

Drought and fire suppression lead to rapid forest composition change in a forest–prairie ecotone

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ARTICLE INFO

Article history:

Received 5 January 2011
Received in revised form 2 February 2011
Accepted 3 February 2011
Available online 1 March 2011

Keywords:

Drought
Fire exclusion
Juniperus virginiana
Quercus marilandica
Quercus stellata
Recruitment

ABSTRACT

Altered fire regimes and increased drought can lead to major vegetation changes, especially in ecotones. A decrease in fire can lead to woody species encroachment in prairies and increasing forest stand density. The threat of global climate change raises questions about potential increases in the length, severity, and incidence of droughts substantially altering species composition. Re-measured upland forests in south-central North America's midcontinent forest–prairie ecotone exhibited major changes in woody species composition and structure over fifty years and successional trajectories appeared to favor invasive *Juniperus virginiana* L. over the previous dominant *Quercus* species. The objective of this study was to determine whether climate and fire exclusion affected the recruitment history of dominant woody species in these upland forests located near the xeric western edge of the eastern deciduous forest biome of North America. We removed cores and cross-sections from 992 *J. virginiana*, *Quercus marilandica* Münchh. and *Q. stellata* Wangenh. trees from eleven forest stands located across central and northwest Oklahoma, and determined their ages using standard dendrochronological methods. Recruitment of all species increased following a severe mid-20th century drought, but a rapid increase in *J. virginiana* recruitment and decrease in *Quercus* recruitment appeared to be linked to a decrease in fire. Future fire regime changes and increased drought due to global climate change could lead to widespread shifts from *Quercus*- to *Juniperus*- dominated forests and cause substantial changes to ecosystem services.

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1. Introduction

Increasing human population, resource development, and changes in land use and management are driving the global transformation of ecosystems at an accelerating rate. For example, altered fire regimes have the potential to cause major changes in plant community composition and structure (Bond et al., 2005; Nowacki and Abrams, 2008). The threat of global climate change raises concerns about the combined effects of increased temperatures, droughts, and changes in land use and management on plant communities (Allen and Breshears, 1998; Suarez and Kitzberger, 2008; Allen et al., 2010). Vegetation in ecotones may be especially sensitive to these combined effects because many species are at the limits of their natural ranges (Gosz, 1992; Risser, 1995).

In south-central North America's midcontinent forest–prairie ecotone, anthropogenic fire helped shape the species composition of plant communities over thousands of years (Pyne, 1982; Bryant and Holloway, 1985). Following 19th century Euro-American settlement, major changes in land use and management occurred as native forest and grassland vegetation was cleared for cropland and rangelands were opened for cattle production (Briggs et al., 2002b; Guyette et al., 2002). Opening this land to settlement in Oklahoma resulted in over 7.3 million ha of native vegetation converted to cropland by 1920 (Phillips, 2003). Much of the cleared land was not suitable for cultivation, and cropland abandonment reduced the area to 6.5 million ha by 1950 and 3.2 million ha today. With the increase in population and property values, the use of fire to maintain prairie dwindled and fire was suppressed to protect property (Bragg and Hulbert, 1976). The exclusion of fire from the landscape led to a major change in vegetation due to woody plant encroachment in grasslands, savannas and forests. In the latter part of the 20th century the decrease in fire and changes in grazing practices led to substantial changes in forest composition and structure (Pyne, 1982; Abrams, 1986; Briggs et al., 2002a).

A substantial increase in *Juniperus virginiana* L. due to a reduction in fire may be among the most important ecosystem changes

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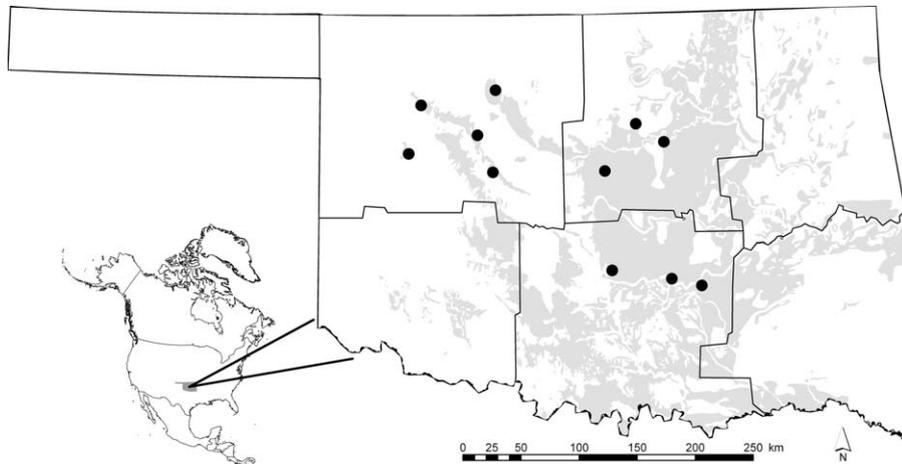


Fig. 1. Location of sampled forest stands within regions of Oklahoma, the Oklahoma Cross Timbers, and North America.

resulting from land management in south-central North America. Here, this native species is invasive (Horncastle et al., 2004; Van Zandt et al., 2005; Ganguli et al., 2008) but easily controlled by fire, especially in areas with grass-dominated understories and abundant herbaceous fuels (Briggs et al., 2002a). As *J. virginiana* increases in size, it becomes less vulnerable to surface fires, and thus less likely to be killed by future burning (Engle and Stritzke, 1995). In addition, a denser and more continuous conifer canopy suppresses the herbaceous understory, thereby reducing fine fuels and making the stand less susceptible to light surface fires that encourage *Quercus* regeneration (Briggs et al., 2002b).

Recent research suggested drought and decreased fire were responsible for changes in the composition and structure of *Quercus*-dominated forests in south-central North America over fifty years (Rice and Penfound, 1959; DeSantis et al., 2010). The conclusion was that invasive *J. virginiana* could eventually replace the dominant *Quercus*. Therefore, we conducted a dendrochronological study to determine the combined effect of fire suppression and drought on the temporal pattern of recruitment of dominant upland forest tree species. We wanted to learn whether changes in the recruitment of the three most important species, *J. virginiana*, *Quercus marilandica* Münchh. and *Q. stellata* Wangenh., could be attributed to changes in fire regime, climate and land use and management.

2. Methods

2.1. Study area

The study area was in the Cross Timbers region which can be characterized as a mosaic of oak forest, oak savanna, and prairie that constitutes a broad ecotone stretching from southeastern Kansas to central Texas (Duck and Fletcher, 1943; Rice and Penfound, 1959; Hoagland et al., 1999). Study sites were forest stands in the central Cross Timbers between 34° 50' and 36° 20' N latitude and between 96° 10' and 99° 10' W longitude (Fig. 1). Mean annual temperature and precipitation range from 15 °C and 71 cm to 19 °C and 102 cm. Temperature generally decreases to the north, precipitation generally decreases to the west, and elevation decreases from 700 to 200 m a.s.l. west to east (Court, 1974; Bell and Hulbert, 1976; Sutherland, 1977). Fine-grained clay soils with limestone and shale parent material generally support grasslands and coarse-grained sandy soils with sandstone parent material generally support forests (Dyksterhuis, 1948; Powell and Lowry, 1980; Rhodes, 1980). *Q. marilandica* and *Q. stellata* were the dominant woody species with *J. virginiana* subdominant and limited to ripar-

ian sites and rocky outcrops sheltered from fire (Johnson and Risser, 1972; Hoagland et al., 1999).

2.2. Vegetation sampling

We re-measured stands first measured by Rice and Penfound (1955, 1959) between 1953 and 1957 for the purpose of characterizing the upland forests of Oklahoma. We measured the woody vegetation of eleven forest stands in three regions of Oklahoma: northwest (5 stands), north-central (3 stands), and south-central (3 stands) (Fig. 1). We chose stands with the least human disturbance (minimal vegetation removal). The stands had a mean area of approximately 50 ha and ranged in size from 16 to 129 ha. All of these stands had a history of fire prior to the 1950s sampling period according to Rice and Penfound (1959). In contrast, we found no recent evidence of fire.

In each stand we used 40 prism plots spaced 22 m apart to measure basal area ($\text{m}^2 \text{ha}^{-1}$) by species using a BAF10 prism (Avery and Burkhart, 1994). We used a 1.83 m wide by 22 m long plot between each prism plot to count the number of tree and sapling stems per plot by species. Stems 2.54–7.62 cm diameter at breast height (dbh) were considered saplings, and stems >7.62 cm dbh were considered trees. We estimated basal area and tree and sapling density (stems ha^{-1}) by stand and by region from these data.

We determined ages for a random sample of stems >2.54 cm dbh for the three dominant tree species which made up over 84% of stand basal area: *J. virginiana*, *Q. marilandica*, and *Q. stellata*. We used tree and sapling density data for these species to determine the diameter of a circular plot necessary to find one stem of each species. The plot diameter was different for each species. We visited at least one-third of the sample plots established in each stand, measured all stems of the desired species on each plot for dbh, and sampled each for age determination. The goal was to sample as many stems as possible throughout the entire stand up to 40 per species. Due to the variability of the distribution of stems within a stand and the size of the stands (16–129 ha), the number of sample stems per stand varied from 16 to 51 for *J. virginiana*, 8 to 42 for *Q. marilandica*, and 12 to 52 for *Q. stellata*. The total number of stems aged was 404 *J. virginiana*, 290 *Q. marilandica*, and 298 *Q. stellata*. All three species were sampled in all stands with the exception of *Q. stellata*, which was absent from three of the five stands in northwest Oklahoma. To determine age we extracted a core from each live stem. When stems were too small or obstructed we removed a 5 cm thick cross-section just above ground level. We dried samples, sanded them with progressively finer grades of sandpaper to distinguish tree rings under a microscope, and dated most annual growth

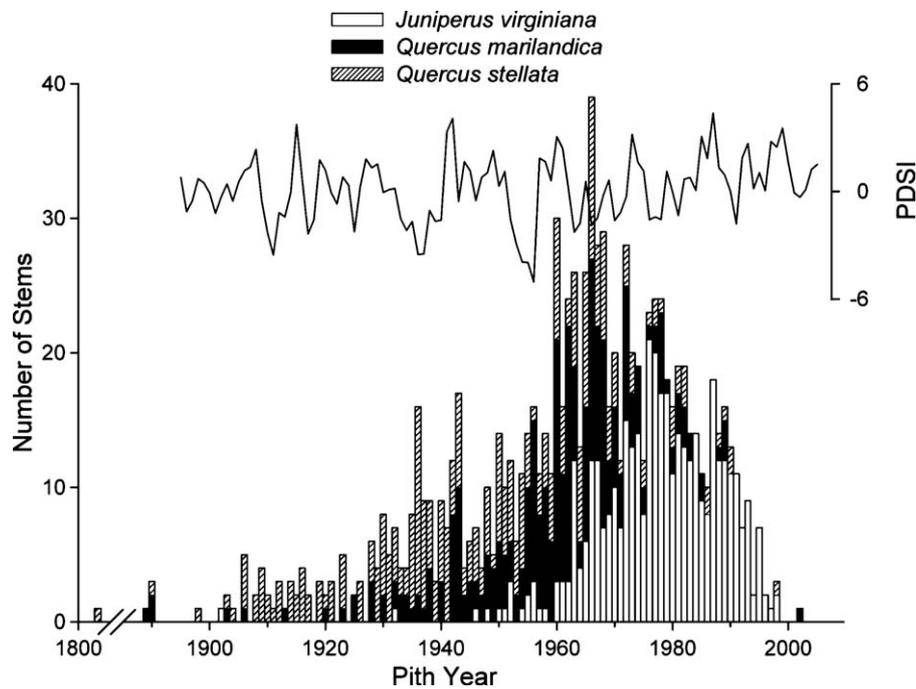


Fig. 2. Age distributions of *Juniperus virginiana*, *Quercus marilandica* and *Quercus stellata*, and instrumental PDSI in upland *Quercus* forests of Oklahoma, USA. Data represent sums of three Oklahoma regions and average of regional PDSI.

rings to their calendar year of formation using dendrochronology (Stokes and Smiley, 1968).

2.3. Environmental data

We used instrumental Palmer Drought Severity Index (PDSI) from 1895 to 2005 to determine the occurrence of abnormally dry and wet periods (NOAA NESDIS, 2010). PDSI ranges from -6 (extreme drought) to $+6$ (extremely wet) (Palmer, 1965). Canonical correspondence analysis (CCA, ter Braak, 1986) previously revealed precipitation had a strong effect on basal area, tree density, and sapling density (DeSantis et al., 2010). Therefore, we used PDSI data collected from the closest geographical locations to each stand and region. For northwest Oklahoma forest stands, we used annual PDSI averaged from monthly values from the Panhandle Division of Oklahoma, for north-central Oklahoma the North Central Division, and for south-central the Central Division (NOAA NESDIS, 2010).

2.4. Data analysis

We analyzed differences between forest stands as well as differences between regions. For all analyses we report here, the experimental unit was the region, with sub-sample plots measured within the region as well as within each stand. Paired Student's *t*-tests were conducted separately on regional means to determine if differences between 1950s and 2000s basal area, tree density, and sapling density were significant.

Standard dendrochronological methods were used to crossdate all cores and cross-sections (Stokes and Smiley, 1968). We crossdated *Q. marilandica* and *Q. stellata* using a local master chronology for *Q. stellata* available on the International Tree-Ring Data Bank (ITRDB, NOAA, 2004), and *J. virginiana* using a local master chronology (J. Edmondson, Department of Geosciences, University of Arkansas-Fayetteville, personal communication). Although *J. virginiana* produces abundant false rings, these growth patterns can be used to augment crossdating (Edmondson, 2010). However, we had difficulties when comparing among regions due to the effect of climatic variability on annual growth rings. Therefore, ages of

J. virginiana should be regarded as ring counts and not exact ages (Schweingruber, 1988). On the other hand, we were confident that despite crossdating discrepancies, our ring counts were within five years of exact ages.

The Superposed Epoch Analysis (SEA) component of FHX2 (Grissino-Mayer, 2001) was used to analyze PDSI and species recruitment dates to determine if PDSI was significantly different than normal from 20 years before to 4 years after each recruitment year. We performed separate SEAs on each species in each stand and region using a list of recruitment years and corresponding annual PDSI values (NOAA NESDIS, 2010).

3. Results

Tree dbh ranged from 3 to 50 cm with a mean of 13.50 cm. Trees ranged in age from 5 to 204 years with a mean age of 44 years (Fig. 2). *J. virginiana* basal area and tree density increased between sampling periods in the northwest region. *Q. stellata* basal area and tree density increased in the north-central region. Total tree density increased in the northwest and south-central regions. Total basal area more than doubled in all three regions (Table 1). *Q. marilandica* tree density decreased in the north-central region and *Q. marilandica* sapling density decreased in the south-central region.

Total recruitment increased in the early 1960s (Figs. 2 and 3). The increased recruitment was initially dominated by the two *Quercus* species; however, *J. virginiana* recruitment increased from the 1960s to 1970s and *Q. marilandica* and *Q. stellata* recruitment decreased from the 1970s to 1980s. From the mid-1970s to 2005 the rate of recruitment slowed and was primarily *J. virginiana* with little *Q. marilandica* or *Q. stellata*.

Recruitment patterns may have been asynchronous among regions because forest stands were spaced out across a very broad area that experienced varying levels of drought intensity and duration (Figs. 1 and 3). Although there was no recruitment of *J. virginiana* before the mid-1940s in the northwest region and before the mid-1960s in the north-central region, there was occasional *J. virginiana* recruitment in the early 1900s in the south-central region. The major acceleration of *J. virginiana* recruitment occurred

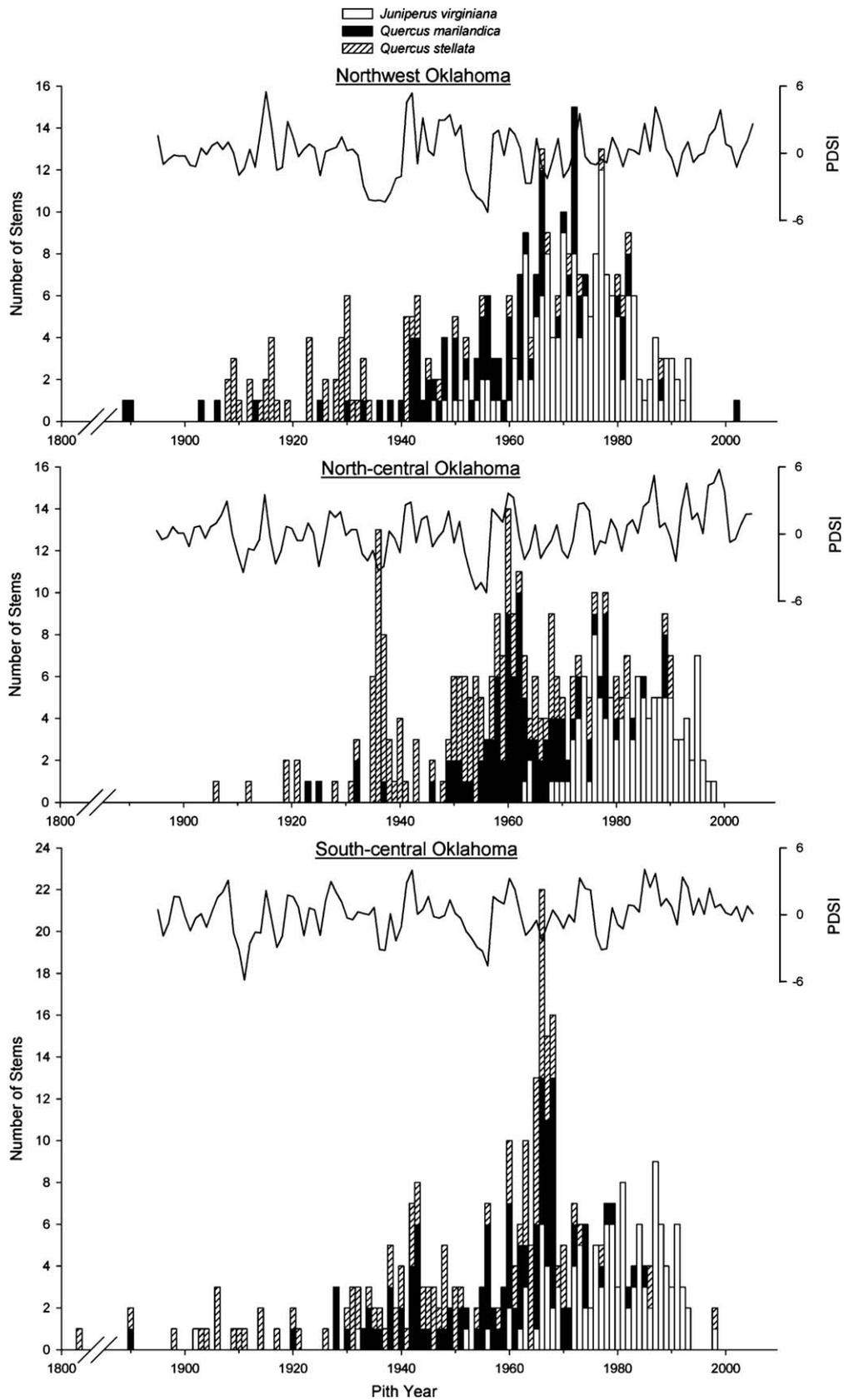


Fig. 3. Age distributions of *Juniperus virginiana*, *Quercus marilandica* and *Quercus stellata*, and instrumental PDSI by region in upland *Quercus* forests of Oklahoma, USA. Data represent sums of stands by region.

Table 1Tree basal area and density, and sapling density for *Juniperus virginiana*, *Quercus marilandica*, and *Quercus stellata* in the 1950s and 2000s in three regions of Oklahoma, USA.

Region Species	Trees				Saplings	
	Basal Area (m ² ha ⁻¹)		Density (stems ha ⁻¹)		Density (stems ha ⁻¹)	
	1950s	2000s	1950s	2000s	1950s	2000s
Northwest						
<i>J. virginiana</i>	0.02 (0.02) 0	10.09 (2.13)* 43	8.69 (5.41) 2	533.75 (192.65)* 56	2.48 (2.48) 1	316.17 (137.88) 38
<i>Q. marilandica</i>	5.22 (2.03) 82	6.79 (2.06) 29	353.95 (108.85) 80	201.53 (35.29) 21	198.71 (60.94) 47	89.92 (23.10) 11
<i>Q. stellata</i>	0.85 (0.57) 13	4.30 (3.67) 18	62.10 (45.80) 14	108.83 (78.43) 11	197.47 (185.30) 46	65.52 (45.22) 8
Total	6.35 (1.90)	23.56 (2.04)*	442.13 (102.83)	958.00 (163.94)*	424.74 (228.58)	838.78 (203.99)
North-central						
<i>J. virginiana</i>	0 0	0.65 (0.34) 3	0 0	81.99 (34.10) 11	0 0	146.64 (62.67) 23
<i>Q. marilandica</i>	4.74 (1.76) 46	2.77 (1.36) 12	211.13 (52.08) 40	58.18 (7.18)* 8	264.94 (147.14) 40	30.26 (6.87) 5
<i>Q. stellata</i>	5.43 (1.10) 52	18.08 (3.34)* 81	312.55 (67.29) 59	547.55 (4.40)* 73	389.14 (188.43) 59	146.26 (46.44) 23
Total	10.37 (0.92)	22.44 (1.69)*	531.96 (90.22)	753.94 (33.21)	662.36 (330.66)	641.70 (24.00)
South-central						
<i>J. virginiana</i>	0.02 (0.02) 0	3.60 (2.91) 17	2.07 (2.07) 0	165.59 (103.74) 17	0 0	142.82 (57.70) 33
<i>Q. marilandica</i>	2.58 (0.63) 27	2.10 (0.26) 10	113.84 (33.31) 27	163.52 (50.36) 17	157.31 (18.40) 26	22.77 (11.52)* 5
<i>Q. stellata</i>	6.22 (2.05) 64	12.87 (2.14) 60	269.08 (25.94) 64	502.98 (201.88) 51	393.28 (219.67) 64	76.59 (27.38) 17
Total	9.68 (2.34)	21.31 (2.03)*	418.12 (47.34)	989.40 (169.09)*	616.82 (207.48)	438.81 (90.79)

Percent of total in bold, percents do not add to 100 due to exclusion of other species from table, totals include all woody species; SE in parentheses; asterisks indicate significant changes, $P < 0.05$.

first in the northwest region (early 1960s), next in the south-central region (mid-1960s) and last in the north-central region (early 1970s).

SEA did not detect a significant relationship between PDSI and recruitment at the regional level but did detect a relationship between PDSI and recruitment at the stand level. For all three species, recruitment events typically occurred from 5 to 20 years after abnormally dry periods and the timing of events differed among stands. SEA detected more correlations between recruitment events and prior drought than between recruitment events and prior wet periods. On the other hand, PDSI was substantially different by region (NOAA NESDIS, 2010; Fig. 3).

4. Discussion

Results from the current study supported the conclusion that a combination of drought-induced tree mortality and decreased fire frequency was the primary cause for major changes in forest composition and structure in south-central North America's midcontinent forest-prairie ecotone. Although these forests had exhibited changes in dominance from xeric fire-tolerant *Quercus* to mesic fire-intolerant tree species (DeSantis et al., 2010), the most noteworthy change was the rapid encroachment of the native invasive *J. virginiana*. For many centuries, anthropogenic fire played a role in the maintenance of upland *Quercus* forests by encouraging *Q. stellata* and *Q. marilandica* regeneration by sprouting (Johnson, 1993; DeSantis, 2010) and by restricting regeneration of *J. virginiana* (Briggs et al., 2002a). The canopy gaps caused by tree mortality during severe droughts would most likely have been filled by *Quercus*. Recent fire suppression has changed the patterns of community succession. Recruitment of *Q. marilandica* and *Q. stellata* appeared to increase along with *J. virginiana* following the locally severe 1950s drought, apparently to fill gaps caused by mortality noted by Rice and Penfound (1959); later recruitment of *Quercus* gradually declined while *J. virginiana* increased. Future forests subjected

to fire suppression and more frequent and prolonged droughts will likely undergo continued changes in species composition away from the fire dependent *Quercus* toward fire-intolerant species such as *J. virginiana*.

In south-central North America's midcontinent forest-prairie ecotone, the balance of evapotranspiration and precipitation permits a wide range of vegetation types to grow in proximity. Because many species are at the limits of their natural ranges, even a small change in climate can lead to major changes in vegetation composition and structure, often in combination with rapid encroachment of invasive species. The midcontinent forest-prairie boundary has shifted back and forth from west to east in response to changes in aridity occurring over hundreds of years during the Holocene (Williams et al., 2009). Severe and prolonged droughts that kill trees can change successional pathways due to variability in drought tolerance among species (Tainter et al., 1990; Jenkins and Pallardy, 1995; Suarez and Kitzberger, 2008). Rapid vegetation shifts can occur in ecotones, where disturbances such as fire and drought play important roles in species composition (Allen and Breshears, 1998). An increase in the number and severity of droughts may lead to rapid transformations becoming more common (Allen et al., 2010).

In south-central North America's midcontinent forest-prairie ecotone, drought occurs approximately every 20 years, and some are severe enough to cause substantial tree mortality (Albertson, 1940; Albertson and Weaver, 1945; Rice and Penfound, 1959; Johnson and Risser, 1975). Drought-induced mortality can be species specific; the 1950s drought appeared to affect mostly *Q. marilandica* (Rice and Penfound, 1959). The greater sensitivity of this species compared to others in the same stand was documented following more recent drought events (Law and Gott, 1987; Jenkins and Pallardy, 1993). *Quercus* includes some of the deepest rooting trees in North America (Kozłowski, 1975; Johnson et al., 2002); so it is not surprising many *Quercus* species are relatively drought tolerant (Rice and Penfound, 1959; Abrams, 1990). Although *J. virginiana* does not have a deep root system like *Quercus* (Albertson,

1940; Hinckley et al., 1981), it is capable of competing in prairies and closed forests (Ormsbee et al., 1976; Lassoie et al., 1983). Part of its success is due to its capability to photosynthesize year round in mild weather, an important advantage over deciduous *Quercus* and grass species. In addition, it is likely more tolerant of drought than most *Quercus* species due to its xylem consisting entirely of tracheids, which are more resistant to drought-induced loss of function due to cavitation than the vessels in *Quercus* xylem (Ginter-Whitehouse et al., 1983; Willson et al., 2008). These adaptations plus production of abundant seeds may explain why *J. virginiana* was found to be especially effective at replacing losses due to drought mortality (Albertson and Weaver, 1945).

South-central North America's midcontinent forest-prairie ecotone is an anthropogenic landscape where fire was used for thousands of years to meet the needs of Native Americans (Albert, 1981; Pyne, 1982; Bryant and Holloway, 1985). The fire return interval likely was one to ten years (Brown, 2000) until after Euro-American settlement 100–150 years ago when fire suppression made it a rare event in many locations (Guyette et al., 2002). Fire altered forest composition by increasing low-moisture microclimates and suppressing later-successional fire intolerant species like *J. virginiana* that are more shade tolerant than *Quercus* (Lassoie et al., 1983; Engle et al., 2006). Fire removed vegetation, increased light to dormant buds near the forest floor, and stimulated new regeneration from exposed stump, seedling, and root sprout buds on xerophytic *Quercus* (Abrams, 2003). Regeneration of *Quercus* species in xeric forests is primarily through sprouting from the root collar and along roots, the former being twice as common as the latter (Larson and Johnson, 1998; Heitzman, 2003; Clark and Hallgren, 2003; DeSantis, 2010). Fire encourages *Quercus* sprouting (Powell and Lowry, 1980; DeSantis, 2010) and favors its success by suppressing fire-intolerant competing vegetation (Crow et al., 1994; Burton et al., 2010). Abundant *Quercus* advance reproduction from sprouts can exist in the understory indefinitely and recruit into the canopy after gaps are created by disturbances (Johnson, 1993).

Although *J. virginiana* does not sprout and may suffer mortality from severe droughts, it may be capable of more rapid recovery from drought than *Quercus* because its seeds are dispersed extensively by birds (Holthuijzen and Sharik, 1984). Most of the seed crop from *J. virginiana* was found to be dispersed more than 12 m from the parent (Holthuijzen et al., 1986). The widespread *J. virginiana* recruitment following the 1950s drought likely benefitted from drought-caused gaps in the *Quercus* forest (Rice and Penfound, 1959) and it occurred at a higher level of abundance than seen before. Fire suppression had removed the force that prevented *J. virginiana* establishment and favored *Quercus* sprouting and establishment. Over time *J. virginiana* likely recruited into canopy gaps and further reduced recruitment of the less shade-tolerant *Quercus* species (Rykiel and Cook, 1986; Briggs et al., 2002a; DeSantis et al., 2010). The commencement and acceleration of *J. virginiana* recruitment was asynchronous among regions; this may have been due to asynchronous fire regime changes among regions. The forest stands we sampled were spread across a broad geographical area and distances between stands were large. Most of these stands were in small land parcels owned by local farmers who likely used or suppressed fire at different times. Therefore, the timing of changes in land management practices may have caused differences in *J. virginiana* recruitment among forest stands.

The widespread encroachment of *J. virginiana* into plant communities may be partly due to the extensive planting of this species for conservation purposes since the 1930s. The Prairie States Forestry Project of the USDA Forest Service was responsible for planting an estimated 1,430,000 *J. virginiana* seedlings in 1900 miles of shelterbelts in Oklahoma between 1935 and 1942 (Smola, 1985). *J. virginiana* was considered the best tree to plant because of its capacity to survive and grow under droughty condi-

tions (Woodruff et al., 1976). Overall survival was estimated to be 72% and in some places it was one of the few trees to survive in large numbers (Read, 1958). The Forest Regeneration Center of the state of Oklahoma began producing *J. virginiana* seedlings in 1979 and shipped over 1,660,000 by 2002. No assessment has ever been made of the impact of these plantings on encroachment of *J. virginiana* into prairies or forests. We found the regular recruitment of *J. virginiana* did not begin until after 1940, rather early to show effects of shelterbelt planting. *J. virginiana* begins to produce seeds after 10 years, and although it produces seeds every year, good crops are produced only every two to three years (Lawson, 2004). *J. virginiana* was known to be the most common natural reproduction from shelterbelts. It seems possible the shelterbelt planting could have contributed to the increase in this species and most likely was not an important contributor until the mid-1950s. In contrast, the plantings from the Forest Regeneration Center were too late to have an effect on the results of our study.

Grazing is a major disturbance factor in south-central North America's midcontinent forest-prairie ecotone. The American bison (*Bos bison* L.) was a dominant force until it was nearly extirpated. Cattle production has been a major industry since Euro-American settlement beginning in the late 1800s. Grazing was found to reduce *J. virginiana* encroachment in grasslands (Owensby et al., 1973). However, due to the reduction in fuel caused by grazing, the combination of fire and grazing was not as effective as fire alone at reducing *J. virginiana* (Schmidt and Stubbendieck, 1993; Briggs et al., 2002b). This may explain the common conclusion overgrazing can actually favor encroachment of woody species (Grover and Musick, 1990; Briggs et al., 2002b). Without similar research in forests we can only speculate these findings may apply under a forest canopy. Grazing was a common use of the grassland, savanna, and forest and may have played a role in the rapid increase in *J. virginiana* by reducing fire intensity, but it was not likely to be as important as the suppression of fire.

5. Conclusions

Research has shown severe and prolonged drought and grazing can influence recruitment and contribute to changes in forest composition and structure in south-central North America's midcontinent forest-prairie ecotone (Rice and Penfound, 1959; Briggs et al., 2002a; DeSantis et al., 2010). However, our findings and previous studies supported the conclusion that a dramatic increase in *J. virginiana* was dependent on fire suppression (Dyksterhuis, 1948; Snook, 1985; Engle and Kulbeth, 1992). Lacking fire to reduce competition from other woody species and stimulate sprouting from exposed dormant buds, *Quercus* regeneration slowed while regeneration of fire-intolerant *J. virginiana* increased (Schmidt and Leatherberry, 1995; Gedalof et al., 2006; Bartolomé et al., 2008; Belden and Pallardy, 2009). Increased stand density due to gap filling and *J. virginiana* regeneration (DeSantis, 2010) further disfavored the light demanding *Quercus* (Rebertus and Burns, 1997; Nowacki and Abrams, 2008; Shinneman and Baker, 2009).

Patterns of species recruitment suggest a continuing shift away from *Quercus* and toward *J. virginiana* in the future (DeSantis et al., 2010). Combined with decreasing fire, an increase in drought severity and duration due to global climate change could have substantial effects on forest composition and structure (Allen et al., 2010). Major changes in vegetation composition such as the accelerated conversion of *Quercus* to *J. virginiana* forests could have substantial implications for ecosystem services, including wildlife habitat, water resources, and support for soil formation, nutrient cycling, and aesthetic and recreational services. This is important information for land managers interested in maintaining *Quercus* forests.

Acknowledgements

We thank the landowners for access to the study sites. Dr. Tom Lynch and Dr. Mike Palmer, Oklahoma State University, provided valuable advice. Thanks to Jake Beale, Kyle Hesse, and Jesse Martin for field and laboratory assistance. Financial support was provided by the Oklahoma State University Department of Natural Resource Ecology & Management and the Oklahoma State University Cooperative Extension Service and Agricultural Experiment Station through a Division of Agricultural Sciences and Natural Resources Team Initiative Project grant.

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