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Positive feedbacks amplify rates of woody encroachment in mesic tallgrass prairie

ZAK RATAJCZAK,† JESSE B. NIPPERT, JEFFREY C. HARTMAN, AND TROY W. OCHELTREE

Division of Biology, Kansas State University, Manhattan, Kansas 66506 USA

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Abstract. Over the last century, many grasslands worldwide have transitioned from a graminoid to a tree/shrub-dominated state in a short period of time, a phenomenon referred to as woody encroachment. Positive feedbacks and bi-stability are thought to be important drivers of woody encroachment, but there is little empirical evidence to suggest that positive feedbacks accelerate the woody encroachment of mesic grasslands. In mesic tallgrass prairie, shrub establishment does not directly facilitate seedling establishment. Yet, shrub establishment may facilitate the clonal spread of existing shrubs into nearby patches, because clonal reproduction might circumvent barriers that typically limit woody seedlings. Our results show that when *Cornus drummondii* (the predominate encroacher of mesic tallgrass prairie) extends rhizomatous stems into open grasslands, these stems use the same deep soil water sources as mature stems—thereby avoiding competition with grasses and gaining access to a reliable water source. In addition, herbaceous fuel concentrations are lower at the shrub/grass interface than in open grasslands, reducing the potential impacts of subsequent grassland fires. We propose that the release from resource and fire limitation results in a positive feedback loop as clonal stems are able to extend into surrounding patches, circumvent demographic barriers, mature, and spread by developing their own clonal stems. Long-term data on site (26 years) corroborates this interpretation: the size of deep-rooted clonal shrub species has increased 16-fold and their cover has increased from 0 to 27%, whereas the cover of shallow-rooted species (both clonal and non-clonal) has only increased marginally. Together, these results suggest that (1) positive feedbacks can facilitate mesic woody encroachment and (2) bi-stability exists in mesic tallgrass prairie.

Key words: *Andropogon gerardii*; bi-stability; bush encroachment; *Cornus drummondii*; $\delta^{18}O$; fire; niche-partitioning; shrub encroachment; source water; tipping points; tree–grass coexistence; two-layer soil model.

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† **E-mail:** zarata@ksu.edu

INTRODUCTION

In the last century, woody encroachment has been reported in grasslands worldwide and across a range of evolutionary histories and climatic conditions (Archer 1995, Van Auken 2000, Roques et al. 2001, Knapp et al. 2008), resulting in changes in ecosystem structure and function (Scholes and Archer 1997, Van Auken 2000, Knapp et al. 2008). Positive feedbacks have been shown to increase the rate and extent of woody encroachment in many grasslands (Schlesinger et al. 1990, Van Auken 2000, Scheffer et al. 2001, Wookey et al. 2009, D'Odorico et al. 2010). However, the study of encroachment feedbacks has focused primarily on semi-arid and arctic grasslands (Archer et al. 1988, Schlesinger et al. 1990, Ravi et al. 2007, Wookey et al. 2009, D'Odorico et al. 2010), with examples in mesic systems restricted to theoretical models (D'Odorico et al. 2006, Baudena et al. 2010). This study addresses the potential for positive feedback mechanisms in mesic tallgrass prairie, a system in which positive feedbacks have not been previously identified.

In semi-arid and arctic grasslands, woody encroachment alters temperature and/or the availability of water and nutrients, which facilitates the establishment of other shrubs and creates a positive feedback loop (Schlesinger et al. 1990, Scheffer et al. 2001, Ravi et al. 2007, Wookey et al. 2009, D'Odorico et al. 2010; see Archer et al. 1988 for mechanisms related to seed dispersal). However, these and other mechanisms have been found to have a minimal impact on encroachment of tallgrass prairie (Briggs et al. 2005, McKinley and Blair 2008). Instead, the nature of feedbacks in tallgrass prairie may involve factors that structure mesic grasslands: pronounced belowground competition in the upper soil layers (Nippert and Knapp 2007*a, b*), frequent and intense fires (Knapp et al. 1998, van Wilgen et al. 2003, Briggs et al. 2005, Bond 2008) and predominance of clonal reproduction (Benson and Hartnett 2006, Dalgleish and Hartnett 2006).

Though mesic grasslands receive enough rainfall to support closed forests, woody plants are commonly excluded because grass dominance decreases water availability in the upper soil and stimulates fires (Scholes and Archer 1997, Sankaran et al. 2005, Bond 2008, Staver et al. 2011). Many adult woody plants escape resource competition because they can access deeper water sources and usually can withstand grassland fires (Walter 1971, Scholes and Archer 1997, Bond 2008). However, grasses can suppress seedling establishment and/or prohibit seedlings from reaching the adult stage, which imposes a demographic bottleneck on woody plant populations (Higgins et al. 2000, Sankaran et al. 2005, Gignoux et al. 2009, Staver et al. 2011). Specifically, when woody species are young they have a shallow and less robust root system, which overlaps with the extensive grass root systems in the upper soil (Wilson 1993, Jackson et al. 1996, Weltzin and McPherson 1997, Partel and Wilson 2002). Because grasses deplete soil moisture in the upper soil, this overlap results in high mortality rates until woody plants develop deeper roots (Scholes and Archer 1997, Jurena and Archer 2003, Bond 2008). Likewise, the thinner bark and lower stature of young woody plants makes them more susceptible to fire than adults (Scholes and Archer 1997, Higgins et al. 2000, Bond 2008, Lawes et al. 2011). Both of these demographic barriers are especially acute in tallgrass prairie, as seedling establishment accounts for less than1% of recruitment each year (Benson and Hartnett 2006) and this system supports high levels of herbaceous productivity (Nippert et al. 2011), which leads to high-intensity fires (Gibson et al. 1990).

Considering the limitations of woody vegetation in mesic grasslands, positive feedbacks that favor encroachment in tallgrass prairie should theoretically reduce competition for water and the impacts of fire during the establishment phase of woody plants. In tallgrass prairie most reproduction occurs by clonal reproduction (Benson and Hartnett 2006), as dominant species become established and then expand radially via rhizomatous clonal stems. Therefore, to test for positive feedbacks in mesic grassland we focused on factors affecting clonal stem production. Using a 26 year species composition data-set, we first identified long-term trends in woody coverage in tallgrass prairie and determined whether changes in cover were the result of the expansion by existing shrubs and/or the establishment of new individuals. We also used this dataset, which occurs over a soil moisture gradient, to determine if water availability limits woody establishment in tallgrass prairie. Then, we explored three specific mechanisms: (1) Do clonal shrub stems use deep soil water to circumvent the competition with grasses? (2) Does shrub establishment alter drivers of fire frequency/intensity in favor of clonal shrub expansion? (3) Early in development, can clonal shrub stems limit light availability to suppress growth of competing grasses?

METHODS

Study site and organisms

The Konza Prairie Biological Station (KPBS) is a native tallgrass prairie (3487 ha) in the Flint Hills of northeast Kansas, USA, where most of the large remnant tracts of tallgrass prairie remain (39°05′ N, 96°35′ W). KPBS is divided

Table 1. Woody species characteristics and long-term cover dynamics.

Species	Life form	Rooting depth§	N-fixing	Cover (%)		Frequency (%)		Size index (%)	
				1983–1985	2007–2009	1983–1985	2007–2009	1983–1985	2007–2009
Cornus drummondii	clonal	deep	no	0.0	18.5	0	35	0	47
Rhus glabora	clonal	deep[1]	no	0.0	8.2	0	28	0	27
Prunus americana	clonal	shallow[1]	no	0.0	4.0	0	13	0	16
Ceanothus americanus	non-clonal	shallow[2]	no	0.0	0.1	0	5	0	2
Amorpha canescens	non-clonal	shallow[2]	yes	4.2	4.7	43	46	5	6
Other species‡	various	unknown	various	0.3	5.7	3 (±2)	8 (±5)	1 (±0.4)	6 (±4)

Note: Sources are: 1, McCarron and Knapp (2004); 2, Nippert and Knapp (2007*a*, *b*).

§ Species were considered to have a shallow rooting depth if they obtained the majority of their water from 0–30 cm, where grass roots predominate.

‡ For ‘Other species’, cover is the aggregate cover of species in this group, whereas frequency and size index are averages of all species. This group is made up of 7 species total. Numbers in parentheses denote ±1 SEM.

into 60 hydrological catchment basins, referred to as watersheds. Each watershed has a prescribed fire frequency (1, 2, 4, or 20 yrs) with most being burned in late April. The estimated historical fire frequency (i.e., prior to European settlement) for this region is every 3 to 4 years (Knapp et al. 1998). All analyses reported here occurred in watersheds that are ungrazed by bison and burned every 3 to 4 years.

Topographic variation at KPBS is dramatic over small scales. Upland locations have thinner soils than lowlands, resulting in lower water availability and lower primary productivity (Nippert et al. 2011). KPBS experiences weather conditions typical of mesic grassland, with 75% of annual rainfall occurring during the growing season of April to September (Hayden 1998). The climate of 2009 was wetter (950 mm) and cooler (11.9°C mean daily air temperature) than the long-term site average (35 year mean: 835 mm precipitation and 12.7°C air temperature). The plant community of KPBS is dominated by perennial C_4 grasses *Andropogon gerardii*, *Sorghastrum nutans*, *Schizachyrium scoparium*, and *Panicum virgatum*, which rely almost exclusively on soil-water from 0–25 cm depth (McCarron and Knapp 2004, Nippert and Knapp 2007*a*, *b*). KPBS was historically devoid of woody vegetation except in riparian areas, but in the last 26 years, woody encroachment has occurred in areas with a fire frequency of 3 years per fire or greater (reviewed in Briggs et al. 2005). More information on KPBS can be found at http://www.konza.ksu.edu.

Long-term cover dynamics

We present changes in the cover dynamics of 5 native deciduous woody species in this study: *Cornus drummondii*, *Rhus glabra*, *Prunus americana*, *Ceanothus americanus* and *Amorpha canescens*. Together, these 5 focal species account for 85% of woody cover in ungrazed watersheds of KPBS burned every four years. We separated these species into either “shallow” or “deep” rooting habits based on whether they obtained more water from deeper soil layers (>25 cm) than the dominant C_4 grass community. Past work has shown that *C. americanus*, *A. canescens*, and *P. americana* rely primarily on upper 25 cm of soil for their water needs (McCarron and Knapp 2004, Nippert and Knapp 2007*a*, *b*) and so, we categorized these species as “shallow-rooted”. In contrast, pre-dawn water potentials of *R. glabra* have been found to be strongly correlated with soil water availability at 75 cm depth (McCarron and Knapp 2004) and therefore, we categorized this species as “deep-rooted”. The source water depth of *C. drummondii* has not been determined previously. We focused most of this study on the shrub *C. drummondii* because it is the predominate encroacher of natural and semi-natural tallgrass prairie in Kansas, USA. Individual *C. drummondii* have been observed to extend clonal rhizomatous stems (hereafter to referred to as clones) into surrounding grasslands patches. *R. glabra* and *P. americana* are also capable of clonal expansion. A summary of life-form (clonal vs. non-clonal), rooting habit and other characteristics of these species can found in Table 1.

Long-term dynamics of shrub expansion

Permanent community composition plots were established at KPBS in 1983. For each fire frequency × grazing combination, two watersheds have been sampled annually. Sampling occured in 10 m^2 circular plots, arrayed equally along 50 m long transects. Within each watershed, 4 such transects were randomly located in upland locations and 4 in lowland locations (i.e., n = 40 plots per watershed, n = 20 per topographic position, per watershed). When transects were established, shrub cover in all permanent plots was minor (<5%). Since then, woody plants have become established throughout these plots. We analyzed this long-term dataset to track the expansion of our 5 focal woody species over the last 26 years (1983–2009). At each plot, approximate canopy cover of each species has been recorded using a permutation of the Daubenmire cover scale (Bailey and Poulton 1968). Cover was recorded as either 0–1%, 1–5%, 5–25%, 25–50%, 50–75%, 75–95%, and 95–100% of the 10 m^2 circle; we used the midpoint of these ranges for our calculations. For our analysis of *C. drummondii* cover dynamics, we treated uplands and lowlands separately, reporting for each year the average cover of *C. drummondii* across all plots, the frequency of plots containing *C. drummondii*, and size index of *C. drummondii* (n = 40 for each topographic location per year). Frequency is the percentage of plots in which *C. drummondii* occurs. Size index is the relative size of each shrub and is calculated as the total cover of *C. drummondii* divided by the number of plots in which it occurs. We consider our estimate of shrub size to be conservative because shrubs that expanded outside of the plots would not be considered as increasing the cover recorded inside the plot area. We also report changes in cover, frequency and size index for the other 4 focal woody species described above and the remaining woody species aggregated (Table 1). When we report data for all species (not just *C. drummondii*), the data reported are from lowlands only, because uplands have experienced minimal encroachment.

Soil water provenance of C. drummondii *and* A. gerardii

C. drummondii occurs as monotypic stands in the grassland matrix. In late May 2009, eight isolated *C. drummondii* were selected in lowlands and slopes between lowlands and uplands, within watersheds burned every 4 years (including the watersheds with permanent community composition plots). All shrubs were at least 300 m apart from each other. Shrubs were 9.5 m (± ~ 1 m) in diameter, including shrub clones. At each shrub, we established a transect perpendicular to the prevailing hill-slope aspect and measured the diameter of the mature shrub. Using this measurement, five equidistant transect intervals were marked starting at the center of each shrub, with points 1–2 being the mature shrub, point 3 the transition from mature shrub to clones, and points 4–5 the zone where developing clonal stems, not mature stems, occur. Clones were smallest at point 5 and interspersed within the grass canopy.

During the growing season, the stable isotopic signature of groundwater on KPBS falls on the meteoric water line ($\delta D = -41.2‰$, $\delta^{18}O = -6.4‰$; Nippert and Knapp 2007*a*) and primarily reflects recharge by winter precipitation (Macpherson 1996, Nippert and Knapp 2007*a*), whereas the stable isotopic signature of shallower soils is evaporatively enriched (Nippert and Knapp 2007*a*). Using this gradient, we sampled surface soils and xylem tissue of *C. drummondii* and *A. gerardii* and extracted water for isotopic analysis, in order to determine source water-use over time. Sampling of xylem tissue and soil occurred during daylong sampling campaigns during the most active portion of the growing season (June 13 and 26, and July 10 and 23, 2009). During each sampling campaign, *C. drummondii* stem samples were collected at all five transect intervals per shrub, while *A. gerardii* samples were collected at intervals 3–5 along the transect because grasses were not present in the mature shrub interior (intervals 1–2). Soil samples were collected at transect intervals 1, 3, and 5, at 8 and 30 cm depth. *C. drummondii* samples consisted of a non-photosynthetic woody stem sample, taken from a single *C. drummondii* stem at about 1.25 m height. To obtain sufficient quantity of *A. gerardii* xylem tissue, we collected and pooled the non-photosynthetic crown tissue of 2–3 tillers at each transect interval. All plant and soil samples were immediately sealed in exetainers (Labco Ltd., UK) and iced in the field. At the end of the day, samples were placed in a freezer at −10°C until they were processed.

Xylem and soil-water was extracted using cryogenic vacuum distillation (Ehleringer and Osmond 1989, Nippert and Knapp 2007*a*).

Samples were analyzed for their stable oxygen and hydrogen isotopic signatures using a Picarro WS-CRDS isotopic water analyzer and referenced to V-SMOW. Within-run variation of a working standard for all runs was $<0.07‰$ and $<0.5‰$ for $\delta^{18}O$ and δD, respectively. The accuracy of all runs was $<0.18‰$ and $<0.6‰$ for $\delta^{18}O$ and δD, respectively, determined from an in-house standard. Isotope ratios were expressed using δ notation: $\delta = (R_{sample}/R_{standard} - 1) \times 1000$, where R is the absolute ratio of the rare to common isotope.

To estimate varying contributions of multiple water sources to the isotopic water mixture in plant stems, we used the isotopic mixing model MixSIR (Semmens and Moore 2008). MixSIR uses a Bayesian approach to estimate probability distributions of multiple sources to the isotopic mixture of xylem samples (or any other isotope mixing model), by incorporating analytical uncertainty into the prediction. We modelled each individual plant sample for each collection period using the corresponding soil water samples, and ran 1.5 million iterations per sample (accuracy of the model increases with the number of iterations). At each individual shrub, 8 cm and 30 cm soil δD and $\delta^{18}O$ and corresponding variance were obtained by averaging data from all transect intervals for the same depth, for each sampling period, because there was no effect of transect position on the isotopic signature of soil water (see *Results*). Groundwater samples were not available at all locations, therefore we used the most depleted δD and $\delta^{18}O$ sample value measured at each transect as a proxy for the deepest soil water source available (>30 cm end member).

Fire fuel dynamics

To test whether *C. drummondii* alter fire dynamics, we compared herbaceous fuel concentrations at different landscape positions (open grassland, shrub edge or shrub center) and below shrubs of different ages. In early June, fire fuel dynamics were assessed for 19 *C. drummondii* shrubs across five watersheds at KPBS with a 4-year burn frequency. In each watershed, four shrubs were chosen randomly. Three randomly placed replicate samples of litter were taken at the center and edge of each shrub island and a paired grassland plot 15 m from the edge of each shrub island. Using a 0.1 m^2 clip frame to denote each replicate, all dead plant material from the ground to 1 m height was gathered and dried at 60°C for five days before being analyzed. Replicates were sorted into woody and herbaceous components and weighed. Within shrub replicates were weighed separately and then averaged prior to statistical analysis.

At each shrub, the largest stem(s) present was harvested to approximate the age of the shrub. A cross-section of each stem was dried, cut, sanded and then scanned using a flatbed scanner at 600 dpi. The scanned images were used to determine the approximate age of oldest standing stems for each shrub by counting growth rings.

Canopy development

To determine the effects of woody expansion on light availability, we measured the leaf area index (LAI), which reflects changes in canopy density per unit ground area. At the same locations used for isotopic analysis, we measured LAI at 8 cm height every two weeks from June11 to August 28, 2009 using a Li-Cor LAI 2000 Plant Canopy Analyzer (Li-Cor, Lincoln, Nebraska, USA). At each transect interval, five individual readings were averaged for each LAI measurement.

Statistical analyses

The stable isotopic signature ($\delta^{18}O$ and δD) of xylem water was analyzed using a mixed-effects model ANOVA in R (www.r-project.org). In the analysis, date of sampling, species (grass or shrub), transect interval, elevation, and their interactions were fixed effects. Data were log-transformed as needed to meet the assumption of normality. Analysis of litter and LAI was performed separately using a mixed-effects model ANOVA with date of sampling, species, transect interval, topographic position, years since last burn, and their interaction as fixed effects. Biomass data was not normally distributed, so a (log + 1) transformation was used. Statistical trends did not vary statistically when analyzed for $\delta^{18}O$ and δD. To simplify the presentation, we present the results of $\delta^{18}O$ rather than δD because oxygen isotopes have been shown to be a more robust indicator of plant source-water use (Ellsworth and Williams 2007).

RESULTS

Long-term C. drummondii *demography and dynamics*

Since 1983, cover of *C. drummondii* in lowlands has increased from $\sim$0% to $\sim$19%, while cover in uplands has remained at or close to 0% throughout the 26-year period (Fig. 1A). In lowlands, the frequency and size of *C. drummondii* has increased, more or less linearly throughout the entire 26-year period (Fig. 1B, C). Notably, there were two punctuated increases in *C. drummondii* cover, from 1999 to 2002 and 2006 to 2009. Both of these increases are commensurate with increases in shrub size over the same period.

In lowlands, species that are clonal and deeply rooted have increased substantially in cover (Fig. 2A) and have become an increasing higher percentage of the total woody community (Fig. 2B). *P. americana*, a shallow-rooted clonal species, has increased slightly, and non-clonal shallow rooted species have not increased significantly (Table 1, Fig. 2A).

Soil water provenance of C. drummondii *and* A. gerardii

The δ^{18}O of soil water varied significantly by sample period ($p < 0.01$), soil depth ($p < 0.01$) and their interaction ($p < 0.05$), but did not vary by transect interval ($p = 0.69$) (Fig. 3). *C. drummondii* had lower δ^{18}O values than *A. gerardii* for all 4 sampling intervals ($p < 0.0001$, Fig. 3). For most sampling periods, the highest proportion of water used by *C. drummondii* came from $>$30 cm soil depths, while the lowest source contribution was from the 8 cm soil (Fig. 4A). In contrast, *A. gerardii* obtained most of its water from sources at 8 cm and 30 cm depths (Fig. 4B). The source fraction of water-use did not vary along the transect interval for *C. drummondii* ($p = 0.88$) or *A. gerardii* ($p = 0.20$). δ^{18}O of *A. gerardii* xylem water was significantly lower on slopes, compared to lowlands ($p < 0.05$).

Fuel dynamics

Herbaceous fuel (i.e., dead herbaceous biomass) was lower at the shrub edge and center than in open grasslands, and declined significantly ($p < 0.05$) with age at the shrub edge (Fig. 5). At the shrub edge, declines in herbaceous biomass were best explained by an exponential curve ($r^2 = 0.60$, compared to $r^2 = 0.47$ for linear). Herbaceous biomass was greater at the shrub edge immediately following fires than in open grasslands ($p < 0.01$ for interaction between

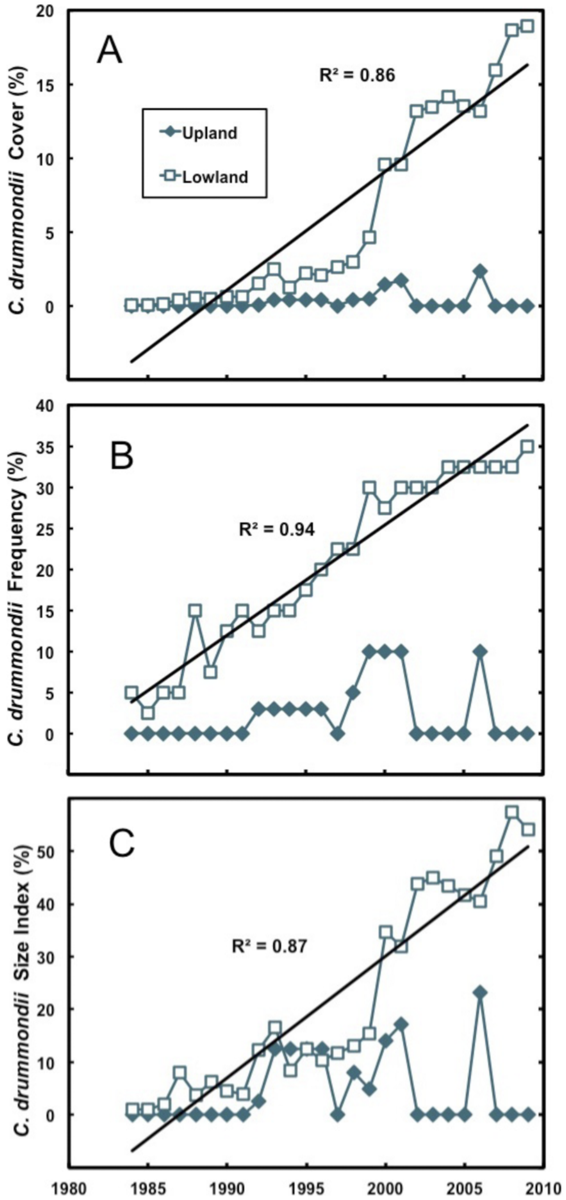

Fig. 1. The long-term trends in (A) aerial cover of the shrub *Cornus drummondii*, (B) the percentage of plots with *C. drummondii* and (C) size index of *C. drummondii* within the permanent community plots ($n = 80$, 10-m^2 plots), measured in uplands (circles) and lowlands (squares). For this analysis, the size index is calculated as the aerial coverage divided by the number of plots containing *C. drummondii*.

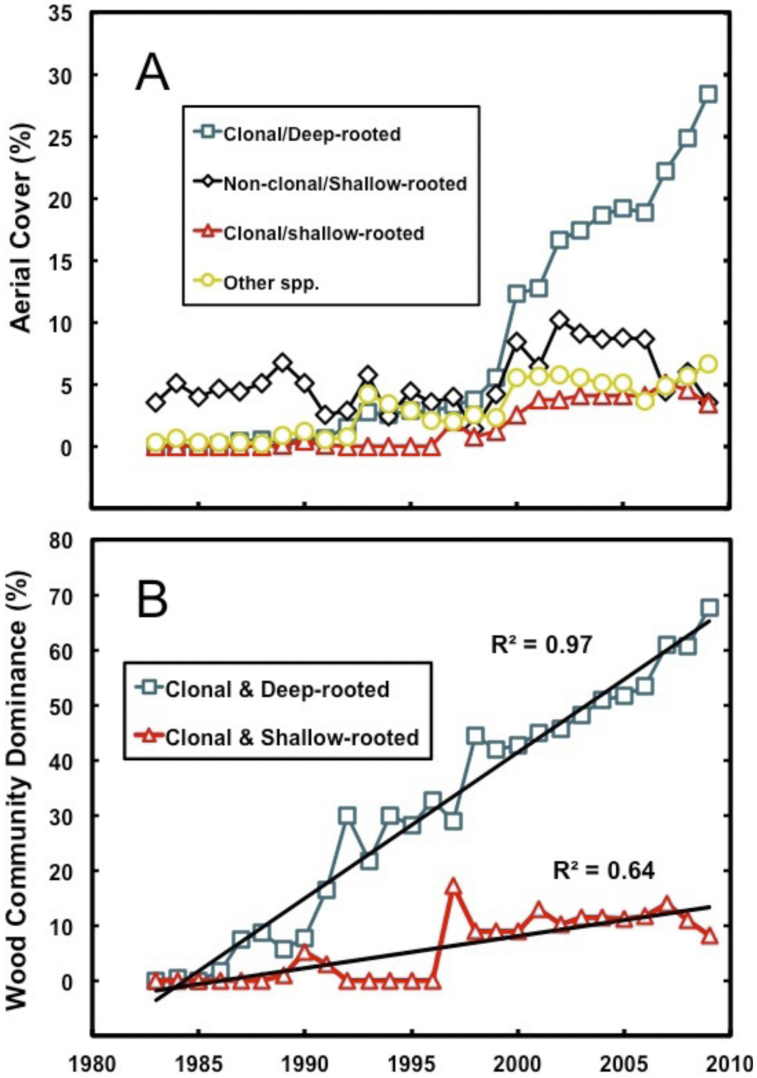

Fig. 2. (A) The long-term changes in cover for 4 woody functional groups over time: species that are clonal and deep-rooted (squares), clonal and shallow-rooted (diamonds), non-clonal and shallow-rooted (triangle) and the remaining species (circles). (B) Change in the percentage of total woody cover that is clonal deep-rooted species (squares) and clonal shallow-rooted species (triangles). Woody Community Dominance = percent cover of woody functional group/percent cover of all woody plants.

location and years post-burn). Age of nearby shrubs had no effect on herbaceous biomass in paired grassland sites.

Canopy development and light limitation

LAI varied significantly by transect interval ($p < 0.0001$) and sample date × transect interval ($p < 0.001$) (Fig. 6). Transect intervals 1 through 3 (the mature shrub) had the most similar values across the growing season and high LAI values early in the season. LAI values at points 4 and 5 (the area dominated by shrub clones) were significantly lower than points 1–3 ($p < 0.05$). LAI values for all transect locations converged by mid-August (Fig. 6).

DISCUSSION

In lowlands the aerial coverage of encroaching *C. drummondii* has increased from 0% to 19% over

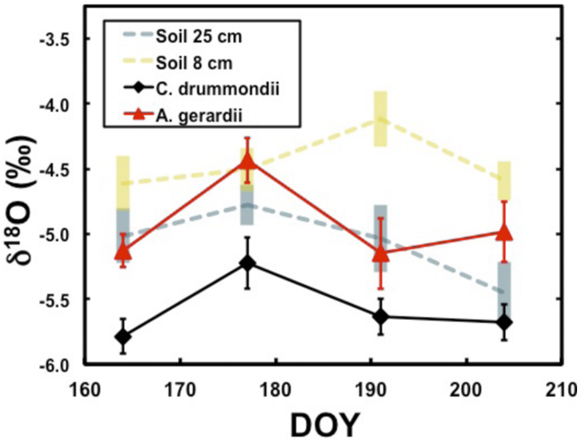

Fig. 3. Temporal trends in δ^{18}O of soil water at 8 cm and 30 cm depth and *Cornus drummondii* (triangles) and *Andropogon gerardii* (diamonds) xylem water. Data are all transect intervals combined. Shaded bars denote (±1 SEM) and correspond to data series of the same color.

the last 26 years, and notably, the size index of *C. drummondii* has increased more than 16-fold. However, *C. drummondii* has not become established in uplands (Fig. 1). Compared to lowlands, uplands have thinner soils and significantly lower water availability (Knapp et al. 1998, Nippert et al. 2011). As a result, uplands also support lower levels of herbaceous biomass (Nippert et al. 2011) and because herbaceous biomass is the primary fuel for fire (van Wilgen et al. 2003), these areas also have lower fire intensities (Gibson et al. 1990). Thus, despite the key role of fire in preventing *C. drummondii* establishment in tallgrass prairie (Heisler et al. 2003, Briggs et al. 2005), water limitation prevents woody establishment under drier conditions, either through outright resource limitation or reducing growth rates to the point at which woody seedlings cannot survive fires of even low intensity.

While resource limitation might constrain establishing *C. drummondii*, our results show that mature *C. drummondii* on slopes and in lowlands avoid competition for water by accessing deeper water sources than primary grass competitors. Across all transect intervals and all sampling periods, δ^{18}O of xylem water in *C. drummondii* was significantly lower than *A. gerardii* (Fig. 3) and on average, *C. drummondii* relied on the upper 30 cm soil for 53% of its water-uptake, compared to 79% in *A. gerardii* (Fig. 4). This represents a substantial degree of niche partitioning, considering Nippert and Knapp (2007*a*, *b*) found that forbs and other woody species in tallgrass prairie usually relied on the upper 25 cm of soil for 70–90% of their water uptake.

The source-water partitioning between *C.*

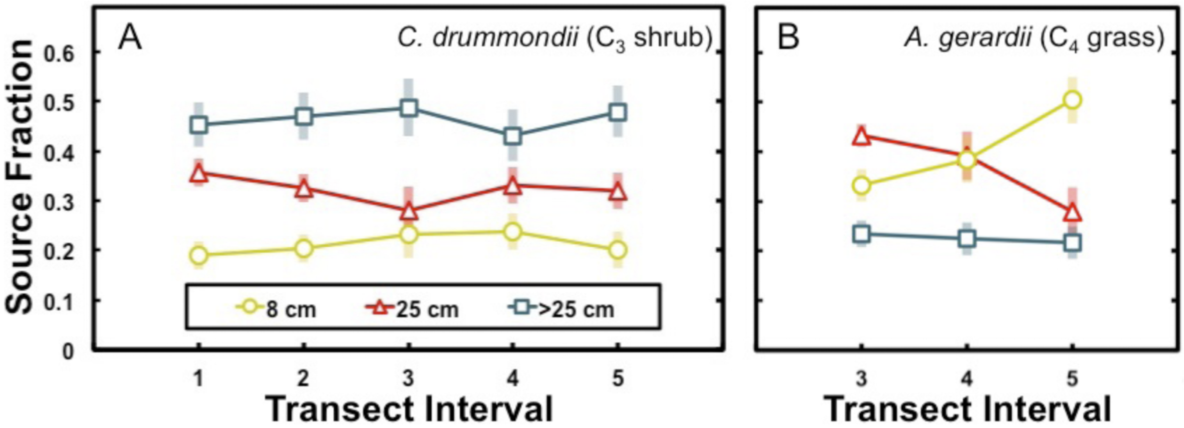

Fig. 4. Mean proportional contributions (±1 SEM) of soil water from different depths to the isotopic mixture of xylem-water for (A) *Cornus drummondii* and (B) *Andropogon gerardii*. Source fraction is the Bayesian estimate of the proportion of source water obtained from each depth by each species, at each transect interval. Transect interval 1 = the center of the mature shrub, 2 = point between the center and edge of the mature shrub, 3 = the edge of the mature shrub, 4 = shrub clones, 5 = shrub that are younger and further away than those at interval 4.

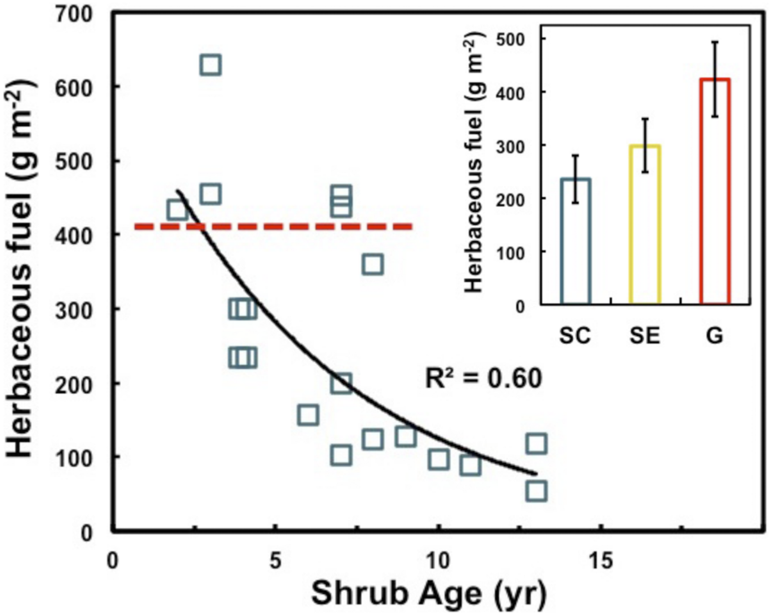

Fig. 5. Herbaceous fuel at the shrub edge (interval 3) in relation to shrub age. The horizontal red line denotes fuel levels in open grassland before burning. Some points are jittered to make them visible. (Inset) average herbaceous fuel at the shrub center (SC), shrub edge (SE) and open grassland (G). Error bars denote ±1 SEM.

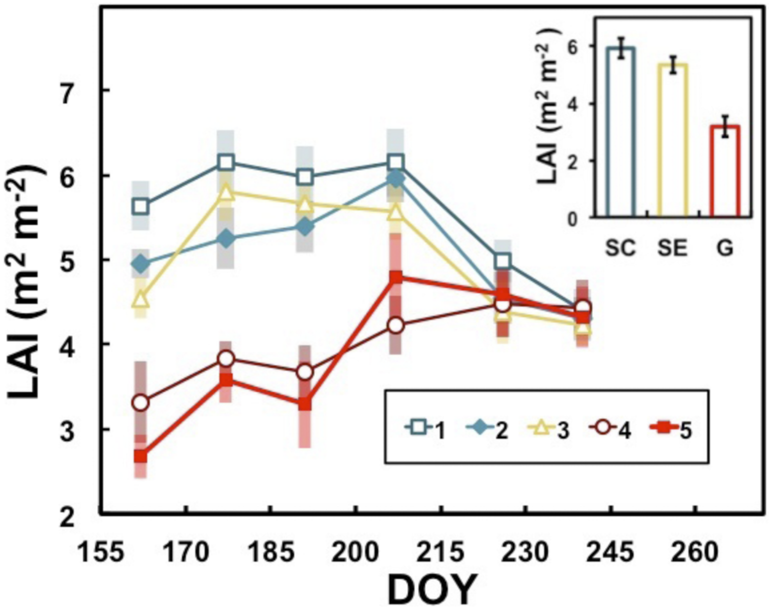

Fig. 6. Mean changes (±1 SE) in LAI from June–September, 2009 for each equidistant transect interval. Intervals 1–3 are the mature shrub while 4–5 are developing clonal stems in the surrounding grass matrix. (Inset) average LAI values for the first 3 sampling periods at the shrub center (SC), shrub edge (SE) and open grassland (G). Error bars denote ±1 SEM.

drummondii and *A. gerardii* is consistent with a large number of studies that have found a vertical separation of tree and grass root systems (Jackson et al. 1996, Weltzin and McPherson 1997, but see Scholes and Archer 1997, Bond 2008, Kulmatiski et al. 2010). However, it is surprising that C. *drummondii* clones measured in the grassland matrix were accessing the same soil water source as the mature shrubs, even up to 5 m from the center of the shrub island ($p > 0.88$ for difference between mature shrub and clones; Fig. 4). We suspect that clonal stems initially access deep soil water through rhizomatous transfer. Survival rates of woody plants in many types of grassland are usually low until root development extends beyond concentrated grass roots in surface soils (Jackson et al. 1996, Partel and Wilson 2002), resulting in competitive release (Walter 1971, Weltzin and McPherson 1997, Jurena and Archer 2003, Bond 2008; Z. Ratajczak *unpublished data*). At KPBS, deep soil water is recharged by winter precipitation and because it is not a primary water source for grasses, this soil-water source is abundant and intra-annually stable (Macpherson 1996, Nippert and Knapp 2007*b*). Therefore, access to deep soil water should allow clonal stems to circumvent the period of water limitation that prevents woody seedling establishment. This can potentially result in a positive feedback system, as niche partitioning allows clonal stems to colonize new patches and then develop their own clonal stems, which can circumvent water competition as well (i.e., Fig. 4). To test this proposed feedback loop, we compared long-term rates of expansion by species with different rooting depths and clonal and non-clonal life forms.

In tallgrass prairie, the two species that account for the majority of woody encroachment (*C. drummondii* and *R. glabra*) are both clonal and more deeply rooted than the dominant grass species (Table 1, Fig. 2). In contrast, there has only been a marginal increase in cover by the clonal, shallow-rooted *P. americana* (McCarron and Knapp 2004) and there has been no increase in cover by non-clonal shallow-rooted species (Table 1, Fig. 2). The increased cover of clonal species was the result of both new shrub establishment, as indicated by an increase in frequency, and the widening of individual shrubs, as indicated by an increase in size index. In fact, all clonal species—even the shallow-rooted *P. americana*—have increased in size index, suggesting that clonality is a key trait for determining whether woody species spread within the areas they colonize (rather than enhanced seedling establishment). However, *P. americana* has only increased half as much in size index and frequency as its more deeply-rooted counterparts. These differences are likely attributable to the increased competition with grasses that is inherent to having a shallower root system (Jackson et al. 1996, Nippert and Knapp 2007*a*, *b*). Together, these results suggest that both clonality and deep roots are needed for woody plants to colonize tallgrass prairie and expand substantially within individual patches.

In addition to changes in competition for water, we also found evidence that individual *C. drummondii* may facilitate their own expansion through localized changes in fire frequency/intensity. The short stature of *C. drummondii* does not permit escape from fire through vertical growth, therefore the most likely way for *C. drummondii* to escape fire is to alter fire dynamics. We found that following fire, large portions of fuel goes un-burned at the shrub edge and center, suggesting that few fires carry into the center of the shrub islands (i.e., fire frequency is effectively reduced). Just preceding fires, fuel loads are lower around *C. drummondii* compared to open grasslands and as *C. drummondii* ages, the amount of herbaceous fuel declines at the shrub grass/interface where clones emerge (Fig. 5). Given the key role of herbaceous biomass in determining fire intensity in tallgrass prairie (Gibson et al. 1990) and elsewhere (Ansley et al. 1998, van Wilgen et al. 2003, Tidwell et al. 2009), these changes in fuel should also reduce fire intensity around shrub islands. Since fire is one of the primary factors limiting shrub establishment in tallgrass prairie and other grasslands (Scholes and Archer 1997, Roques et al. 2001, Briggs et al. 2005, Bond 2008), the creation of a low fire frequency/intensity zone around shrubs should decrease the mortality of mature and clonal shrub stems, which would contribute to the clonal expansion described above. Indeed, reductions of fuel by woody vegetation have been shown to result in positive feedbacks in savanna models (Scholes and Archer 1997, D'Odorico et al. 2006) and localized fuel alterations have been shown to reduce fire mortality for woody plants in other grasslands (Tidwell et al. 2009).

In contrast to changes in water competition and fire, we found that changes in light availability do not appear to contribute directly to clonal stem establishment. If emerging *C. drummondii* clones could reduce light availability early in their development, this would limit grass growth and thereby, total water and nutrient uptake by grasses (e.g., Knapp and Seastedt 1986). However, LAI values were low where developing clones predominated (Fig. 6) and similar to those measured in open tallgrass prairie during the same time (Nippert et al. 2011). Although light interception might not have a direct effect, changes in light availability may indirectly contribute to the subsequent expansion of shrubs. LAI values inside the mature shrub and at the shrub edge were high early in the growing season (Fig. 6), which is a critical growth period for competing C_4 grasses (Knapp et al. 1993, Nippert and Knapp 2007*a*). Because light availability limits productivity in tallgrass prairie (Knapp and Seastedt 1986), these differences in LAI are probably partially responsible for the observed decline in fuel outlined above (Fig. 5).

Conclusion

The combination of long-term and physiological data presented in this study provides evidence that positive feedbacks contribute to the woody encroachment of tallgrass prairie, but by different mechanisms than those reported in other systems. The cover of deep-rooted clonal species—*C. drummondii* and *Rhus glabra*—has increased substantially over the last 25 years, whereas the cover of non-clonal and shallow-rooted species has not (Table 1). Clonal expansion has been an important driver of this increase in cover; if the average size of *C. drummondii* were the same size as it was from 1983–1985 (the beginning of the data-set) the contemporary aerial coverage would be only 6% of its current site coverage. Thus, the increasing cover of woody plants in tallgrass prairie is largely the result of expansion by established shrubs, rather than the more commonly reported pattern where encroachment facilitates establishment of new individuals (i.e., Archer et al. 1988, Schlesinger et al. 1990, Ravi et al. 2007, Wookey et al. 2009, D'Odorico et al. 2010).

Many potential positive feedback mechanisms in tallgrass prairie have already been explicitly or implicitly refuted, including grazing pressure and shrub-mediated changes in water/nitrogen availability (reviewed in Briggs et al. 2005). Based on the shared rooting characteristics of encroaching species and noted changes in herbaceous fuels, we propose the following positive feedback loop for shrub encroachment of tallgrass prairie: (1) global change facilitates initial *C. drummondii* establishment; (2) *C. drummondii* develops deep roots and reduces herbaceous fuel concentrations; (3) *C. drummondii* extends clonal stems into surrounding patches; (4) a high percentage of clonal stems survive and mature because they can use deep soil water and are less susceptible to fire; (5) now mature clonal stems develop deep roots and produce new clonal stems, allowing them to expand into new patches. To date, some shrubs have reached an area of 200 m^2 in this way (Z. Ratajczak, *unpublished data*). As far as we are aware, these mechanisms have not been reported for other systems where woody encroachment of grasslands is occurring. This disparity reflects the unique demographic barriers of mesic North American grasslands (Dalgleish and Hartnett 2006) and that most studies of encroachment feedbacks have focused on drier ecosystems or modeled fire-feedbacks for larger scales (Schlesinger et al. 1990, Scheffer et al. 2001, D'Odorico et al. 2006, Ravi et al. 2007, Wookey et al. 2009, Baudena et al. 2010, D'Odorico et al. 2010).

While the mechanisms underlying encroachment of different grasslands may vary, many examples of encroachment exhibit a pattern of rapidly increasing woody coverage and sustained encroachment (Schlesinger et al. 1990, Briggs et al. 2005, Wookey et al. 2009), which is diagnostic of bi-stability (Scheffer et al. 2001). Notably, the mechanisms that facilitate woody encroachment of tallgrass prairie represent an inversion of the mechanisms that maintain grass dominance in mesic grasslands (i.e., intensified competition for water and increased fire intensity; Scholes and Archer 1997, Knapp et al. 1998, Sankaran et al. 2005, Bond 2008, Staver et al. 2011). Taken together with the observation that current encroachment of tallgrass prairie occurs despite historical fire frequencies (Briggs et al. 2005), this contrast highlights the likely possibility that tallgrass prairie is a bi-stable system as well.

This and other studies (Schlesinger et al. 1990, D'Odorico et al. 2006, Ravi et al. 2007, Wookey et al. 2009, Baudena et al. 2010, D'Odorico et al. 2010, Staver et al. 2011) suggest that woody plants have a strong propensity for expansion into grasslands following initial shrub establishment. Therefore, to separate the mechanisms of initial establishment from trajectories of woody encroachment, future work needs to identify how global change phenomena are affecting rates of recruitment from seedling to adult stages. Because woody encroachment of tallgrass prairie occurs even in areas with greater fire intensities than those that existed prior to European settlement (e.g., Knapp et al. 1998, Briggs et al. 2005), we suspect that global drivers such as CO_2 emissions and N-deposition may be inciting the initial establishment of shrubs in tallgrass prairie.

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