Mountains, Russia: advantages of combined remote sensing and dendroecological approaches. *Applied Vegetation Science*, **17**, 6-16.
- McAllister C.A., Knapp A.K. & Maragni L.A. (1998) Is leaf-level photosynthesis related to plant success in a highly productive grassland? *Oecologia*, **117**, 40-46.
- McPherson G.R. (1997) *Ecology and management of North American savannas*. University of Arizona Press.
- Nippert J.B., Fay P.A. & Knapp A.K. (2007) Photosynthetic traits in C3 and C4 grassland species in mesocosm and field environments. *Environmental and Experimental Botany*, **60**, 412-420.
- Nippert J.B. & Knapp A.K. (2007) Linking water uptake with rooting patterns in grassland species. *Oecologia*, **153**, 261-272.
- Nowacki, G.J., and Abrams, M.D. (2008) The demise of fire and "Mesophication" of forests in the eastern United States. *Bioscience*, **58**, 123-138.

Dee, J. D. and Palmer, M. W.

Annual rings in the U.S. prairie – forest ecotone

- Nuzzo V.A. (1986) Extent and status of Midwest oak savanna: presettlement and 1985. *Natural Areas Journal*, **6**, 6-36.
- Olano J.M., Almería I., Eugenio M. & Arx G. (2013) Under pressure: how a Mediterranean high-mountain forb coordinates growth and hydraulic xylem anatomy in response to temperature and water constraints. *Functional Ecology*, **27**, 1295-1303.
- Overbeck G.E., Müller S.C., Fidelis A., Pfadenhauer J., Pillar V.D., Blanco C.C., Boldrini I.I., Both R. & Forneck E.D. (2007) Brazil's neglected biome: the South Brazilian Campos. *Perspectives in Plant Ecology, Evolution and Systematics*, **9**, 101-116.
- Pedersen B.S. (1998) The role of stress in the mortality of midwestern oaks as indicated by growth prior to death. *Ecology*, **79**, 79-93.
- Pederson N., Dyer J.M., McEwan R.W., Hessler A.E., Mock C.J., Orwig D.A., Rieder H.E. & Cook B.I. (2014) The legacy of episodic climatic events in shaping temperate, broadleaf forests. *Ecological Monographs*, **84**, 599-620.
- Peterson D.W. & Reich P.B. (2001) Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. *Ecological Applications*, **11**, 914-927.
- Peterson D.W., Reich P.B. & Wragge K.J. (2007) Plant functional group responses to fire frequency and tree canopy cover gradients in oak savannas and woodlands. *Journal of Vegetation Science*, **18**, 3-12.
- Powell J. & Lowry D. (1980) Oak (*Quercus* spp.) sprouts growth rates on a central Oklahoma shallow savannah range site. *Journal of Range Management Archives*, **33**, 312-313.
- Pratt R., Jacobsen A., Ewers F. & Davis S. (2007) Relationships among xylem transport, biomechanics and storage in stems and roots of nine Rhamnaceae species of the California chaparral. *New Phytologist*, **174**, 787-798.
- R Core Team (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Reich P.B., Peterson D.W., Wedin D.A. & Wragge K. (2001) Fire and vegetation effects on productivity and nitrogen cycling across a forest-grassland continuum. *Ecology*, **82**, 1703-1719.
- Rogers W.E. & Hartnett D.C. (2001) Temporal vegetation dynamics and recolonization mechanisms on different-sized soil disturbances in tallgrass prairie. *American Journal of Botany*, **88**, 1634-1642.
- Rowe, J. S. (1983) Concepts of fire effects on plant individuals and species. Pages 135-154 in R. W. Wein and D. A. MacLean, editors. *The role of fire in northern circumpolar ecosystems*. John Wiley, New York, New York, USA.

Dee, J. D. and Palmer, M. W.

Annual rings in the U.S. prairie – forest ecotone

- Sankaran M., Ratnam J. & Hanan N.P. (2004) Tree–grass coexistence in savannas revisited—insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters*, **7**, 480-490.
- Scholes R. & Archer S. (1997) Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, 517-544.
- Schweingruber F.H., Börner A. & Schulze E.-D. (2011) *Atlas of stem anatomy in herbs, shrubs and trees* (vol. 1). Springer Science & Business Media.
- Seastedt T. (1985) Canopy interception of nitrogen in bulk precipitation by annually burned and unburned tallgrass prairie. *Oecologia*, **66**, 88-92.
- Speer J.H. (2010) *Fundamentals of tree-ring research*. University of Arizona Press.
- Stahle D.W. & Hehr J.G. (1984) Dendroclimatic relationships of post oak across a precipitation gradient in the southcentral United States. *Annals of the Association of American Geographers*, **74**, 561-573
- Teskey R., Wertin T., Bauweraerts I., Ameye M., McGuire M.A. & Steppe K. (2015) Responses of tree species to heat waves and extreme heat events. *Plant, Cell & Environment*, **38**, 1699-1712.
- Turner C. & Knapp A. (1996) Responses of a C4 grass and three C3 forbs to variation in nitrogen and light in tallgrass prairie. *Ecology*, 1738-1749.
- Umbanhowar C.E., Camill P., Geiss C.E. & Teed R. (2006) Asymmetric vegetation responses to mid-Holocene aridity at the prairie–forest ecotone in south-central Minnesota. *Quaternary Research*, **66**, 53-66.
- Velmex Inc. (2009) Velmex Measurement System.
- Vermeire L.T., Wester D.B., Mitchell R.B. & Fuhlendorf S.D. (2005) Fire and grazing effects on wind erosion, soil water content, and soil temperature. *Journal of Environmental Quality*, **34**, 1559-1565.
- Voelker S.L., Meinzer F.C., Lachenbruch B., Brooks J.R. & Guyette R.P. (2014) Drivers of radial growth and carbon isotope discrimination of bur oak (*Quercus macrocarpa* Michx.) across continental gradients in precipitation, vapour pressure deficit and irradiance. *Plant, Cell & Environment*, **37**, 766-779.
- von Arx G., Archer S.R. & Hughes M.K. (2012) Long-term functional plasticity in plant hydraulic architecture in response to supplemental moisture. *Annals of Botany*, **109**, 1091-1100.

Dee, J. D. and Palmer, M. W.

Annual rings in the U.S. prairie – forest ecotone

Voor Tech Consulting (2008) Measure J2X.

Wan S., Hui D. & Luo Y. (2001) Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. *Ecological Applications*, **11**, 1349-1365

Wyckoff P.H. & Bowers R. (2010) Response of the prairie–forest border to climate change: impacts of increasing drought may be mitigated by increasing CO₂. *Journal of Ecology*, **98**, 197-208.

Tables and Figures

Table 1. Results from the randomization tests testing for evidence of patch fidelity amongst the forb and tree species from the two study locations. Formulae for each Ω_x may be found in the methods.

<u>Species</u>	<u>Ω_x (fidelity test statistic)</u>	<u>P value for randomization test</u>
<i>Asclepias viridis</i>	$\Omega_1 = 0.10$	0.0003
<i>Quercus stellata</i>	$\Omega_1 = 0.06$	< 0.0001
<i>Lespedeza capitata</i>	$\Omega_1 = 0.27$	< 0.0001
<i>Quercus macrocarpa</i>	$\Omega_1 = 0.10$	0.0202
TP - Species fidelity	$\Omega_3 = 0.50$	< 0.0001
CC - Species fidelity	$\Omega_3 = 0.27$	< 0.0001
Test of the strength of patch fidelity of forbs compared to trees of TP	$\Omega_2 = 0.04$	0.0388
Test of the strength of patch fidelity of forbs compared to trees of CC	$\Omega_2 = 0.17$	< 0.0001

Table 2. Results for yearly one-way ANOVA comparisons between standardized ring widths and the occurrence of fire as well as correlations with climatic variables for spring and summer for each of the four species. Results from this table should be used with Figures 3 and 4.

<u>Species</u>	<u>Fire (year)</u>	<u>F (df)</u>	<u>Sig.</u>
<i>Asclepias viridis</i>	2009	11.09 (df = 45)	.002
	2010	1.55 (df = 53)	.218
	2011*	N/A	N/A
	2012*	N/A	N/A
	2013	0.36 (df = 68)	.551
	2014	0.03 (df = 68)	.875
	<u>Seasonal climate</u>	<u>Correlation coefficient</u>	<u>Sig.</u>
		(df=374)	
	Spring temp.	-.242	.000
	Spring precip.	.213	.000
	Summer temp.	-.267	.000
	Summer precip.	.132	.011
<i>Quercus stellata</i>	2009	3.21 (df = 68)	.078
	2010	5.00 (df = 68)	.029
	2011*	N/A	N/A
	2012*	N/A	N/A
	2013	0.04 (df = 59)	.844
	2014	0.18 (df = 68)	.674
	<u>Seasonal climate</u>	<u>Correlation coefficient</u>	<u>Sig.</u>
		(df=392)	
	Spring temp.	-.258	.000
	Spring precip.	-.053	.294
	Summer temp.	-.281	.000
	Summer precip.	.445	.000
<i>Lespedeza capitata</i>	2011	14.32 (df = 52)	.000
	2012	6.18 (df = 51)	.016
	2013	41.56 (df = 51)	.000
	2014	0.18 (df = 51)	.455
	2015	10.71 (df = 51)	.002
	<u>Seasonal climate</u>	<u>Correlation coefficient</u>	<u>Sig.</u>
		(df=265)	
	Spring temp.	-.126	.040
	Spring precip.	.219	.000
	Summer temp.	-.288	.000
	Summer precip.	.236	.000
<i>Quercus macrocarpa</i>	2011	2.11 (df = 39)	.154
	2012	0.02 (df = 38)	.881
	2013	2.73 (df = 38)	.104
	2014	1.74 (df = 38)	.195
	2015	4.30 (df = 33)	.056
	<u>Seasonal climate</u>	<u>Correlation coefficient</u>	<u>Sig.</u>
		(df=196)	
	Spring temp.	-.029	.686
	Spring precip.	-.256	.294
	Summer temp.	.116	.104
	Summer precip.	-.288	.000

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Figure 1. Ring chronologies for the four species amongst the two study locations. The left side includes *Quercus macrocarpa* and *Lespedeza capitata* of the Cedar Creek, Minnesota location. The right side includes *Quercus stellata* and *Asclepias viridis* of the Tallgrass Prairie Preserve, Oklahoma location. Along with the chronologies shown in RWI sites, the dark gray background represents each year's sample depth.

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Figure 2. Boxplots for the intra-patch and inter-patch pairwise correlations amongst series for the forbs and trees: **A.** Intra-patch (within) correlations for the two species from TP, **B.** Intra-patch correlations for the two species from CC, **C.** Inter-patch (among) correlations for the four species where *AV* = *Asclepias viridis*, *QS* = *Quercus stellata*, *LC* = *Lespedeza capitata*, and *QM* = *Quercus macrocarpa*. All mean pairwise correlations are calculated by averaging pairwise correlation amongst all individuals either within a patch (Intra-patch) or among patches (Inter-patch).

Figure 3. Associations between standardized annual ring widths, yearly occurrence of fire, and climate for **A.** *Asclepias viridis* and **B.** *Quercus stellata* of the TP site. Different letters above a pair of 95% confidence intervals in any given year signifies a significant effect of burning on that year's standardized ring widths, whereas corresponding f scores and *p* values can be found on Table 2. The chosen climatic variable in either panel corresponds to the seasonal climatic variable which had the highest correlation with either species standardized ring widths, for all other seasonal climatic variable correlations with ring widths refer back to Table 2. For these correlations, the specific months used for summer climatic variables are June - September for each corresponding year. Note that 2011 and 2012 could not be tested for a fire effect since all patches were burned in 2011 and unburned in 2012.

Figure 4. Associations between standardized annual ring widths, yearly occurrence of fire, and climate for **A.** *Lespedeza capitata* and **B.** *Quercus macrocarpa* of the CC site. Different letters above a pair of 95% confidence intervals in any given year signifies a significant effect of burning on that year's standardized ring widths, whereas corresponding f scores and p values can be found on Table 2. The chosen climatic variable in either panel corresponds to the seasonal climatic variable which had the highest correlation with either species standardized ring widths, for all other seasonal climatic variable correlations with ring widths refer back to Table 2. For these correlations, the specific months used for summer climatic variables are June - September for each corresponding year.

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Figure 5. Correlation coefficients between the ring widths of the two species and PDSI from **A.** TP, and **B.** CC. The lower case “p” represents the intra-annual season previous to the year used in analysis. * = significance $p < 0.10$ level, ** = significance $p < 0.05$ level.

Supplemental Figure 1. Histograms representing the difference between average within and among patch correlation per each of the 10,000 iterations for **A.** *Asclepias viridis*, **B.** *Quercus stellata*, **C.** *Lespedeza capitata*, and **D.** *Quercus macrocarpa*. Gray vertical lines represent the approximate location of the test statistic for each species, though in most cases these are at the right hand terminus of the histogram since the test statistic is beyond the maximum bin assignment. P value corresponds to the significance of the one tailed test, if below 0.025 then we have evidence of site fidelity.

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Supplemental Figure 2. Histograms representing the average within patch correlation per each of the 10,000 iterations where individuals, regardless of species, were randomly assigned to any patch for **A.** TP and **B.** CC. Gray vertical lines represent the approximate location of the fidelity test statistic for each species, though in both cases these are at the right hand terminus of the histogram since the fidelity test statistic is beyond the maximum bin assignment. *P* corresponds to the significance of the one tailed test, if below 0.025 then we have evidence of species fidelity.

Supplementary material: Annual rings of perennial forbs and mature oaks show similar effects of climate but inconsistent responses to fire in the North American prairie –forest ecotone

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Supplementary Figure S1. Histograms representing the difference between average within and among patch correlation per each of the 10,000 iterations for **A.** *Asclepias viridis*, **B.** *Quercus stellata*, **C.** *Lespedeza capitata*, and **D.** *Quercus macrocarpa*. Gray vertical lines represent the approximate location of the test statistic for each species, though in most cases these are at the right hand terminus of the histogram since the test statistic is beyond the maximum bin assignment. *P* value corresponds to the significance of the one tailed test, if below 0.025 then we have evidence of site fidelity.

Supplementary Figure S2. Histograms representing the average within patch correlation per each of the 10,000 iterations where individuals, regardless of species, were randomly assigned to any patch for **A.** TP and **B.** CC. Gray vertical lines represent the approximate location of the fidelity test statistic for each species, though in both cases these are at the right hand terminus of the histogram since the fidelity test statistic is beyond the maximum bin assignment. P corresponds to the significance of the one tailed test, if below 0.025 then we have evidence of species fidelity.