

Vegetation dynamics in a *Quercus-Juniperus* savanna: An isotopic assessment

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Abstract. Woody plants are increasing in many grassland and savanna ecosystems around the world. As a case in point, the Edwards Plateau of Texas, USA, is a vast region (93 000 km²) in which rapid woody encroachment appears to be occurring. The native vegetation (prior to the Anglo-European settlement 150 - 200 yr ago) and the biogeochemical consequences of woody encroachment in this region, however, are poorly understood. To assess these matters we measured plant and soil $\delta^{13}\text{C}$, soil organic C and soil N content from grasslands and two important woody patch types (mature *Quercus virginiana* clusters and *Juniperus ashei* woodlands) in this region. Soil $\delta^{13}\text{C}$ values showed that relative productivity of C₃ species has increased in grassland and both woody habitats in recent times. $\delta^{13}\text{C}$ of SOC in grasslands and *Q. virginiana* clusters increased with depth from the litter layer to 30 cm (grasslands = -21 to -13‰; *Q. virginiana* clusters = -27 to -17‰) and were significantly different between habitats at all depths, indicating that *Q. virginiana* has been a long-term component of the landscape. In *J. ashei* woodlands, soil $\delta^{13}\text{C}$ values (at 20 - 30 cm depth) near the woodland edge (-13‰) converged with those of an adjacent grassland (-13‰) while those from the woodland interior (-15‰) remained distinct, indicating that the woodland has been present for many years but has recently expanded. Concentrations and densities of SOC and total N were generally greater in woody patches than in grasslands. However, differences in the amount of SOC and N stored beneath the two woody patch types indicates that C and N sequestration potentials are species dependent.

Keywords: ¹³C natural abundance; C₃; C₄; CAM; Soil organic carbon; Soil total nitrogen; Stable carbon isotope; Woody plant encroachment.

Nomenclature: Jones et al. (1997).

Abbreviations: SOC = soil organic carbon; SOM = soil organic matter.

Introduction

Savannas are dynamic and patchy ecosystems in which the composition, distribution and abundance of the woody and herbaceous patches are strongly influenced by variation in climate, fire, soils and herbivory (Huntley & Walker 1982; Sarmiento 1984; Skarpe 1992; Belsky & Canham 1994; Scholes & Archer 1997). Many savannas throughout the world have experienced a dramatic increase in woody plant cover over the past 100-200 years (Archer 1994; McPherson 1997; Van Auken 2000), driven primarily by intensified livestock grazing and reduced fire frequency (Archer et al. 1995), although elevated atmospheric CO₂ concentration (Polley et al. 1996) and increased atmospheric nitrogen deposition (Köchy & Wilson 2001) may also contribute. This change in ecosystem structure has strong potential to modify biogeochemistry at both ecosystem (Archer et al. 2001; Jackson et al. 2002) and global (Schlesinger et al. 1990; Goodale & Davidson 2002) scales. Ecosystem level studies have generally indicated that soil C and N increase following woody encroachment into grasslands (e.g. Jackson et al. 1990; Mordelet et al. 1993; San Jose et al. 1998; Geesing et al. 2000; Archer et al. 2001). However, one study has shown that densities of these elements may decrease following woody invasion into grasslands with mean annual precipitation > 600 mm (Jackson et al. 2002). Recent estimates suggest that woody encroachment may represent a sink for 0.12 Pg-C.yr⁻¹ (1 Pg = 10¹⁵ g) in the USA alone (Houghton et al. 2000; Pacala et al. 2001) and perhaps as much as 0.8 Pg-C.yr⁻¹ globally (Tilman et al. 2000).

Although woody plant encroachment is a general phenomenon of many contemporary savannas, not all woody species present in savannas show this increase and, indeed, some appear to be stable or declining in abundance (Allen-Diaz et al. 1999; van de Vijver et al. 1999; Weltzin & McPherson 1999). A number of stud-

ies have documented the rates and patterns of woody species that are increasing in savannas (Archer et al. 1988; Brown & Carter 1998; Skowno et al. 1999; Ansley et al. 2001). Less attention, however, has been paid to characterizing the patch dynamics of invasive and non-invasive native woody species within the same ecosystem.

The Edwards Plateau of central Texas (93000 km²), USA is covered with savannas and parklands dominated by two woody species: *Quercus virginiana* var. *fusiformis* and *Juniperus ashei* (McMahan et al. 1984). *Q. virginiana* var. *fusiformis* is a sprouting, fire resistant species (Muller 1951) that is thought to have been common in upland grasslands and savanna parklands for centuries (Olmstead 1857; Buechner 1944). Its populations, however, appear to have remained static or declined in recent times (Russell & Fowler 1999). In some cases it has been replaced by *J. ashei* (Smeins & Fuhlendorf 1997; Wu et al. 2001), a non-sprouting, fire sensitive species (Fonteyn et al. 1988; Fuhlendorf et al. 1996), which is thought to have been restricted to fire protected refugia (e.g. rocky outcrops, steep cliffs or drainages) at times in the past (Foster 1917; Smeins 1980; Terletzky & Van Auken 1996). In recent times, however, *J. ashei* appears to have invaded many grasslands and open parklands (Smeins & Merrill 1988; Blomquist 1990; Van Auken 1993; Fuhlendorf & Smeins 1997; Wu et al. 2001). This invasion of *J. ashei* into native grasslands appears to have been accompanied by an increase in grazing tolerant herbaceous C₃ species, perhaps in response to chronic or intense grazing by domestic livestock (Smeins & Merrill 1988; Fuhlendorf & Smeins 1997).

At present, evidence for the historical distribution and abundance of these two prominent woody species is largely anecdotal and, therefore, often biased, imprecise and sometimes even contradictory (Smeins 1980; Smeins et al. 1997). Growth rings from large *Q. virginiana* and *J. ashei* trees in this region are difficult to obtain and interpret (Van Auken 1993; Russell & Fowler 1999). Although analyses of aerial photographs have documented recent increases (e.g. 1950 - present) in woody plant cover on the Edwards Plateau (Blomquist 1990; Wu et al. 2001), they were not able to address the status of woody vegetation at, or prior to, settlement. However, stable carbon isotope ratios ($\delta^{13}\text{C}$) of soil organic carbon (SOC) can be used to infer vegetation change in mixed C₃/C₄ ecosystems over longer periods of time (Stout & Rafter 1978; Dzurec et al. 1985; Boutton 1996). Previous studies have used the stable carbon isotope composition of vegetation and SOC to document the recent invasion of woody C₃ plants into C₄ dominated grasslands (McPherson et al. 1993; Schwartz et al. 1996; Boutton et al. 1998), as

well as the historical decline of C₃ vegetation in communities that are currently dominated by C₄ plants (Hendy et al. 1972; Dzurec et al. 1985; Victoria et al. 1995). Because the mean residence time of bulk SOC generally increases from ca. 50 - 100 yr in surface horizons (0-15 cm) to ca. 200 - 500 yr at depths of 15-30 cm (Scharpenseel & Neue 1984; Boutton et al. 1998; Trumbore 2000), isotopic analyses of relatively shallow soil depths can be used to investigate vegetation change over the recent centuries.

In this study we used carbon isotopic and elemental analyses of plants and soils to investigate historical vegetation changes and woody patch dynamics in a subtropical *Q. virginiana*-*J. ashei* savanna in the eastern Edwards Plateau of Texas, and the consequences of these vegetation changes for soil carbon and nitrogen storage. Specifically, we tested the hypotheses that: (1) the relative contribution of C₄ species to productivity in upland grasslands has decreased over the recent past; (2) discrete *Q. virginiana* clusters have been long-term, persistent woody patches in upland savanna parklands; (3) mature *J. ashei* woodlands were historically associated with steep cliffs or drainages but the boundaries of these woody patches with grasslands have expanded over the recent past and (4) relative to grasslands, *Q. virginiana* clusters and *J. ashei* woodlands represent sites of increased soil carbon and nitrogen storage.

Methods

Study area

Studies were conducted at the 1700 ha Southwest Texas State University Freeman Ranch (29° 56' N, 98° W; max. altitude 274 m a.s.l.) located in the eastern Edwards Plateau of Texas. Mean annual temperature and precipitation are 19.4 °C and 857 mm, respectively (Dixon 2000). Soils have been classified in the Rump-Comfort association and the Comfort-Rock outcrop complex (Anon. 1984), which are shallow (typically ≤ 30 cm), well drained Argiustolls that have developed over indurated limestone. These soils are near neutral in pH, with mean clay and sand contents of 40.3 and 22.5%, respectively, in the upper 0 - 20 cm. (Jessup 2001).

Although long-term records are incomplete, it is thought that the Freeman Ranch has experienced moderate to heavy grazing pressure since the mid 1800s. In general, the contemporary vegetation of the site is typical of this region: savanna parklands occupy the uplands while evergreen woodlands and deciduous forest occur on slopes and along drainages (Barnes et

al. 2000). Upland grasslands are currently vegetated by a sparse canopy of grazing tolerant perennial grasses, i.e. *Nassella leucotricha* (C₃) and *Bouteloua rigidisetata* (C₄) and weedy C₃ dicots, e.g. *Croton monanthogynus* and *Gutierrezia texana*. *Q. virginiana* trees in upland habitats are present within grasslands as part of discrete tree-shrub clusters, which include a central oak and a woody understorey of up to 11 species of shrubs or small trees (including *J. ashei*), all of which exhibit the C₃ photosynthetic pathway (Phillips & Barnes 2003). Common herbaceous understorey species include the C₃ graminoids *N. leucotricha* and *Carex planostachys*. Some cacti (primarily *Opuntia leptocaulis*) also occur, while epiphytic CAM species (*Tillandsia recurvata* and *T. usneoides*) may be abundant in these oak clusters. Although *J. ashei* is abundant in savanna parklands and mixed woodlands throughout the Freeman Ranch, field observations and analyses of aerial photographs dating back to the 1950s indicated that woodlands containing mature (i.e. potentially old-growth) patches of *J. ashei* were rare on this property. Putative mature *J. ashei* patches appear to be associated with steep cliffs and escarpments and are dominated by relatively large, widely spaced *J. ashei* trees, with a sparse herbaceous understorey dominated by *C. planostachys*.

Field sampling

Sampling in upland savanna parklands was conducted in separate pastures ($n = 6$). Four of the six pastures were grazed by livestock (primarily cattle) at the time of sampling, while two pastures had not experienced livestock grazing within the past 5 yr. Within each pasture, a single sampling location was chosen that consisted of a discrete *Q. virginiana* cluster (typically containing a single, large *Q. virginiana*; mean DBH = 1.3 m) and a nearby grassland area. These sampling locations were relatively flat (slope < 4°) and occurred at least 100 m from major drainages. Due to the rarity of mature *J. ashei* woodlands, all sampling for this habitat was confined to a single location at the top of a steep, north-facing cliff that bordered an intermittent drainage. At this location, five 50-m transects were established parallel to the cliff edge: three within the *J. ashei* woodland: T1 20 m from the cliff edge; T2 80 m from the edge and T3 100 m from the edge at the ecotone with an adjacent grassland; the remaining two transects T4 and T5 were established within the adjacent grassland, at distances of 20 m and 80 m from the ecotone, respectively. Within each transect, three sampling sites were established ca. 20 m apart.

To assess the isotopic composition of the above-ground organic matter inputs from current vegetation

(hereafter referred to as 'litter'), woody and herbaceous litter together with live and standing dead herbaceous plant material was collected and pooled from three 0.5 m × 0.5 m plots at each sampling location. Samples from the *Q. virginiana* clusters were taken well within the edge of the oak canopy (1–3 m from the central *Q. virginiana* trunk), while those from grassland habitats were collected 10–30 m from the nearest *Q. virginiana* cluster. In the *J. ashei* woodland, litter samples were collected at 5-m intervals along each transect.

Following the removal of surface litter, soil samples (ca. 55 cm³) were obtained beneath each of the three plots using a soil sampling tube or by excavating pits. The rocky substrate prevented collection of soil below 30 cm at most sites; consequently, samples were collected from four depths: 0–5, 5–10, 10–20 and 20–30 cm. Visual inspection revealed no anomalous soil development (e.g. buried horizons) at any sampling site. As was the case for litter, the three soil samples collected at each location were pooled prior to analysis. Three additional soil cores were taken from each of three *Q. virginiana* and grassland patches, and from T1 of the *J. ashei* woodland, to assess bulk density using the core method (Culley 1993).

Seasonal shifts in the relative biomass contribution from C₃ and C₄ plants are known to occur in mixed prairie systems (Boutton et al. 1980; Ode et al. 1980). Because the current organic matter inputs (litter + standing crop) were collected from our grassland sites during one month of the year (July), we wished to determine if these samples were representative of the overall contribution of C₃ and C₄ species to the annual production in these grasslands. For this test, two 20-m transects located ca. 200 m apart were established within a 5-yr old grazing enclosure. Standing live and dead biomass were clipped and collected from ten 0.5 m × 0.5 m plots (five per transect) in January, April, July and October. These mixed samples were then analysed for δ¹³C as described below.

Elemental and isotopic analyses

Prior to isotopic analysis, plant and soil samples were oven dried at 80 °C for 48 hr. Dried plant tissue was then ground and homogenized in a commercial blender until able to pass through a 0.25-mm sieve. These plant samples were then weighed into tin capsules for δ¹³C, %C and %N measurements.

Dried soil was first passed through a 2-mm sieve where large rocks and roots were removed. Soil samples were then ground to pass through a 0.25 mm sieve and re-mixed by hand for 2 min to homogenize samples. From each soil sample, a sub-sample was

weighed into silver capsules and treated with 3N HCl until no reaction occurred (Nieuwenhuize et al. 1994) to remove inorganic carbon (CaCO_3). This subsample was used to measure percentage organic carbon content on a whole soil basis. A second subsample (not subjected to acid treatment) was weighed into tin capsules to measure percentage total nitrogen. Finally, a third subsample was used for $\delta^{13}\text{C}$ determination of older, more resistant, humified forms of soil organic matter. Fine roots, leaf litter and other undecomposed organic debris (i.e. the 'light fraction') were removed from this subsample by flotation in a saturated NaCl solution (density = 1.2 g.cm^{-3}) (Dzurec et al. 1985; McPherson et al. 1993; Wolf et al. 1994), the soil was then washed with distilled water, weighed into silver capsules and treated with 3N HCl.

Measurements of $\delta^{13}\text{C}$, %C and %N were made using an elemental analyzer (Carlo Erba EA-1108, Lakewood, NJ, USA) interfaced with a Delta Plus plusotope ratio mass spectrometer (ThermoFinnigan, Bremen, Germany) operating in continuous flow mode. Precision for the $\delta^{13}\text{C}$ measurements was $<0.1\%$. $\delta^{13}\text{C}$ values were expressed relative to the V-PDB standard (Coplen 1995).

Estimates of the proportion of carbon in litter derived from C_3 , C_4 or C_4+CAM species were made using a mass balance equation:

$$\delta^{13}\text{C} = (\delta^{13}\text{C}_{\text{C}_4}) (\chi) + (\delta^{13}\text{C}_{\text{C}_3}) (1 - \chi) \quad (1)$$

where $\delta^{13}\text{C}$ is the $\delta^{13}\text{C}$ value of the mixed sample, $\delta^{13}\text{C}_{\text{C}_4}$ is the average $\delta^{13}\text{C}$ value of known C_4 plants (or CAM components where appropriate), $\delta^{13}\text{C}_{\text{C}_3}$ is the mean $\delta^{13}\text{C}$ value of known C_3 species, χ is the proportion of carbon derived from C_4 (or CAM) species and $1 - \chi$ is the proportion of carbon derived from C_3 species. Standard error values for source proportion estimates were calculated according to Phillips and Gregg (2001). To determine $\delta^{13}\text{C}_{\text{C}_4}$ and $\delta^{13}\text{C}_{\text{C}_3}$, $\delta^{13}\text{C}$ measurements were determined for foliar and stem tissue of all major C_4 , CAM and C_3 species of the three sampling habitats (Table 1).

Samples from herbaceous plants consisted of all live + dead above-ground tissue, while samples from woody plants were derived from a mixture of live green foliage plus dead leaves and small diameter stem material collected from beneath the plant. For mass balance calculations in grasslands and the *J. ashei* woodland, the mean $\delta^{13}\text{C}$ value of C_4 grasses (-14.0% ; Table 1) was used for the 100% C_4 ($\delta^{13}\text{C}_{\text{C}_4}$) endpoint. Because CAM rather than C_4 plants were present in the *Q. virginiana* clusters, the $\delta^{13}\text{C}_{\text{C}_4}$ value for this habitat was calculated from the $\delta^{13}\text{C}$ of CAM species present and weighted according to their approximate abundance, i.e.:

$$\delta^{13}\text{C}_{\text{C}_4} = [(3 \times \text{Ts } \delta^{13}\text{C}) + (1 \times \text{Ol } \delta^{13}\text{C})]/4 = (-15.5\%)$$

where Ts = *Tillandsia* spp. and Ol = *Opuntia leptocaulis*. The 100% C_3 ($\delta^{13}\text{C}_{\text{C}_3}$) endpoint for grasslands was the mean $\delta^{13}\text{C}$ for all C_3 herbaceous (grass and forb) species (-28.8%), while that for the *Q. virginiana* and *J. ashei* habitats was the pooled mean $\delta^{13}\text{C}$ of herbaceous and woody C_3 species (-28.3%).

Statistical analyses

Because of differences in sampling design, degree of replication, and site conditions, the soil and litter data from grassland and *Q. virginiana* habitats were analysed separately from the *J. ashei* woodland data. For purposes of comparison, however, we show data from all three habitats together. All variables from the *Q. virginiana* and grassland habitats were initially tested in a multivariate ANOVA and were found to differ significantly ($P < 0.05$) among habitats. Separate univariate ANOVA tests were then performed on each dependent variable. For these analyses, data were analysed in a split plot factorial design, where habitat was a fixed main plot effect and depth increment was a fixed split-plot effect. If the assumption of multisample sphericity was not tenable for the split-plot factorial designs, the *F*-statistics were tested using adjusted (more conservative) critical values (Kirk 1995).

The $\delta^{13}\text{C}$ data from the *J. ashei* woodland study were analysed as a completely randomized factorial design (Kirk 1995), with site and depth as fixed effects. Simple effects contrasts were performed using Student's *t*-test (if contrasts were orthogonal) or Holm's sequentially rejective Bonferroni test (if contrasts were non-orthogonal) (Kirk 1995). In most cases, the assumption of homogeneity of variances was not met and thus the *t*-statistic was replaced with the *t'*-statistic in either of the two previous tests and used with Welch's modified degrees of freedom (Kirk 1995). In comparisons between *Q. virginiana* cluster and grassland habitats, differences were considered statistically significant when $P < 0.05$.

Results

Soil and litter chemistry

Soil and litter associated with *Q. virginiana* clusters, the *J. ashei* woodland and upland grasslands varied considerably with respect to organic carbon and total nitrogen. When mean values were calculated over depth (0 - 30 cm), both C and N concentrations (Fig. 1a, b) were ca. twofold higher ($P = 0.002$) in soils beneath *Q. virginiana* ($C = 55 \text{ g.kg}^{-1}$; $N = 4 \text{ g.kg}^{-1}$) than in nearby grasslands ($C = 29 \text{ g.kg}^{-1}$; $N = 2 \text{ g.kg}^{-1}$), while soil [C] and [N] were intermediate in the *J. ashei* woodland ($C = 48 \text{ g.kg}^{-1}$; $N = 3 \text{ g.kg}^{-1}$). Both soil C and N decreased significantly ($P < 0.05$) with depth in all habitats, and habitat differences were greatest in surface (0 - 5 cm) layers.

Despite grassland patches having greater soil (0 - 10 cm) bulk density values than in *Q. virginiana* clusters or the *J. ashei* woodland (0.9, 0.5 and 0.6 g.cm^{-3} , respectively), soils (0-10 cm) beneath *Q. virginiana* clusters contained a significantly greater ($P < 0.05$) density of organic carbon ($5802 \pm 519 \text{ g.m}^{-2}$) than did those of grasslands ($3757 \pm 335 \text{ g.m}^{-2}$), while SOC for the *J. ashei* woodland ($4384 \pm 85 \text{ g.m}^{-2}$) was intermediate (Fig. 1c). Soil total N density (Fig. 1d) for this depth was also significantly greater in live oak clusters ($446 \pm 51 \text{ g.m}^{-2}$) than grasslands ($295 \pm 26 \text{ g.m}^{-2}$), but was comparable between grasslands and the juniper woodland ($287 \pm 14 \text{ g.m}^{-2}$).

Litter C:N ratios were statistically comparable ($P > 0.05$) between *Q. virginiana* clusters and grasslands, (mean = 28 and 33, respectively), but were generally higher and more variable in the *J. ashei* woodland (range = 31 to 50). Soil C:N ratios were significantly lower ($P < 0.01$) than surface litter values in all habitats, but showed no significant variation ($P > 0.05$) between soil depths or habitats (data not shown).

Stable isotopes in grasslands and *Q. virginiana* clusters

Above-ground standing crop biomass of the ungrazed grassland ranged from 120 g.m^{-2} in January to 290 g.m^{-2} in July, mean value was 179 g.m^{-2} over the entire growing season (Fig. 2). The majority (77%) of the annual above-ground production was contributed by C_4 plants, but the relative C_3/C_4 composition varied over time. Whereas C_4 contribution was greatest in autumn (October 87%), C_3 contribution peaked in the early spring (April 43%). The mean $\delta^{13}\text{C}$ value for the year, when weighted according to production, was the same as the mean for the July samples (i.e. -17.4‰). Thus, it was concluded that the $\delta^{13}\text{C}$ values of grassland litter samples that were collected in July provided a reason-

Table 1. $\delta^{13}\text{C}$ values of above-ground parts (live and dead) of plant species in upland grasslands, upland *Quercus virginiana* var. *fusiformis* clusters and *Juniperus ashei* woodlands at Freeman Ranch. Replicates were collected from different seasons and/or sites to capture variation within a species. $N = 2$ for all species, except those denoted by * for which $n = 3$. ‡Lichen samples represent a mixture of dominant fruticose, foliose and crustose lichen species occurring on *Q. virginiana* in the study area. Samples denoted by ** represent a mixture of common species within a genera.

Life form / Species	Mean	s.e.
C_3 woody		
<i>Berberis trifoliolata</i>	-27.6	0.7
<i>Celtis laevigata</i>	-28.1	0.4
<i>Diospyros texana</i>	-28.6	0.3
<i>Forestiera pubescens</i>	-26.7	0.5
<i>Juniperus ashei</i> *	-26.7	0.2
<i>Quercus virginiana</i> var. <i>fusiformis</i> *	-27.1	0.3
<i>Ulmus crassifolia</i>	-27.2	0.8
C_3 forb		
<i>Ambrosia psilostachya</i>	-29.4	0.4
<i>Croton fruticosus</i>	-28.7	0.4
<i>Croton monanthogynus</i>	-28.7	0.3
<i>Gutierrezia texana</i>	-29.3	0.1
<i>Ratibida columnifera</i>	-28.5	0.4
<i>Wedelia texana</i>	-28.6	0.1
C_3 graminoid		
<i>Bromus</i> spp.**	-30.5	0.3
<i>Carex planostachys</i>	-28.0	0.3
<i>Elymus</i> spp.**	-29.4	0.1
<i>Nassella leucotricha</i> *	-28.4	0.6
<i>Panicum oligosanthes</i>	-27.8	0.5
Mean of all C_3 species	-28.3	0.2
Mean of herbaceous C_3 species only	-28.8	0.2
C_4 grass		
<i>Andropogon gerardii</i> *	-12.3	0.2
<i>Aristida</i> spp.**	-14.6	0.7
<i>Bothriochloa ischaemum</i>	-14.9	1.0
<i>Bothriochloa laguroides</i>	-12.8	0.1
<i>Bouteloua curtipendula</i>	-14.4	0.1
<i>Bouteloua hirsuta</i>	-14.1	0.8
<i>Bouteloua rigidiseta</i>	-15.1	0.6
<i>Buchloë dactyloides</i>	-15.7	1.0
<i>Eragrostis</i> spp.**	-13.6	0.3
<i>Schizachyrium scoparium</i>	-13.1	0.1
<i>Sorghastrum nutans</i>	-13.6	0.4
Mean of C_4 species	-14.0	0.3
CAM		
<i>Opuntia engelmannii</i>	-13.5	0.2
<i>Tillandsia</i> spp.**	-16.1	0.3
Mean of CAM species	-14.8	1.3
Other		
Lichen‡	-22.3	0.3

able estimate of integrated annual C_3/C_4 composition in this habitat.

The $\delta^{13}\text{C}$ of current above-ground organic matter inputs (i.e. litter) differed significantly ($P < 0.05$) between grasslands and *Q. virginiana* clusters (Fig. 3a). Mean $\delta^{13}\text{C}$ values of litter for these two habitats ($-20.8 \pm 1.3\text{‰}$ for grasslands and $-26.7 \pm 0.2\text{‰}$ for *Q. virginiana* clusters), yielded calculated mean (\pm s.e.) C_3 contents of 46 ± 8 and $88 \pm 3\%$, respectively. Because C_4 grasses

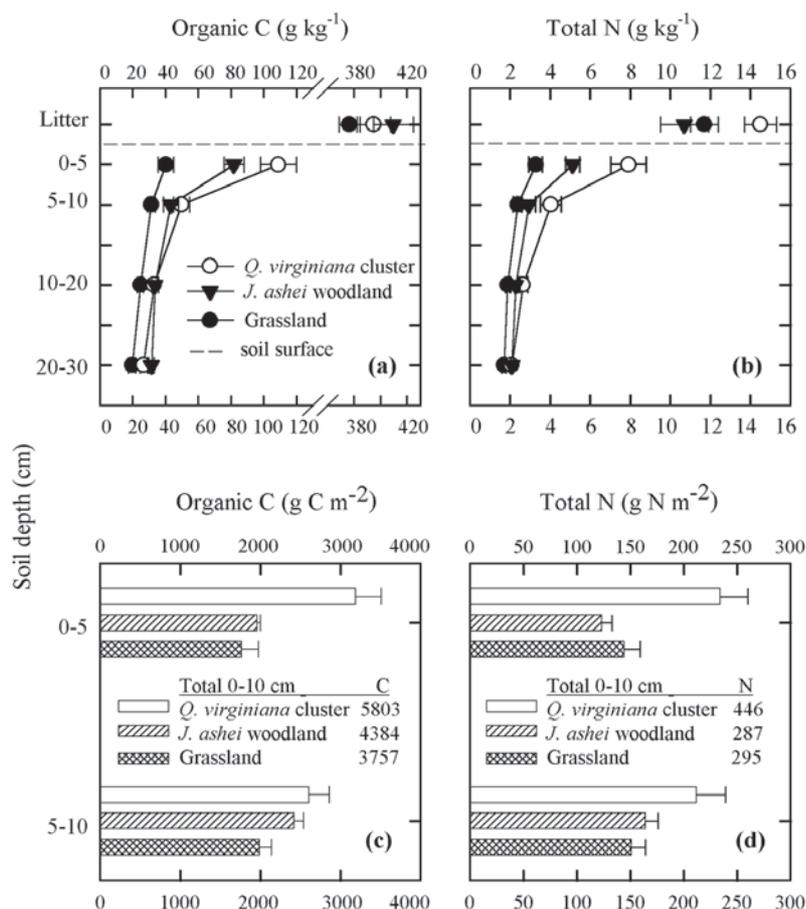


Fig. 1. a. Organic carbon concentration, b. total nitrogen concentration, c. organic carbon density and d. total nitrogen density with soil depth beneath *Q. virginiana* clusters, *J. ashei* woodland transect T1 and grasslands in the *Q. virginiana*-*J. ashei* savanna. Data are means \pm 1 s.e.; $n = 5$ for *Q. virginiana* clusters and grasslands, $n = 3$ for *J. ashei* woodland.

were not observed within the *Q. virginiana* clusters, all of the modern non-C₃ contribution to this habitat (ca. 12%), was likely derived from the CAM species, particularly *Tillandsia* spp.

Soil $\delta^{13}\text{C}$ increased significantly with depth ($F_{4,40} = 86.79$, $P < 0.001$) in both habitats (Fig. 3a), indicating that the relative productivity of C₄ species was greater historically not only in the grassland patches, but also in the *Q. virginiana* clusters (which currently have no input from C₄ sources). Soil $\delta^{13}\text{C}$ also differed between these two habitats at all depths ($F_{1,10} = 91.97$, $P < 0.001$ for habitat effect; $F_{4,40} = 1.44$, $P = 0.24$ for habitat \times depth interaction), indicative of a long-term presence of the woody *Q. virginiana* patches in these savannas. In the deepest soil increment (20-30 cm), the mean $\delta^{13}\text{C}$ of soil organic C was $-16.7 \pm 0.3\text{‰}$ beneath *Q. virginiana* clusters and $-13.2 \pm 0.1\text{‰}$ beneath grasslands.

Stable isotopes in the *J. ashei* woodland

The $\delta^{13}\text{C}$ values of surface litter from the three transects currently occupied by *J. ashei* woodland (i.e. T1, T2 and T3) were similar to one another (ca. -27‰ ; Fig. 3b), but were more negative ($P < 0.01$) than those of

litter collected from transects in the adjacent grassland (T4 = $-20.3 \pm 0.3\text{‰}$; T5 = $-22.8 \pm 0.4\text{‰}$). These litter $\delta^{13}\text{C}$ values indicate that C₃ species contribute ca. 90% of current above-ground inputs to soil organic matter (SOM) within the woodland and 40-60% in the nearby grassland. As was the case for *Q. virginiana* habitats, soil $\delta^{13}\text{C}$ values for all transects at this site increased significantly with depth ($P < 0.01$), indicating that relative C₄ productivity was greater historically throughout this *J. ashei* woodland. Despite clear differences between the litter $\delta^{13}\text{C}$ of the *J. ashei* woodland and adjacent grassland sites, soil $\delta^{13}\text{C}$ values for the outermost woodland transects (T2 and T3 = ca. -13.5‰) converged with those of the grassland sites (T4 not shown and T5 = ca. -13.7‰), such that at 20-30 cm, soil $\delta^{13}\text{C}$ values from these four transects were similar to one another, but significantly different ($P < 0.05$) from those of the most interior woodland transect (T1 = $-15.9 \pm 0.7\text{‰}$). This indicates that, although *J. ashei* has had a long-term presence at the most interior woodland site, the outer portions of this woodland were formed more recently.

Discussion

Historical vegetation and woody patch dynamics

The potential vegetation within grasslands of the Edwards Plateau has been classified as grading from tall-grass prairie in the east to mixed prairie in the west (Allred 1956) and it is widely believed that C_4 tall- and mid-grasses were historically much more prevalent in this region than they are today (Launchbaugh 1955; Anon. 1984; Riskind & Diamond 1988). Although our research cannot address the precise species composition of historical grasslands in this region, the findings support the hypothesis that relative C_4 productivity is much less today than previously. This reduction is perhaps a result of chronic grazing pressure by domestic livestock following Anglo-European settlement (Smeins & Merrill 1988; Fuhlendorf & Smeins 1997). Previous research has shown that continuous grazing reduced C_4 grass contribution to SOM in a tall-grass prairie in east-central Texas (Boutton et al. 1993) and in subtropical grasslands in southern Texas (Boutton et al. 1998).

The finding that soil $\delta^{13}C$ from *Q. virginiana* clusters had a stronger C_3 signature than grasslands throughout the upper 30 cm of the profile (radiocarbon dating of similar soils near this region showed mean residence times of 40 - 100 yr in the upper 15 cm of the profile and 200 - 500 yr at 15 - 30 cm for bulk soil organic carbon (Boutton et al. 1998)) supports the hypothesis that upland *Q. virginiana* patches have been long-term components of this savanna ecosystem (Olmstead 1857; Buechner 1944).

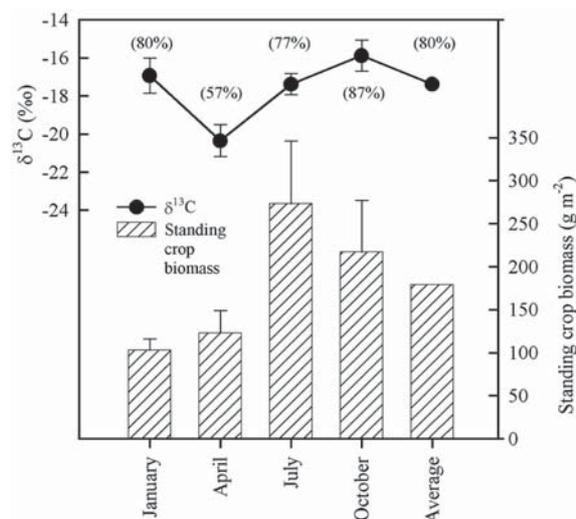


Fig. 2. Mean standing crop biomass and associated $\delta^{13}C$ values in grasslands of the *Q. virginiana*-*J. ashei* savanna. % C_4 contribution (determined by mass balance) for each sample date is shown adjacent to the appropriate $\delta^{13}C$ value. Samples were taken in a 5-yr grazing enclosure between 30-07-1999 and 30-04-2000. Data are means \pm 1 s.e.; $n = 10$. The mean $\delta^{13}C$ value was calculated by weighting the $\delta^{13}C$ for each sample date by its respective standing crop biomass.

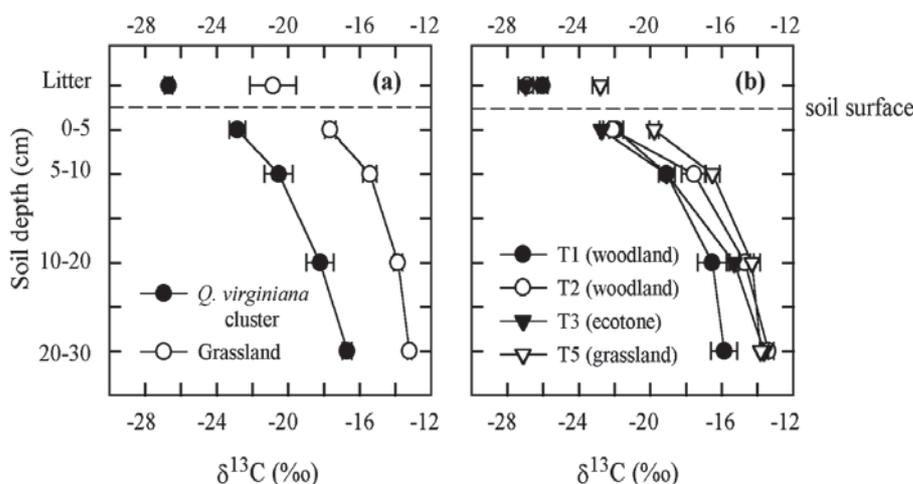


Fig. 3. Mean $\delta^{13}C$ values for litter and soils in (a) *Q. virginiana* clusters and grasslands and (b) *J. ashei* woodland in the *Q. virginiana*-*J. ashei* savanna. In (b), transect T1 is the most interior woodland site (at the cliff edge), T2 is within the woodland (80 m from the cliff edge), T3 is within the woodland at the ecotone of the *J. ashei* woodland and grassland, T5 is within the grassland (80 m from the ecotone). The profile for T4 (grassland, 20 m from the ecotone) is similar to T5 and is not shown for clarity. Data are means \pm 1 s.e.; $n = 6$ in (a) and $n = 3$ in (b).

The enrichment in soil $\delta^{13}\text{C}$ with depth beneath *Q. virginiana* patches probably reflects C_3/C_4 compositional shifts that occurred during development and expansion of these tree-shrub clusters (e.g. the growth of the live oak and understory shrubs progressively contributed more C_3 biomass while simultaneously reducing C_4 biomass by shading out grasses). This woody cluster formation has been hypothesized to occur similarly in other savannas (Archer et al. 1988; Fowler 1988) and was probably facilitated in this region by a reduction in fire frequency following Anglo-European settlement (Fuhlendorf & Smeins 1997).

Within the *J. ashei* woodland, we found that soil $\delta^{13}\text{C}$ profiles from the most interior portions were significantly lower than those from an adjacent grassland throughout the entire soil profile. The clear C_3 isotopic signal in the innermost part of the woodland (at depths where bulk SOC has a mean residence time > 200 yr (Boutton et al. 1998)), together with the general characteristics of the inner woodland (i.e. widely spaced and large *J. ashei* trees with basal diameters > 1 m), suggest that the invasive *J. ashei* was already present at this site prior to Anglo-European settlement. However, our data also support the hypothesis that the boundary of this *J. ashei* woodland has not been stable, since soil $\delta^{13}\text{C}$ profiles from the outer woodland converged with the grassland profiles at depth. These data indicate that the *J. ashei* woodland has recently encroached into surrounding grassland and supports the general notion that at times in the past when fires set by lightning strikes and/or Native Americans were common, *J. ashei* was restricted to relatively cool and moist sites (e.g. near steep cliffs or drainages) similar to that of the innermost portion of this woodland (Foster 1917; Smeins 1980; Terletzky & Van Auken 1996). These results agree with findings from demographic analyses (Van Auken 1993), long-term vegetation studies (Smeins & Merrill 1988) and analyses of aerial photographs (Blomquist 1990; Wu et al. 2001) which indicate that *J. ashei* has been increasing in abundance and distribution in the grasslands of the Edwards Plateau. This increase has been attributed to reductions in fire frequency (Weniger 1984; Smeins et al. 1997) and also coincides with the increase in abundance of other species of *Juniperus* in other regions of Texas (Foster 1917; Ansley et al. 1995) and throughout western North America (Miller 1921; Leopold 1924; Emerson 1932; Cottam & Stewart 1940; Christensen & Johnson 1964; Burkhardt & Tisdale 1969; Briggs et al. 2002).

For each habitat in this study, it is possible that at least part of the observed enrichment in $\delta^{13}\text{C}$ with depth is due to factors unrelated to vegetation change. Others have shown that changes in soil $\delta^{13}\text{C}$ with depth can occur on sites where the vegetation is known to have

been compositionally stable (e.g. Nadelhoffer & Fry 1988; Balesdent et al. 1993). The exact causes of this difference (typically an enrichment with depth of ca. 1 - 3‰) are not completely understood, though a number of possible explanations have been suggested. These include a decrease in the $\delta^{13}\text{C}$ of atmospheric CO_2 , fractionation by microbial decomposers and the addition of relatively enriched root tissue to deeper soils (Boutton 1996; Biedenbender 1999). Garten et al. (2000) found that for several forested locations, this background enrichment was positively correlated with the mean annual temperature of the site. Although our study site has less woody cover than those used by Garten et al. (2000), in order to estimate the background enrichment at our site we combined our temperature data with their regression model, predicting a background enrichment of 3.7‰ for the 20 cm depth. If this background enrichment is accounted for, our interpretations are not affected since we continue to detect significant ($P < 0.01$) shifts in soil $\delta^{13}\text{C}$ with depth in each habitat, and significant differences between grasslands and woody patches.

Woody plant effects on biogeochemistry

The increase in woody plant abundance documented in this study (e.g. expanded range of *J. ashei*) and relative productivity (e.g. increased woody biomass of *Q. virginiana* clusters) has altered ecosystem biogeochemistry. Soils associated with *Q. virginiana* clusters and the *Juniperus ashei* woodland had greater concentrations of SOC and total N than did those of adjacent grassland patches. These findings correspond with those of Marshall (1995) from *Q. virginiana*-*J. ashei* savannas in the more arid, western part of the Edwards Plateau and are in agreement with other studies showing greater C and N concentrations in soils beneath woody plants than in soils of grasslands (e.g. Klopatek 1987; Jackson et al. 1990; McPherson et al. 1993; Hibbard et al. 2001). In addition, densities ($\text{g}\cdot\text{m}^{-2}$) of SOC and total N in the upper 10 cm of the profile were generally greater in soils beneath the woody species than in grassland soils. Other studies report similar patterns at this soil depth (Jackson et al. 1990; Hibbard et al. 2001), which though generally considered 'shallow' represents a considerable fraction of the soil profile for this region given that consolidated limestone in our habitats was usually ≤ 30 cm depth.

The results of our research suggest several conclusions about the history and consequences of woody plant dynamics in these savannas. First, although *Q. virginiana* has been a long-term component of the Edwards Plateau region, if the increase in relative C_3 productivity within *Q. virginiana* clusters documented by our isotopic data reflects increased contribution to

SOM from woody sources via the growth of the central *Q. virginiana* and development of a woody understorey, then these clusters represent sites where SOC and N stores have increased in the last several hundred years. Secondly, our results confirm that, where mechanical clearing or fire have been absent, *J. ashei* woodlands have been expanding in range since Anglo-European settlement, and that this expansion into grazed grasslands appears to be accompanied by increases in SOC, with little or no change to soil N stores. Finally, since SOC and soil N were lower in the mature *J. ashei* woodland than in *Q. virginiana* clusters, if *Q. virginiana* is replaced by *J. ashei* following drought or mechanical clearing (Smeins & Fuhlendorf 1997; Wu et al. 2001) soil C and N stores may be reduced, suggesting that a quantitative assessment of landscape and regional level carbon and nitrogen sequestration associated with woody plant increase in dryland ecosystems (Scholes & Archer 1997; Scholes & Noble 2001; Pacala et al. 2001) requires an understanding of the temporal and spatial dynamics of the specific types of woody plants involved.

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