

Changes in aboveground primary production and carbon and nitrogen pools accompanying woody plant encroachment in a temperate savanna

R. FLINT HUGHES*, STEVEN R. ARCHER†, GREGORY P. ASNER‡, CAROL A. WESSMAN§, CHAD McMURTRY†, JIM NELSON¶ and R. JAMES ANSLEY||

*Institute of Pacific Islands Forestry, USDA Forest Service, PO Box 4370, 60 Nowelo Street, Hilo, HI 96720, USA, †School of Natural Resources, University of Arizona, Tucson, AZ 85721-0043, USA, ‡Department of Global Ecology, Carnegie Institute of Washington, Stanford University, Stanford, CA 94305, USA, §Cooperative Institute for Research in Environmental Sciences & Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309-0216, USA, ¶Department of Plant & Soil Science, University of Kentucky, Lexington, KY 40546-0091, USA, ||Texas Agricultural Experiment Station, PO Box 1658, 11708 Highway 70 South, Vernon, TX 76384, USA

Abstract

When woody plant abundance increases in grasslands and savannas, a phenomenon widely observed worldwide, there is considerable uncertainty as to whether aboveground net primary productivity (ANPP) and ecosystem carbon (C) and nitrogen (N) pools increase, decrease, or remain the same. We estimated ANPP and C and N pools in aboveground vegetation and surface soils on shallow clay and clay loam soils undergoing encroachment by *Prosopis glandulosa* in the Southern Great Plains of the United States. Aboveground *Prosopis* C and N mass increased linearly, and ANPP increased logarithmically, with stand age on clay loam soils; on shallow clays, *Prosopis* C and N mass and ANPP all increased linearly with stand age. We found no evidence of an asymptote in trajectories of C and N accumulation or ANPP on either soil type even following 68 years of stand development. Production and accumulation rates were lower on shallow clay sites relative to clay loam sites, suggesting strong edaphic control of C and N accumulation associated with woody plant encroachment. Response of herbaceous C mass to *Prosopis* stand development also differed between soil types. Herbaceous C declined with increasing aboveground *Prosopis* C on clay loams, but increased with increasing *Prosopis* C on shallow clays. Total ANPP (*Prosopis* + herbaceous) of sites with the highest *Prosopis* basal area were $1.2 \times$ and $4.0 \times$ greater than those with the lowest *Prosopis* basal area on clay loam and shallow clay soils, respectively. *Prosopis* ANPP more than offset declines in herbaceous ANPP on clay loams and added to increased herbaceous ANPP on shallow clays. Although aboveground C and N pools increased substantially with *Prosopis* stand development, we found no corresponding change in surface soil C and N pools (0–10 cm). Overall, our findings indicate that *Prosopis* stand development significantly increases ecosystem C and N storage/cycling, and the magnitude of these impacts varied with stand age, soil type and functional plant traits

Keywords: ANPP, biomass, facilitation, productivity, *Prosopis glandulosa*, sequestration, soil nitrogen, soil organic carbon, tree–grass interactions, woody plant encroachment

Received 22 September 2005; revised version received 24 March 2006; accepted 1 May 2006

Introduction

Land cover change is an important component of global environmental change (Vitousek, 1994; DeFries *et al.*,

2004). Woody encroachment, defined here as the establishment, development and spread of tree or shrub species, is one such change that has occurred over the past century in many grassland/savanna ecosystems of North and South America, Africa and Australia (Van Auken, 2000; Archer *et al.*, 2001; Bowman, 2002). These

Correspondence: R. Flint Hughes, e-mail: fhughes@fs.fed.us

ecosystems occur in both temperate and tropical regions, constitute over 45% of the Earth's land surface (Bailey, 1998), and account for 30–35% of global terrestrial net primary productivity (NPP) (Field *et al.*, 1998). When increasing woody species abundance transforms grasslands into savannas and savannas into shrublands or woodlands, substantial alterations in the sequestration and cycling of carbon (C) and nitrogen (N) are likely to occur.

Woody plant proliferation in grassland/savanna ecosystems has been proposed as a significant terrestrial sink for atmospheric CO₂ (Geesing *et al.*, 2000; Pacala *et al.*, 2001; Scholes & Noble, 2001; Houghton, 2003). Such estimates are, however, characterized by a high degree of uncertainty regarding how the biomass and productivity of herbaceous and woody components interact in response to shifts in plant life form composition. Using modeling approaches, Hibbard *et al.* (2003) estimated that woody proliferation in southern Texas would lead to *Prosopis* woodlands with aboveground C stocks 15–24 times greater than those of grasslands they replaced. Asner *et al.* (2003) used remote sensing techniques to estimate a 30% net increase in woody plant cover across 400 km² of northern Texas during a 63-year period that resulted in a 32% increase in aboveground woody plant C pools. Additionally, they detected a strong edaphic influence on aboveground *Prosopis* C mass at the landscape scale; clay loam and shallow clay soil formations are intermixed across this region (SCS, 1962), and clay loam soils supported substantially larger C pools than shallow clay soils (Asner *et al.*, 2003).

Edaphic properties strongly influence the size, density and patterning of woody plants in arid and semi-arid systems. Regional assessments typically predict an inverse relationship between woody plant abundance and clay content (Johnson & Tothill, 1985; Williams *et al.*, 1996). This relationship is thought to be based on how the contrasting root systems of grass and woody plant life forms access moisture from coarse- and fine-textured soils (Scholes & Archer, 1997; Breshears *et al.*, 1999; Rodriguez-Iturbe, 2000). Sites with fine-textured soils may support open savanna grasslands because grasses with shallow, fibrous root systems are favored by clayey soils that retain water in upper layers. In contrast, coarse-textured soils that allow percolation of rainfall to deeper depths may support higher densities of trees and shrubs with deeper, more extensive root systems (Knoop & Walker, 1985). Sites with fine-textured soils may thus be more resistant to woody plant encroachment, whereas sites characterized by coarse-textured soils may be more prone to increases in tree or shrub abundance.

Although Asner *et al.* (2003) estimated dynamics of the C pools of woody species in communities on con-

trasting soils experiencing woody encroachment, they did not account for possible coincident changes in aboveground herbaceous pools and productivity. As woody plant abundance increases, grass productivity typically decreases (Scholes & Archer, 1997), potentially negating increases in C storage by woody vegetation. Yet, few studies have quantified the net effect of shifts in grass-woody abundance on ecosystem (woody + herbaceous) productivity. In addition, studies investigating the sign and magnitude of response of soil C and N pools to woody encroachment have documented decreases (Jackson *et al.*, 2002), increases (Connin *et al.*, 1997; Gill & Burke, 1999; McCulley *et al.*, 2004), and spatial redistribution – though not necessarily a change – in absolute amounts (Schlesinger & Pilmanis, 1998; Wilson & Thompson, 2005).

House *et al.* (2003) present four possible scenarios for tree, herbaceous and total NPP response to woody encroachment. The first two scenarios define zero-sum relationships in which grass and tree NPP vary proportionally and inversely with woody encroachment, resulting in no net change to total NPP. The third scenario, termed facilitation optimum, defines an inverse relationship between grass and tree NPP, with increasing tree NPP outpacing decreasing herbaceous NPP during the early stages of woody encroachment and leading to a peak in total NPP during early to middle stages of encroachment. The fourth scenario, termed asymmetric, describes increases in tree NPP that are greater than coincidental decreases in herbaceous NPP throughout all stages of the encroachment process, resulting in consistent increases in total ecosystem NPP. To date, these scenarios stand as conceptual possibilities owing to the lack of field studies accounting for both herbaceous and woody plant productivity in areas undergoing woody encroachment.

Abundance of the N₂-fixing woody plant, *Prosopis glandulosa* (honey mesquite) (Johnson & Mayeux, 1990; Zitzer *et al.*, 1996), has increased markedly during the past century (Ansley *et al.*, 2001; Asner *et al.*, 2003) in the Southern Great Plains of the United States. In this study, we (1) estimated aboveground herbaceous and woody plant biomass and aboveground net primary productivity (ANPP) across a range of *Prosopis* stand age states on both clay loam and shallow clay soil types within this Southern Great Plains region, and (2) determined the sign and magnitude of change to C and N pools in aboveground biomass and surface soils (0–10 cm) when *Prosopis* stands develop in grasslands of this region. Our expectation was that proliferation of *Prosopis* would result in consistent increases in total ANPP as *Prosopis* productivity offsets declines in herbaceous productivity throughout all stages of the encroachment process (i.e. scenario #4 of House *et al.*, 2003). We expected this

scenario to apply on both clay loam and shallow clay soils, but that, based on results of Asner *et al.* (2003), both *Prosopis* and herbaceous productivity would be lower on shallow clays compared with clay loams. We also expected that increases in aboveground *Prosopis* C and N mass would be accompanied by increases in surface soil C and N pools.

Methods

Study area

The study was conducted on the 230 000 ha W. T. Waggoner Estate (Clayton, 1993) located on the eastern edge of the Rolling Plains (McMahan *et al.*, 1984) in north-central Texas, near the town of Vernon (34°09'06"N, 99°16'57"W; elevation ca. 350–400 m above sea level). Climate of the region is semiarid continental, characterized by warm, moist periods during spring and autumn; hot, dry summers; and cool winters. Mean annual precipitation is 665 mm (Heitschmidt *et al.*, 1986). Annual precipitation during the course of the study, as measured by rain gauges scattered throughout the study site and maintained by the Texas A&M Research and Extension Center in Vernon (<http://vernon.tamu.edu/>), was 861 mm in 1997 (one gauge maintained during this year), 426–482 mm in 1998 and 589–622 mm in 1999. Mean annual temperature is 17 °C, with mean monthly temperatures ranging from –2.5 °C (January) to 36 °C (July) (Heitschmidt *et al.*, 1986). Soils of the region are generally classified as fine, mixed thermic, Typic Paleustolls of the Tillman association (SCS, 1962). Within this general classification, soils range from deep clay loams (Tillman series) to relatively shallow clay loams (Vernon series) and hardlands of exposed red-bed clays and shales.

Vegetation of the region is classified as temperate savanna and shares structural/functional characteristics with many other semiarid savanna systems. The N₂-fixing, winter deciduous tree *P. glandulosa* var. *glandulosa* (honey mesquite) (nomenclature follows Correll & Johnston, 1979) accounts for 95–99% of the woody biomass on upland sites in the study area. Other occasional woody species include *Celtis laevigata* (hackberry), *Ziziphus obtusifolia* (lotebush), and *Acacia greggii* (catclaw acacia). Herbaceous composition and production varies across the site, depending on livestock (cattle) grazing and woody plant cover/density. During the last 20 years, cattle stocking rates on the Waggoner Ranch have been maintained at ca. 10–12 ha per head; before that time, grazing pressure was much higher (ca. 2 ha per head) (Teague *et al.*, 1997). Common grasses native to the region include: *Bouteloua curtipendula* (side-oats grama), *Nasella* (formerly *Stipa*) *leucotrica* (Texas

wintergrass), *Sporobolus asper* (meadow dropseed) and *Buchlœe dactyloides* (buffalograss). The introduced annual grass, *Bromus japonicus* (Japanese brome), is locally abundant as well. Common herbaceous dicots include *Xanthocephalum texanum* (Texas broomweed) and *Aster ericoides* (heath aster). The succulent, *Opuntia* spp. (prickly pear cactus) is also locally abundant throughout the area (Heitschmidt & Dowhower, 1991).

Historically, vegetation across this region of Texas was thought to have been composed of grassland and open savanna (Küchler, 1964; Weltzin *et al.*, 1997). By the mid-1900s, however, woody encroachment by *Prosopis* had progressed to the point that land managers vigorously pursued a variety of techniques (e.g. prescribed burning, mechanical removal and herbicide application) to control the spread and reduce the cover of this species (Fisher, 1942, 1950). These activities continue through recent times (e.g. Heitschmidt *et al.*, 1989; Ansley *et al.*, 1998; Teague, 1999), resulting in landscapes comprised of a mosaic of *Prosopis* stands that vary in canopy cover, stature and stem density (Ansley *et al.*, 2001; Asner *et al.*, 2003).

Measures of *Prosopis* stand structure, age, biomass and production

Our overall objective was to quantify how ecosystem properties change as *Prosopis* stands develop. Logistical constraints limited the number of sites and stands that could be studied, and the spatial variability in primary production is such that a random selection of a few stands is seldom sufficient for adequate replication (Huenneke *et al.*, 2001). We, therefore, opted for a regression, rather than an ANOVA design, approach, and directed our sampling to span the observed range of *Prosopis* stand age states on the two most spatially extensive soil types (clay loams and shallow clays). Ranges in stand age states were achieved by sampling stands on landscapes at different stages of recovery from past disturbance. Information regarding the disturbance history of each stand was obtained from Waggoner Ranch managers and scientists at the Texas A&M Research and Extension Center, Vernon, TX. A total of 24 stands were sampled (Table 1). We sampled more stands on clay loam soils ($n = 18$) than on shallow clay soils ($n = 6$), because field observations indicated a broader range of *Prosopis* stem sizes and densities on the former.

A single 60 × 60 m² plot was established at a randomly-selected location within each target stand. Within each plot, six 5 × 60 m² belt transects were systematically located at 10 m intervals beginning at the 5 m point along the bottom line of each plot. During

Table 1 Name and age of *Prosopis* stands sampled on Waggoner Ranch, Texas, the soil types on which they occur, and the variables measured within each stand

Stand name	Aboveground <i>Prosopis</i> bio-, C, and N mass	Aboveground herb and litter bio-, C and N mass	Surface soil bulk density, C and N mass
SC12	(6)	Away (6)	
SC14	(6)	Away (6)	
SC15	(6)	Away (6)	
SC18	(6)	Under (10) and away (10)	
SC20	(6)	Under (10) and away (10)	
SC27	(6)	Under (10) and away (10)	
CL18	(6)		
CL19	(6)	Away (6)	
CL20a	(6)	Away (6)	
CL20b	(6)	Away (6)	
CL20c	(6)	Away (6)	
CL21a	(6)	Away (6)	
CL21b	(6)	Under (10) and away (10)	(30)
CL23a	(6)	Away (6)	(30)
CL23b	(6)		
CL24a	(6)	Away (6)	(30)
CL24b	(6)	Under (10) and away (10)	
CL24c	(6)	Under (10) and away (10)	(30)
CL27	(6)	Under (10) and away (10)	
CL30	(6)	Under (10) and away (10)	(30)
CL33	(6)	Under (10) and away (10)	
CL35	(6)	Under (10) and away (10)	(30)
CL48	(6)		
CL68	(6)	Under (10) and away (10)	(30)

Stand codes refer to soil type (SC, shallow clay; CL, clay loam) and stand age (years). A value indicates that the variable was sampled in that stand, and sampling intensity (i.e. *n*). For herb and litter components, under and away indicates that samples were collected both under and away from *Prosopis* canopies; 'away' indicates that samples were collected only away from *Prosopis* canopies.

May, June and October of 1998, *Prosopis* stems within each belt were counted and their basal diameter measured at ca. 10 cm height. Plot values for basal area ($\text{m}^2 \text{ha}^{-1}$), and stem density (stems ha^{-1}) are given as the mean + 1 standard error (SE) of the six belt transects.

Allometric equations relating stem basal diameter to total aboveground *Prosopis* dry biomass (foliar + stem) and foliar dry biomass (Table 2) were developed by destructively harvesting and weighing 120 plants from the vicinity of sampled stands during July and August of 1998 and 1999. Harvested plants encompassed the range of sizes occurring in sampled plots on both soil types. Biomass of each harvested stem was separated into foliar and woody components, and equations generated from harvested trees were used to convert basal diameter of *Prosopis* stems encountered in belt transects to aboveground dry biomass. Diameter–biomass relationships were statistically comparable for trees on clay loam and shallow clay sites. Consequently, data were

pooled to generate regression equations for total aboveground and foliar biomass (Table 2); stem biomass was calculated by subtracting foliar biomass from total aboveground biomass of each stem.

Grab samples of foliage ($n = 29$) and stem ($n = 38$) tissue were also collected from *Prosopis* individuals on both shallow clay and clay loam soils. Samples were dried to a constant weight at 70 °C and ground (Tecator Cyclotec 1093 sample mill, Herndon, VA, USA) to pass through a 40-mesh (0.55 mm) screen. Total C and N concentrations were determined using a Carlo-Erba NA Series 1500 CN analyzer (Fisons Instruments, Danvers, MA, USA) (Nelson & Sommers, 1982). Because concentrations of C and N in *Prosopis* foliage and stem tissues were statistically comparable (two-tailed *t*-tests, $P < 0.05$) among plants on shallow clay and clay loams and among stem diameter classes (e.g. main trunk vs. small branches and twigs), values were consolidated to generate single mean values for leaves and wood. Woody and foliar biomass values were multiplied by

Table 2 Equations used to estimate aboveground *Prosopis* biomass and stem age from basal stem diameter (BD, cm) on clay loam and shallow clay soils in a temperature savanna in northern Texas, USA

Parameter	Equation	<i>n</i>	<i>R</i> ²	<i>P</i> -value
Total aboveground <i>Prosopis</i> biomass (kg)	$= 17.4 \times \exp(0.76BD) - 21.06$	120	0.98	<0.0001
<i>Prosopis</i> leaf biomass (kg)	$= 1.68 \times \exp(0.048BD) - 1.75$	120	0.87	<0.0001
<i>Prosopis</i> stem age on clay loam soils (year)	$= (2.23 \times BD) - 0.59$	67	0.87	<0.0001
<i>Prosopis</i> stem age on shallow clay soils (year)	$= (2.89 \times BD) + 4.5$	18	0.70	<0.0001

Regressions predicting *Prosopis* biomass were statistically comparable on clay loam and shallow clay sites, so data were pooled to develop a single equation.

these %C and %N values to estimate C and N mass of *Prosopis* plants in plots.

Basal diameter-age relationships were developed from a subset of stems harvested for biomass determination ($n = 67$ on clay loam sites; $n = 18$ on shallow clay sites). Basal cross-sections were sanded and stained to reveal annual growth rings which were counted as described by Flinn *et al.* (1994) who had previously established that ring counts of stem cross-sections from *Prosopis* plants in this area provided accurate estimates of stem age. Ring counts were regressed against basal diameter, and resulting soil-type specific equations (Table 2) were used to convert stem diameters measured in belt transects to individual stem ages. Stand age was estimated to be the third year of the oldest three consecutive years that contained one or more individuals (defining stand age based on the single oldest plant may be misleading, because a given disturbance may not affect all plants in a stand). Estimates were corroborated with ranch management records where possible, but stand ages were based on *Prosopis* stem ages rather than on management records, as the latter were typically qualitative pasture-scale assessments that would not necessarily apply to a specific plot within a management unit (e.g. some stands within a given management unit may have escaped fire, herbicide applications, etc.).

To estimate aboveground biomass and net primary production of *Prosopis*, we used an allometric approach similar to those described in Huenneke *et al.* (2001) and Norris *et al.* (2001). We estimated aboveground biomass of wood and foliage of each *Prosopis* stem encountered during the Spring and Summer of 1998 within belt transects using the aforementioned allometric equations (Table 2). Stem biomass values were summed within, and averaged across, belt transects to generate plot- or stand-level aboveground bio- C- and N-mass values. Annual production of leaves and wood for each *Prosopis* stem encountered within study plots was estimated as the difference in biomass between 1998 and 1999, where biomass in 1999 was projected by adding the average annual increase in basal diameter (i.e. the slope of the

linear relationship between stem basal diameter and stem age) to the 1998 measurements and applying these new basal diameter values to the appropriate allometric equations (Table 2). For each year, wood and leaf biomass values were multiplied by their respective C and N concentrations to estimate *Prosopis* wood and foliage C and N mass and annual rates of C and N production (Table 3).

Measurement of herbaceous and soil C and N pools

Aboveground C and N pools in the herbaceous layer were determined in August 1999 – the typical period of peak biomass (Heitschmidt & Dowhower, 1991). Herbaceous biomass was sampled in pairs of 0.1 m² quadrats located both under and away from *Prosopis* canopies at 11 of the 24 plots (10 paired quadrats per plot). Herbaceous biomass was sampled away from *Prosopis* canopies in an additional 10 study sites where *Prosopis* canopies were of a limited extent ($n = 6$ quadrats per plot) (Table 1). Although herbaceous biomass could not be sampled at all 24 plots due to logistical constraints, the subset of plots sampled were selected to encompass the range in stand age and *Prosopis* stem density on both clay loam and shallow clay soil types. Herbaceous biomass in quadrats was clipped at ground level and separated into standing live, standing dead and litter fractions. Standing fractions were considered to approximate the current year's production (live + senescent dry biomass); the litter fraction consisted of unattached herbaceous biomass from previous years and fine *Prosopis* litter (i.e. leaves and stems <2 cm diameter). Samples were oven-dried at 70 °C and weighed. A subset of samples of each herbaceous fraction was ground and analyzed for C and N as described for *Prosopis* tissue. Concentrations of C and N for each herbaceous fraction did not differ with respect to soil type (two-tailed *t*-tests, $P < 0.05$), so values were consolidated (Table 3). These pooled C and N concentrations were then multiplied by biomass to estimate herbaceous and litter C and N mass.

Bulk density and C and N concentrations of surface soils (0–10 cm depth) were determined in seven of the

Table 3 Mean (\pm SE) carbon and nitrogen concentration of selected plant fractions used to calculate C and N mass in *Prosopis*, herbaceous (live and dead) and litter biomass in a temperate savanna in northern Texas, USA

Tissue type	%C	%N
<i>Prosopis</i>		
Foliage ($n = 29$)	49.2 \pm 0.21	2.62 \pm 0.06
Stems ($n = 38$)	47.3 \pm 0.11	1.15 \pm 0.03
Herbaceous Layer		
Under <i>Prosopis</i> canopies		
Live ($n = 10$)	43.9 \pm 0.19	1.38 \pm 0.03
Dead ($n = 10$)	43.7 \pm 0.19	0.99 \pm 0.07
Litter ($n = 9$)	41.6 \pm 0.64	1.88 \pm 0.13
Away from <i>Prosopis</i> canopies		
Live ($n = 15$)	45.3 \pm 0.43	1.32 \pm 0.07
Dead ($n = 18$)	42.8 \pm 0.37	0.85 \pm 0.04
Litter ($n = 16$)	39.1 \pm 0.55	1.29 \pm 0.07

C and N concentration in *Prosopis* foliage and stem tissue did not differ significantly (two-tailed *t*-tests, $P < 0.05$) with respect to soil type (shallow clay vs. clay loam) or stem size (e.g. large trunk vs. small stem tissue) so mean of pooled samples are presented. Values for herbaceous fractions did not differ with respect to soil type (two-tailed *t*-tests, $P < 0.05$, so consolidated values are shown.

60 \times 60 m² plots (clay loam sites only). As was the case with herbaceous sampling, logistical constraints limited the number of plots that could be sampled. We chose to sample only clay loam soils because they supported a broader range of *Prosopis* stem densities than did shallow clay plots. Although we were limited to sampling only seven of the 18 plots on clay loam soils, those seven plots nearly covered the complete range in *Prosopis* stand age and stem density represented by the 18 plots (Table 1). Soil cores (5.1 cm diameter) were collected in each of these plots at 10 m intervals along the six belt transects (five cores per transect; 30 cores per plot). Each sample point was recorded as being either under or away from a *Prosopis* canopy. As a result, the proportion of samples collected under and away from *Prosopis* canopies varied among sites. Soils were sieved to remove roots and rocks greater than 2 mm in diameter, dried, weighed, ground and analyzed for C and N concentrations as described earlier. Tests indicated that no carbonates were present in these samples (Kunze & Dixon, 1986). Soil C and N mass (kg ha⁻¹) was computed by multiplying concentration by bulk density.

Statistical analyses

Metrics were expressed as means +1 SE throughout. Linear and nonlinear regression analyses (SAS, version 8.02) were used to determine relationships between mea-

sured parameters (e.g. *Prosopis* basal diameter and individual tree biomass, stand age and stand C and N mass). Two-tailed Student *t*-tests (Systat, version 10) were used to ascertain significant differences in plant and soil nutrient mass under and away from *Prosopis* canopies. One-way ANOVAs and *post hoc* Tukey tests (SAS, version 8.02) were used to determine differences in surface soil C and N mass among sites.

Results

Prosopis stand structure and ANPP

Prosopis stands ranged from 12 to 68 years in age (Appendix A), and stands on shallow clay sites were relatively young (12–27 yr) compared with those on clay loam sites (18–68 yr). Aboveground C and N mass of *Prosopis* stands increased linearly with stand age on both clay loam and shallow clay sites, with clay loam sites exhibiting a much greater range of stand ages and C mass values and higher rates of C mass accumulation (Fig. 1). Six of the seven sites with the lowest stand-level *Prosopis* C and N mass values occurred on shallow clay

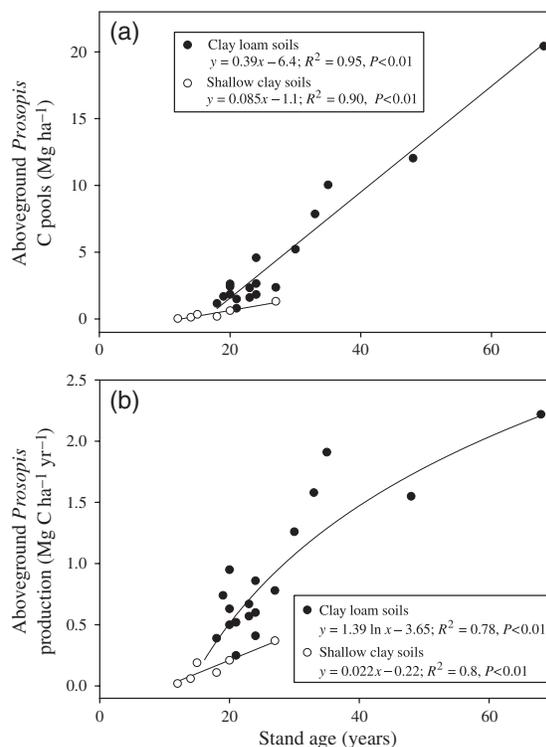


Fig. 1 Relationships between *Prosopis* stand age and (a) mean *Prosopis* plot-scale aboveground C mass (Mg ha⁻¹) and (b) *Prosopis* productivity (Mg C ha⁻¹ yr⁻¹) on shallow clay (○) and clay loam (●) soils in a temperate savanna in northern Texas, USA.

Table 4 Mean (\pm SE) bulk density and mass of surface soil C and N (0–10 cm depth) pools under and away from *Prosopis* canopies at selected clay loam (CL) sites in a temperate savanna in northern Texas, USA

Stand name	Bulk density (g cm ⁻³)	C (Mg ha ⁻¹)			N (Mg ha ⁻¹)		
		Away	Under	Combined	Away	Under	Combined
CL21b	1.3 \pm 0.02 b	22 \pm 1.1	22 \pm 2.4	22 \pm 0.9 b	2.0 \pm 0.09	2.1 \pm 0.24	2.0 \pm 0.09 c
CL23a	1.5 \pm 0.02 a	16 \pm 0.3	16 \pm 1.0	16 \pm 0.3 a	1.5 \pm 0.03	1.5 \pm 0.09	1.5 \pm 0.03 a,b
CL24a	1.4 \pm 0.02 b,c	17 \pm 0.7	19 \pm 2.9	17 \pm 0.8 a,c	1.7 \pm 0.05	1.8 \pm 0.16	1.7 \pm 0.05 a,d
CL24c	1.3 \pm 0.02 a,c	15 \pm 0.5	17 \pm 0.8	15 \pm 0.5 a	1.5 \pm 0.05	1.6 \pm 0.06	1.5 \pm 0.04 b
CL30	1.4 \pm 0.02 a	18 \pm 1.0	22 \pm 1.1	20 \pm 0.8 b,c	1.8 \pm 0.09	2.1 \pm 0.09	1.9 \pm 0.07 c,d
CL35	1.3 \pm 0.02 b,c	18 \pm 1.2	19 \pm 1.0	19 \pm 0.7 b,c	1.8 \pm 0.09	1.8 \pm 0.08	1.8 \pm 0.06 c,d
CL68	1.2 \pm 0.02 b,c	19 \pm 0.9	21 \pm 1.3	20 \pm 1.0 b,c	1.8 \pm 0.08	2.0 \pm 0.11	1.9 \pm 0.08 c,d

The 'combined' columns is the mean of pooled under and away samples. An asterisk denotes a significant difference between 'under' and away samples determined from two-tailed *t*-tests assuming unequal variances ($P < 0.05$). Combined values which share the same letter within each column were not significantly different from one another ($P < 0.05$).

substrates. The youngest stands on clay loam soils (i.e. CL18, CL20b, CL20c, CL2a) also had relatively small *Prosopis* C and N pools, whereas the two *Prosopis* stands that had experienced the longest period of uninterrupted development had the largest aboveground C and N pools (Appendix A).

Aboveground ANPP (Mg C ha⁻¹ yr⁻¹) increased logarithmically with stand age within clay loam sites and linearly with stand age on shallow clay sites (Fig. 1b). As with C and N pools, ANPP of clay loam sites covered a much broader and higher range of values relative to shallow clay sites. *Prosopis* ANPP was lowest in the youngest stand on shallow clay soils (SC12) and highest in the oldest stand on clay loam soils (CL68) (Appendix B). Patterns of ANPP-N *Prosopis* stands were generally similar to those shown for ANPP-C (graphics not shown; see Appendix B for values).

Aboveground herbaceous pools and production

Pools of C and N in aboveground herbaceous biomass varied by one to two orders of magnitude, and variation corresponded to differences in soil type and levels of *Prosopis* biomass among plots. Herbaceous C and N mass values were lowest in the CL68 site and highest in the SC27 site (Appendix B). Of the 11 study plots where herbaceous C and N pools were sampled both under and away from *Prosopis* canopies, a significant canopy effect was found within only one stand (SC27; Appendix B). In contrast, when plots were grouped by soil type, increasing *Prosopis* C mass corresponded to exponential declines in herbaceous C mass on clay loam soils ($R^2 = 0.73$, $P < 0.001$) and linear increases in herbaceous C mass on shallow clays ($R^2 = 0.70$, $P < 0.04$). Herbaceous N pools followed patterns similar to those of herbaceous C pools; herbaceous N mass was inver-

sely related to *Prosopis* N mass on clay loams ($R^2 = 0.65$, $P < 0.001$) and positively related to *Prosopis* N mass on shallow clays ($R^2 = 0.66$, $P < 0.05$). (see values in Appendix B).

Soil C and N pools

Surface (0–10 cm) soil C and N pools ranged from 15 Mg C ha⁻¹ and 1.5 Mg N ha⁻¹ at the CL24c site to 22 Mg C ha⁻¹ and 2.0 Mg N ha⁻¹ at the CL21b site (Table 4). Surface soil C and N pools under *Prosopis* canopies were generally similar to those away from *Prosopis* canopies; the only exception to this occurred in stand CL30 where C and N pools were significantly higher under, compared to away from, *Prosopis* canopies. However, we did not detect a statistically significant relationship between soil C or N pool size and *Prosopis* stand biomass ($R^2 = 0.11$, $P = 0.46$ for soil C; and $R^2 = 0.13$, $P = 0.43$ for soil N).

C and N pools and production in plants and surface soils

How does ecosystem ANPP (woody + herbaceous) change with increasing *Prosopis* abundance? To answer this question we used peak standing pools of herbaceous C and N (Appendix B) as an approximation of total annual herbaceous C and N production in conjunction with estimates of *Prosopis* stand C and N production.

As woody plant basal area increased on clay loam sites, declines in herbaceous C production were more than offset by increases in *Prosopis* C production. As a result, stand-level ANPP-C increased from ca. 2.2 Mg ha⁻¹ yr⁻¹ in open grassland to ca. 2.5 Mg ha⁻¹ yr⁻¹ in *Prosopis* woodland (Fig. 2a). Likewise, increases in *Prosopis* N production with increasing

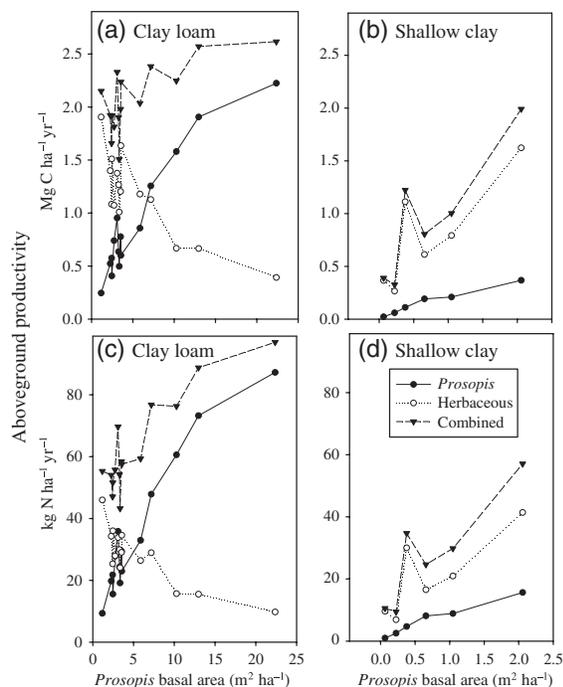


Fig. 2 Relationships between *Prosopis* stand basal area and aboveground C and N production of *Prosopis* plants, herbaceous vegetation and combined vegetation (*Prosopis* + herbaceous) on clay loam soils (a, c) and shallow clay soils (b, d), respectively, in a temperate savanna in northern Texas, USA. Note differences in x-axis scales for clay loam and shallow clay soils.

basal area more than offset associated declines in herbaceous N production (Fig. 2c). The net result was a near doubling of N production (i.e. from ca. 55 to 90 kg ha⁻¹ yr⁻¹) and a concomitant decrease in C:N ratios of production (i.e. from 39 to 27). Total ANPP increased with woody plant proliferation on shallow clay sites as well. However, in contrast to clay loam sites, ANPP in shallow clay sites was characterized by dual increases in herbaceous and *Prosopis* C and N production, with contributions dominated by herbaceous components in all stands (Figs 2b, d). In addition, C:N ratios of production on shallow clay sites decreased only slightly (i.e. 37–35) with increasing *Prosopis* stand basal area.

Stand level (*Prosopis* + herbaceous) C and N pools increased with *Prosopis* basal area on clay loam soils (Figs 3a, c), but the contribution of herbaceous vegetation to these increases in pool size were minimal relative to *Prosopis*. Aboveground pools of C and N on shallow clay sites also increased with increasing *Prosopis* basal area (Figs 3b, d). In contrast to clay loam soils, C and N pools on shallow clays consisted of roughly equivalent contributions from both herbaceous and

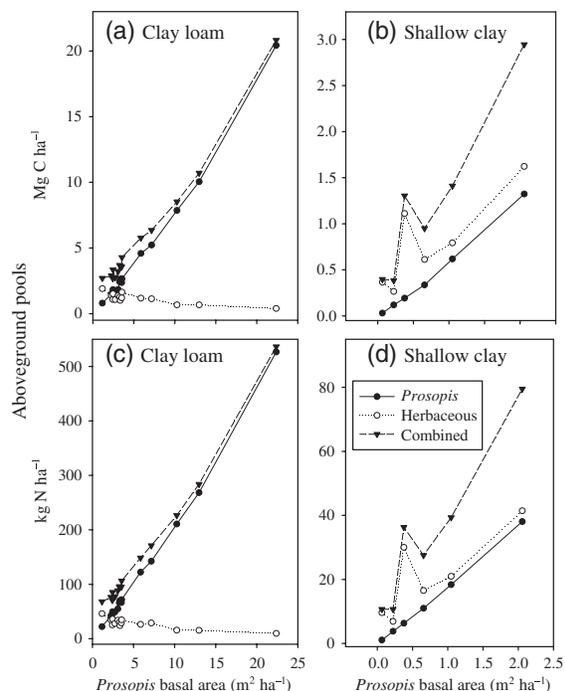


Fig. 3 Relationships between *Prosopis* stand basal area and C and N mass of *Prosopis* plants, herbaceous vegetation and total vegetation (*Prosopis* + herbaceous) on clay loam soils (a, c) and shallow clay soils (b, d), respectively, in a temperate savanna in northern Texas, USA. Note scale differences in x- and y-axis.

Prosopis components, with contributions from herbaceous components somewhat exceeding those from *Prosopis*.

Combined aboveground and surface soil pools (i.e. aboveground *Prosopis* + herbaceous + litter + upper 10 cm of soil) were estimated for a subset of seven clay loam stands ranging from 21 to 68 years in age. Combined C pools ranged from 19 to 43 Mg ha⁻¹, and N pools ranged from 1.6 to 2.5 Mg ha⁻¹ (Fig. 4). Both C and N pools increased in a nonlinear fashion with increasing stand age, with increases in aboveground *Prosopis* pools primarily responsible for the positive relationships. Soils accounted for 48–85% of C pools and 76–95% of N pools. Aboveground *Prosopis* biomass accounted for 7–48% of combined C pools, and 2–21% of N pools. Contributions of herbaceous vegetation to ecosystem C and N pools ranged from 1 to 6% and 1% to 2%, respectively; contributions from litter were 3–6% for C and 1–3% for N.

Discussion

Our investigation revealed several facets of the effects of woody plant encroachment on ecosystem function

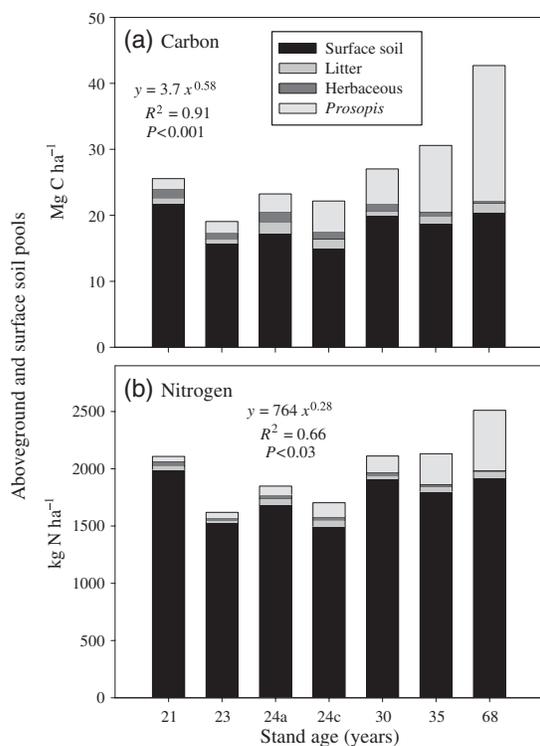


Fig. 4 Mass of carbon (a) and nitrogen (b) in combined surface soils (0–10 cm), litter, herbaceous biomass and *Prosopis* biomass for a range of *Prosopis* stand age states on clay loam soils in a temperate savanna in northern Texas, USA. Nonlinear equations and R^2 values denote relationships between stand age and total combined C mass and stand age and N mass, respectively.

across regions of northern Texas: (1) Aboveground *Prosopis* C and N mass increased linearly, and productivity increased logarithmically, with stand age on clay loam soils, with trajectories of C and N accumulation and ANPP showing no signs of an asymptote even following 68 years of stand development. (2) On shallow clay soils *Prosopis* C and N mass and ANPP increased linearly with stand age, but at slower rates relative to clay loam sites. (3) Herbaceous biomass response to *Prosopis* stand development differed between the two soil types; herbaceous C pools declined with increasing aboveground *Prosopis* C mass on clay loam soils, but increased with increasing *Prosopis* C on shallow clays. (4) Aboveground productivity of the plant community as a whole increased substantially with *Prosopis* stand development on both soil types, but via different mechanisms; *Prosopis* production offset coincidental declines in herbaceous productivity on clay loam soils, but promoted herbaceous productivity on shallow clay soils. (5) Although aboveground C and N pools increased markedly with *Prosopis* stand devel-

opment, corresponding changes in surface soil C and N pools and spatial patterns were not evident. The contrasting ecosystem response to *Prosopis* encroachment on clay loam and shallow clay soils suggests that caution must be exercised when generalizing about woody plant encroachment effects on ANPP and soil C and nutrient pools.

Development of *Prosopis* stands

Our estimates of stand-level ANPP accompanying woody encroachment on clay loam soils in this temperate savanna of northern Texas ($2.0\text{--}2.5\text{ Mg C ha}^{-1}\text{ yr}^{-1}$) were substantially greater than ANPP values reported for populations of *P. glandulosa* that have invaded Chihuahuan Desert grasslands ($<1.1\text{ Mg C ha}^{-1}\text{ yr}^{-1}$; Huenneke *et al.*, 2002). Northern Texas ANPP values were somewhat greater than those reported for subtropical landscapes undergoing *Prosopis*-mixed shrub encroachment in southern Texas ($0.9\text{--}1.5\text{ Mg C ha}^{-1}\text{ yr}^{-1}$; Hibbard *et al.*, 2003), and for temperate landscapes experiencing oak (*Quercus* spp.) proliferation in Minnesota, USA ($1.4\text{ Mg C ha}^{-1}\text{ yr}^{-1}$; Tilman *et al.*, 2000). However, our ANPP values were less than those reported for *Juniperus* stands that have developed in Kansas Tallgrass Prairie ($3.2\text{ to }4.7\text{ Mg C ha}^{-1}\text{ yr}^{-1}$; Norris *et al.*, 2001). The extent to which these differences in ANPP represent climatic, edaphic, growth-form or land use history differences is not known. Stand level ANPP estimates of our shallow clay sites undergoing woody encroachment ($0.3\text{--}2.0\text{ Mg C ha}^{-1}\text{ yr}^{-1}$) were comparable to values reported by Huenneke *et al.* (2002), Hibbard *et al.* (2003) and Tilman *et al.* (2000).

Trends of increasing C accumulation and ANPP with increasing stand age suggest that in the absence of management intervention, wildfire, or severe and prolonged drought, *Prosopis* stands in these northern Texas landscapes will continue to accumulate aboveground biomass well beyond the 68-year period represented in this study. This projection is consistent with dynamic model simulations of *Prosopis* encroachment in subtropical savannas in southern Texas, where biomass accumulation is predicted to occur for another 100–200 years (Hibbard *et al.*, 2003) and result in aboveground C stocks 15–24 times greater than those of grasslands they have replaced. We found that after only 15 and 49 years of stand development on shallow clay and clay loam soils, respectively, total above ground C pools (woody + herbaceous + litter) of the oldest stands (SC 27 and CL68) were already 7–8 times greater than sites with the lowest amount of *Prosopis* biomass (SC12 and CL19). Total aboveground N pools followed a similar pattern; amounts were $10\times$ and $7\times$ greater following 15- and 49-year periods of *Prosopis* stand development on

shallow clay and clay loam soils, respectively (Appendices A and B)

Rates and spatial patterns of woody encroachment are strongly influenced by topographic factors (McAuliffe, 1994; Archer, 1995; Wu & Archer, 2005); soils and topography interact with these vegetation changes to influence patterns and distribution of ecosystem C and N mass (Garten & Ashwood, 2002; Hicke *et al.*, 2004; Kulmatiski *et al.*, 2004). The contrasting patterns and rates of change in ANPP, C and N accumulations and woody/herbaceous interactions on clay loam and shallow clay soil types observed in this study underscore the importance of explicitly accounting for spatial variation in edaphic properties when predicting or modeling the effects of encroaching woody plants on ecosystem function. Our results also confirm broad regional-scale remote sensing assessments that C mass in *Prosopis* stands on clay loam sites exceeds that of *Prosopis* on shallow clay sites by 60–70% (Asner *et al.*, 2003).

Response of herbaceous vegetation to Prosopis stand development

Although providing insight into herbaceous response to woody encroachment, our estimates of herbaceous aboveground production should be interpreted with the caveat that they are based on measures of annual peak standing biomass in an area where the prevailing land use is managed livestock grazing. Our production values are, thus, likely to underestimate productivity by not accounting for biomass consumed by grazers or biomass of early season forbs and grasses that may have senesced before sampling (Singh *et al.*, 1975; Sala *et al.*, 1981). However, our study was not designed to assess how herbaceous biomass or ANPP might be affected by grazing. Rather, we sought to ascertain the outcome of woody plant–herbaceous interactions within the context of a common and widespread land use: landscapes grazed by free-ranging livestock. In that context, the range in C mass values we observed was comparable to peak standing herbaceous C mass measured in the region by others (0.3–1.3 Mg C ha⁻¹; Heitschmidt *et al.*, 1986; Ansley *et al.*, 2004).

Effects of woody plants on herbaceous vegetation can range from positive to neutral to negative and depend on a variety of interacting factors (Belsky, 1990; Scholes & Archer, 1997; Tewksbury & Lloyd, 2001). Within the bioclimatic zone of northern Texas, the general response of herbaceous biomass to *Prosopis* stand development was strongly influenced by soils, such that herbaceous production was promoted by *Prosopis* on shallow clay sites (facilitation) and suppressed by *Prosopis* on clay loam sites (competition). The negative relationship be-

tween woody and herbaceous biomass documented on clay loam soils in our study has been widely reported in savannas worldwide and is an expected dynamic (reviewed by Scholes & Archer, 1997). Facilitation of herbaceous plants by trees and shrubs has also been widely reported; and typically occurs in areas where woody plant densities are relatively low. We can only speculate as to the basis for the facilitation observed in this study, but favorable modifications of microclimate, soil nutrient availability or soil moisture regimes by *Prosopis* plants are potential mechanisms (Belsky & Canham, 1994; Zitzer *et al.*, 1996; Hultine *et al.*, 2003). Whether this facilitation will persist at higher woody plant densities on this soil type; or if higher woody plant densities will even occur on this soil type is unknown. It is tempting to speculate as to why the outcome of tree–grass interactions differ so markedly on the two soil types investigated here, but that is beyond the scope of this paper (but see Jeltsch *et al.*, 2000; Callaway, 2002; House *et al.*, 2003 for relevant discussions).

Ecosystem productivity and woody plant encroachment

Which of the four possible tree, herbaceous, and total ANPP interaction models postulated by House *et al.* (2003), is applicable to our observed results? The answer depends on soil type. ANPP dynamics on clay loam soils investigated here conform to the asymmetric model in which ANPP contributed by encroaching *Prosopis* plants more than compensated for coincidental declines in herbaceous ANPP, resulting in a slight (ca. 20%) increase in total ANPP. In contrast, shallow clays conformed most closely to the facilitation optimum model whereby the ANPP contributed by encroaching *Prosopis* plants led to a 4 × increase in total ANPP by stimulating herbaceous ANPP. However, our assessment of ANPP dynamics on shallow clays was constrained to less than 27 years of stand development. It remains to be seen (1) to what extent *Prosopis* basal area might further increase on shallow clay sites, and (2) whether potential increases of *Prosopis* basal will begin to suppress herbaceous ANPP. Dynamics on our clay loam soils are similar to those documented in temperate oak savannas in the northern Great Plains (Minnesota) where woody ANPP increased exponentially with increases in woody plant cover whereas grass ANPP decreased linearly (Reich *et al.*, 2001). By contrast, the ANPP contributed by encroaching xerophytic shrubs only partially offset concomitant declines in ANPP of desert grasses in New Mexico, resulting in a reduction in ecosystem ANPP with shifts from grass to woody plant dominance (Huenneke *et al.*, 2002). Additional cross-site studies and synthesis are required to develop

robust generalizations concerning woody plant encroachment effects on ecosystem ANPP.

Response of soil C and N pools to woody encroachment

Despite substantial increases in aboveground C and N pools with woody encroachment, we did not see significant changes in C and N pools in the upper 10 cm of the soil. This is consistent with observations for *Juniperus* encroachment in Kansas prairie (Smith & Johnson, 2004), but contrasts with other observations for *Prosopis* in northern Texas where SOC pools decreased 10–11% (Jackson *et al.*, 2002) and observations in southern Texas (Boutton *et al.*, 1998; Geesing *et al.*, 2000; Hibbard *et al.*, 2001; McCulley *et al.*, 2004) and Arizona (Tiedemann & Klemmedson, 2004) where encroachment by *Prosopis* increased near-surface soil C and N pools. Additionally, and in contrast to Schlesinger & Pilmanis (1998), we did not detect increased localization of soil C and N mass – the ‘islands of fertility’ phenomenon – with *Prosopis* stand development. Reasons for these discrepancies are elusive and may reflect differences in land use/disturbance history, soil physical properties, and climate (e.g. Tiedemann & Klemmedson, 2004; Williams *et al.*, 2004; Wessman *et al.*, 2005). It is also important to note that our results, and the conclusions that can be drawn from them, are based on a sampling of the top 10 cm of the soil profile. Although soil C and root biomass for grasses and shrubs are typically greatest at this depth and decline exponentially, the accumulated changes that may occur with increasing depth when woody plants replace grasses may be significant (e.g. Jackson *et al.*, 2002).

Overall, our findings underscore the substantial impacts of woody encroachment on C and N dynamics in savanna systems of the Southern Great Plains of North America. Given the large increases in aboveground C and N pools resulting from *Prosopis* stand development and concomitant changes in herbaceous productivity and standing stocks (increases on shallow clays, decreases on clay loams), it is clear that woody encroachment alters the functioning of these ecosystems and represents a potentially significant terrestrial C sink. *Prosopis*-mediated impacts presented here gain additional importance when considering the global nature of the woody encroachment phenomenon (Archer *et al.*, 2001; Bowman, 2002), and how it affects not only of terrestrial storage and dynamics of C and N, but the ecosystem functions and processes that are largely driven by those dynamics (e.g. trace gas flux, decomposition rates and nutrient availability). Our results also highlight the complexity of patterns and potential impacts of woody encroachment; though *Prosopis* stand development increased C sequestration, the magnitude

of sequestration varied with respect to stand age and soil type. As woody encroachment is likely to continue within arid and semiarid systems on virtually every continent, an improved understanding and better quantification of the local-, regional- and global-scale impacts of this phenomenon is needed to inform discussions on greenhouse gas abatement strategies (e.g. Gifford & Howden, 2001; Henry *et al.*, 2002; Hurtt *et al.*, 2002).

Acknowledgements

We are very grateful to Annalee Hughes, Kye LeBoeuf, Dave Hadersbeck, Jeremiah Ford, Cristina Rumbaitis-del Rio, Nancy Golubiewski, Jonathan Carrasco, Seth Zunker, Paul Jurena, Tamatha Gunn and Colin McIntyre for assistance in collecting, processing, and analyzing field data. We thank Margaret Lefer for help with laboratory analysis and Jim Baldwin for help with statistical analysis. We also thank Eric Davidson, Mark Norris and two anonymous reviewers whose constructive suggestions greatly improved upon earlier drafts of the manuscript. This work was supported by a Cooperative Institute for Research in Environmental Sciences (CIRES) Visiting Post-Doctoral Fellowship, and by a Department of Environmental, Population and Organismic Biology Biosphere-Atmosphere Research Training Program grant (NSF) from the University of Colorado at Boulder, NASA grants NAG5-6134 and NAG5-11238, NSF grants DEB-0303886 and DEB-9981723 and Texas Agriculture Experiment Station project H6717. We thank Richard Teague, and Bill Pinchak of the Texas Agricultural Experiment Station, Vernon, Texas for sharing knowledge and providing logistical support during the research. Finally, we thank the managers of Waggoner Ranch for providing access to field research sites.

References

- Ansley RJ, Jones DL, Tunnell TR *et al.* (1998) Honey mesquite canopy responses to single winter fires: relation to herbaceous fuel, weather and fire temperature. *International Journal of Wildland Fire*, **8**, 241–252.
- Ansley RJ, Pinchak WE, Teague WR *et al.* (2004) Long-term grass yields following chemical control of honey mesquite. *Journal of Range Management*, **51**, 345–352.
- Ansley RJ, Wu XB, Kramp BA (2001) Observation: long-term increases in mesquite canopy cover in North Texas. *Journal of Range Management*, **54**, 171–176.
- Archer S (1995) Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstructing the past and predicting the future. *Ecoscience*, **2**, 83–99.
- Archer S, Boutton TW, Hibbard KA (2001) Trees in grasslands: biogeochemical consequences of woody plant expansion. In: *Global Biogeochemical Cycles in the Climate System* (eds Schulze ED, Heimann M, Harrison S, Holland E, Lloyd J, Prentice I, Schimel D), pp. 115–138. Academic Press, San Diego.
- Asner GP, Archer S, Hughes RF *et al.* (2003) Net changes in regional woody vegetation cover and carbon storage in Texas drylands, 1937–1999. *Global Change Biology*, **9**, 316–335.
- Bailey RG (1998) *Ecoregions: the Ecosystem Geography of the Oceans and Continents*. Springer, New York.

- Belsky AJ (1990) Tree/grass ratios in East African savannas: a comparison of existing models. *Journal of Biogeography*, **17**, 483–489.
- Belsky AJ, Canham CD (1994) Forest gaps and isolated savanna trees: an application of patch dynamics in two ecosystems. *Bioscience*, **44**, 77–84.
- Boutton TW, Archer SR, Midwood AJ *et al.* (1998) $\delta^{13}\text{C}$ values of soil organic carbon and their use in documenting vegetation change in a subtropical savanna ecosystem. *Geoderma*, **82**, 5–41.
- Bowman DMJS (2002) Preface: measuring and imagining: exploring centuries of Australian landscape change (Special 50th Anniversary Issue). *Australian Journal of Botany*, **50**, i–iii.
- Breshears D, Fairley D, Barnes J (1999) Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. *Landscape Ecology*, **14**, 465–478.
- Callaway RM (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–848.
- Clayton L (1993) *Historic Ranches of Texas*. University of Texas Press, Austin.
- Connin SL, Virginia RA, Chamberlain (1997) Carbon isotopes reveal soil organic matter dynamics following arid land shrub expansion. *Oecologia*, **110**, 374–386.
- Correll DS, Johnston MC (1979) *Manual of the vascular plants of Texas*, 2nd edn. University of Texas Press, Dallas, Richardson, TX.
- DeFries R, Asner G, Houghton R (2004) *Ecosystems and Land Use Change. Geophysical Monograph Series*, **153**. American Geophysical Union, Washington, DC.
- Field CB, Behrenfeld MJ, Randerson JT *et al.* (1998) Primary production of the biosphere: integrating terrestrial and oceanic components. *Science*, **281**, 237–240.
- Fisher CE (1942) Mesquite eradication studies at Spur, Texas. *The Cattleman*, **28**, 34–37.
- Fisher CE (1950) The mesquite problem in the Southwest. *Journal of Range Management*, **3**, 60–70.
- Flinn RC, Archer S, Boutton TW *et al.* (1994) Identification of annual rings in an arid-land woody plant, *Prosopis glandulosa*. *Ecology*, **75**, 850–853.
- Garten CTJ, Ashwood TL (2002) Landscape level differences in soil carbon and nitrogen: implications for soil carbon sequestration. *Global Biogeochemical Cycles*, **16**, 1114.
- Geesing D, Felker P, Bingham RL (2000) Influence of mesquite (*Prosopis glandulosa*) on soil nitrogen and carbon development: implications for global carbon sequestration. *Journal of Arid Environments*, **46**, 157–180.
- Gifford RM, Howden SM (2001) Vegetation thickening in an ecological perspective: significance to national greenhouse gas inventories and mitigation policies. *Environmental Science and Policy*, **4**, 59–72.
- Gill RA, Burke IC (1999) Ecosystem consequences of plant life form changes at three sites in the semiarid United States. *Oecologia*, **121**, 551–563.
- Heitschmidt RK, Dowhower SL (1991) Herbage response following control of honey mesquite within single tree lysimeters. *Journal of Range Management*, **44**, 144–149.
- Heitschmidt RK, Dowhower SL, Pinchak WE *et al.* (1989) Effects of stocking rate on quantity and quality of available forage in a southern mixed grass prairie. *Journal Range of Management*, **42**, 468–473.
- Heitschmidt RK, Schultz RD, Scifres CJ (1986) Herbaceous biomass dynamics and net primary production following chemical control of honey mesquite. *Journal of Range Management*, **39**, 67–71.
- Henry BK, Danaher T, McKeon GM *et al.* (2002) A review of the potential role of greenhouse gas abatement in native vegetation management in Queensland's rangelands. *Rangeland Journal*, **24**, 112–132.
- Hibbard KA, Archer S, Schimel DS *et al.* (2001) Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. *Ecology*, **82**, 1999–2001.
- Hibbard KA, Schimel D, Archer S *et al.* (2003) Grassland to woodland transitions: integrating changes in landscape structure and biogeochemistry. *Ecological Applications*, **13**, 911–926.
- Hicke JA, Sherriff RL, Veblin TT *et al.* (2004) Carbon accumulation in Colorado ponderosa pine stands. *Canadian Journal of Forest Research*, **34**, 1283–1295.
- Houghton RA (2003) Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850–2000. *Tellus*, **55B**, 378–390.
- House JI, Archer S, Breshears DD *et al.* (2003) Conundrums in mixed woody-herbaceous plant systems. *Journal of Biogeography*, **30**, 1765–1777.
- Huenneke LF, Aderson JP, Rimmenga M *et al.* (2002) Desertification alters patterns of aboveground net primary production in Chihuahuan ecosystems. *Global Change Biology*, **8**, 247–264.
- Huenneke LF, Clason D, Muldavin E (2001) Spatial heterogeneity in Chihuahuan Desert vegetation: implications for sampling methods in semi-arid ecosystems. *Journal of Arid Environments*, **47**, 257–270.
- Hultine KR, Williams DG, Burgess SSO *et al.* (2003) Contrasting patterns of hydraulic redistribution in three desert phreatophytes. *Oecologia*, **135**, 167–175.
- Hurt GC, Pacala SW, Moorcroft PR (2002) Projecting the future of the U.S. carbon sink. *Proceedings of the National Academy of Sciences*, **99**, 1389–1394.
- Jackson RB, Banner JL, Jobbágy EG *et al.* (2002) Ecosystem carbon loss with woody plant invasion of grasslands. *Nature*, **418**, 623–626.
- Jeltsch F, Weber GE, Grimm V (2000) Ecological buffering mechanisms in savannas: a unifying theory of long-term tree-grass coexistence. *Plant Ecology*, **150**, 161–171.
- Johnson HB, Mayeux Jr. HS (1990) *Prosopis glandulosa* and the nitrogen balance of rangelands: extent and occurrence of nodulation. *Oecologia*, **84**, 176–185.
- Johnson RW, Tothill JC (1985) Definition and broad geographic outline of savanna lands. In: *Ecology and Management of the World's Savannas* (eds Tothill JC, Mott JJ), pp. 1–13. Australian Academy of Science, Canberra.
- Knoop WT, Walker BH (1985) Interactions of woody and herbaceous vegetation in southern African savanna. *Journal of Ecology*, **73**, 235–253.
- Kulmatiski A, Vogt DJ, Sciccama TG *et al.* (2004) Landscape determinants of soil carbon and nitrogen storage in southern

- New England. *Soil Science Society of America Journal*, **68**, 2014–2022.
- Kunze GW, Dixon JB (1986) Pretreatment for mineralogical analysis. In: *Methods of Soil Analysis; Part 1: Physical and Mineralogical Methods*, 2nd edn (ed. Klute A), pp. 91–99. Soil Science Society of America, Madison, WI, USA.
- Küchler AW (1964) *The potential natural vegetation of the conterminous United States*. American Geographical Society, New York.
- McAuliffe JR (1994) Landscape evolution, soil formation, and ecological patterns and processes in Sonoran desert bajadas. *Ecological Monographs*, **64**, 111–148.
- McCulley RL, Archer SR, Boutton TW *et al.* (2004) Soil respiration and nutrient cycling in wooded communities developing in grassland. *Ecology*, **85**, 2804–2817.
- McMahan CA, Frye RG, Brown KL (1984) *The Vegetation Types of Texas*. Texas Parks and Wildlife, Austin, TX.
- Nelson DW, Sommers SE (1982) Total carbon, organic carbon, and organic matter. In: *Methods of Soil Analysis, 2nd edn. Part 2. Chemical and Microbiological Properties* (eds Page AL, Miller RH, Kinney DR), pp. 961–1010. Soil Science Society of America, Madison WI, USA.
- Norris MD, Blair JM, Johnson LC *et al.* (2001) Assessing changes in biomass, productivity, and C and N stores following *Juniperus virginiana* forest expansion into tallgrass prairie. *Canadian Journal of Forest Research*, **31**, 1940–1946.
- Pacala SW, Hurtt GC, Baker D *et al.* (2001) Convergence of land- and atmosphere-based US carbon sink estimates. *Science*, **292**, 2316–2320.
- Reich PB, Peterson DA, Wrage K *et al.* (2001) Fire and vegetation effects on productivity and nitrogen cycling across a forest-grassland continuum. *Ecology*, **82**, 1703–1719.
- Rodriguez-Iturbe I (2000) Ecohydrology: a hydrologic perspective of climate-soil-vegetation dynamics. *Water Resources Research*, **36**, 3–9.
- Sala O, Dergibus V, Shlichter T *et al.* (1981) Productivity dynamics of a native temperate grassland in Argentina. *Journal of Range Management*, **34**, 48–51.
- Schlesinger WH, Pilmanis AM (1998) Plant-soil interactions in deserts. *Biogeochemistry*, **42**, 169–187.
- Scholes RJ, Archer SR (1997) Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, **28**, 517–544.
- Scholes RJ, Noble IR (2001) Storing carbon on land. *Science*, **294**, 1012–1013.
- SCS (1962) *Soil survey of Wilbarger County, Texas*, Soil Survey Series 1959, Number 18. USDA-SCS, Fort Worth, TX.
- Singh JS, Lauenroth WK, Steinhorst RK (1975) Review and assessment of various techniques for estimating net aerial primary production in grasslands from harvest data. *Botanical Review*, **41**, 181–232.
- Smith D, Johnson L (2004) Vegetation-mediated changes in microclimate reduce soil respiration as woodlands expand into grasslands. *Ecology*, **85**, 3348–3361.
- Teague WR (1999) *Rolling plains ranching systems report*. Vernon Center Technical Report 99-100, Texas A&M Research and Extension Center, Vernon, TX.
- Teague WR, Borchardt R, Ansley J *et al.* (1997) Sustainable management strategies for mesquite rangeland: the Waggoner Kite project. *Rangelands*, **19**, 4–8.
- Tewksbury JJ, Lloyd JD (2001) Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia*, **127**, 425–434.
- Tiedemann AR, Klemmedson JO (2004) Response of desert grassland vegetation to mesquite removal and regrowth. *Journal of Range Management*, **57**, 455–465.
- Tilman D, Reich P, Phillips H *et al.* (2000) Fire suppression and ecosystem carbon storage. *Ecology*, **81**, 2680–2685.
- Van Auken OW (2000) Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics*, **31**, 197–215.
- Vitousek PM (1994) Beyond global warming: ecology and global change. *Ecology*, **75**, 1861–1876.
- Weltzin JF, Archer S, Heitschmidt RK (1997) Small-mammal regulation of vegetation structure in a temperate savanna. *Ecology*, **78**, 751–763.
- Wessman CA, Archer S, Johnson LC *et al.* (2005) Woodland expansion in US grasslands: assessing land-cover change and biogeochemical impacts. In: *Land Change Science: Observing, Monitoring and Understanding Trajectories of Change on the Earth's Surface* (eds Gutman G, Janetos A, Justice CO, *et al.*), pp. 185–205. Kluwer Academic Publishers, Dordrecht.
- Williams RJ, Duff GA, Bowman D *et al.* (1996) Variation in the composition and structure of tropical savannas as a function of rainfall and soil texture along a large-scale climatic gradient in the northern territory, Australia. *Journal of Biogeography*, **23**, 747–756.
- Williams RJ, Hutley LB, Cook GD *et al.* (2004) Assessing the carbon sequestration potential of mesic savannas in the Northern Territory, Australia: approaches uncertainties and potential impacts of fire. *Functional Plant Biology*, **31**, 415–422.
- Wilson TB, Thompson TL (2005) Soil nutrient distributions of mesquite-dominated desert grasslands: changes in time and space. *Geoderma*, **126**, 301–315.
- Wu XB, Archer SR (2005) Scale-dependent influence of topography-based hydrologic features on vegetation patterns in savanna landscapes. *Landscape Ecology*, **20**, 733–742.
- Zitzer SF, Archer SR, Boutton TW (1996) Spatial variability in the potential for symbiotic N₂ fixation by woody plants in a subtropical savanna ecosystem. *Journal of Applied Ecology*, **33**, 1125–1136.

Appendix A

Table A1 Characteristics of *Prosopis* stands at study sites located in a temperature savanna in northern Texas, USA

Stand name	Age (years)	Stem density (stems ha ⁻¹)	Basal area (m ² ha ⁻¹)	Aboveground biomass (Mg ha ⁻¹)	Aboveground C pool (Mg ha ⁻¹)	Aboveground N pool (Mg ha ⁻¹)	Aboveground C production (Mg ha ⁻¹ yr ⁻¹)	Aboveground N production (Mg ha ⁻¹ yr ⁻¹)
SC12	12	789 ± 192	0.06 ± 0.03	0.06 ± 0.03	0.03 ± 0.02	1.1 ± 0.49	0.02 ± 0.01	0.96 ± 0.37
SC14	14	1250 ± 376	0.22 ± 0.07	0.25 ± 0.08	0.12 ± 0.04	3.8 ± 1.21	0.06 ± 0.02	2.55 ± 0.77
SC15	15	4483 ± 475	0.66 ± 0.07	0.70 ± 0.08	0.34 ± 0.04	11.0 ± 1.16	0.19 ± 0.02	8.12 ± 0.80
SC18	18	2500 ± 272	0.38 ± 0.05	0.40 ± 0.06	0.19 ± 0.03	6.3 ± 0.82	0.11 ± 0.01	4.69 ± 0.45
SC20	20	1928 ± 418	1.05 ± 0.19	1.30 ± 0.24	0.62 ± 0.11	18.4 ± 3.37	0.21 ± 0.04	8.87 ± 1.65
SC27	27	4083 ± 613	2.06 ± 0.45	2.78 ± 0.65	1.32 ± 0.31	38.1 ± 8.60	0.37 ± 0.07	15.66 ± 3.01
CL18	18	2461 ± 353	1.72 ± 0.43	2.44 ± 0.64	1.16 ± 0.30	32.6 ± 8.31	0.39 ± 0.08	14.85 ± 3.04
CL18	19	3892 ± 496	2.73 ± 0.20	3.54 ± 0.28	1.68 ± 0.13	49.0 ± 3.64	0.74 ± 0.06	27.82 ± 2.15
CL20a	20	7106 ± 811	3.10 ± 0.27	3.87 ± 0.36	1.84 ± 0.17	54.7 ± 4.92	0.95 ± 0.08	35.87 ± 3.04
CL20b	20	4594 ± 1057	3.27 ± 0.81	5.10 ± 1.36	2.42 ± 0.64	66.1 ± 17.06	0.63 ± 0.13	24.29 ± 4.81
CL20c	20	1539 ± 198	3.34 ± 1.64	5.53 ± 2.77	2.62 ± 1.32	70.0 ± 34.76	0.50 ± 0.21	19.14 ± 8.18
CL21a	21	1433 ± 147	1.16 ± 0.33	1.68 ± 0.50	0.80 ± 0.24	22.2 ± 6.45	0.25 ± 0.06	9.32 ± 2.18
CL21b	21	2383 ± 262	2.26 ± 0.30	3.14 ± 0.45	1.49 ± 0.21	42.1 ± 5.79	0.52 ± 0.06	19.76 ± 2.23
CL23a	23	3322 ± 235	2.43 ± 0.43	3.37 ± 0.66	1.60 ± 0.31	45.3 ± 8.48	0.57 ± 0.07	21.76 ± 2.84
CL23b	23	2344 ± 246	3.36 ± 0.71	4.90 ± 1.06	2.33 ± 0.50	64.4 ± 13.81	0.67 ± 0.13	25.51 ± 4.78
CL24a	24	1711 ± 85	3.55 ± 1.08	5.58 ± 1.86	2.65 ± 0.88	71.7 ± 23.11	0.60 ± 0.13	22.96 ± 4.95
CL24b	24	883 ± 164	2.46 ± 0.38	3.85 ± 0.60	1.83 ± 0.28	49.4 ± 7.66	0.41 ± 0.06	15.54 ± 2.37
CL24c	24	1456 ± 221	5.87 ± 1.97	9.66 ± 3.36	4.58 ± 1.59	122.2 ± 42.05	0.86 ± 0.25	32.95 ± 9.81
CL27	27	3239 ± 338	3.52 ± 0.48	4.97 ± 0.71	2.36 ± 0.34	66.3 ± 9.29	0.78 ± 0.09	29.40 ± 3.60
CL30	30	2961 ± 234	7.17 ± 1.25	11.00 ± 2.09	5.22 ± 0.99	142.2 ± 26.21	1.26 ± 0.17	47.86 ± 6.48
CL33	33	3628 ± 486	10.27 ± 2.07	16.57 ± 3.42	7.86 ± 1.62	210.7 ± 43.14	1.58 ± 0.29	60.61 ± 11.14
CL35	35	3522 ± 492	12.97 ± 2.31	21.18 ± 3.79	10.04 ± 1.80	268.3 ± 47.87	1.91 ± 0.33	73.27 ± 12.79
CL48	48	1411 ± 231	13.82 ± 2.88	25.41 ± 5.54	12.04 ± 2.62	313.3 ± 67.55	1.55 ± 0.29	60.20 ± 11.32
CL68	68	1611 ± 147	22.37 ± 2.23	43.12 ± 4.56	20.43 ± 2.16	526.7 ± 55.11	2.22 ± 0.19	87.25 ± 7.67

Values are mean ± 1 SE. Parameters are exclusive to *Prosopis* stands and do not include the herbaceous component of each site. See Table 1 for an explanation of site name codes and Table 4 for concentration values used to derive C and N pools.
SC, shallow clay; CL, clay loam.

Appendix B

Table B1 Mean (\pm SE) mass of C and N in herbaceous biomass (live + standing dead) and litter sampled under any away from *Prosopis* canopies at selected in a temperature savanna of northern Texas, USA

Stand code	Herbaceous (live + standing dead)				Litter			
	C (Mg ha ⁻¹)		N (kg ha ⁻¹)		C (Mg ha ⁻¹)		N (kg ha ⁻¹)	
	Away	Under	Away	Under	Away	Under	Away	Under
SC12	0.37 \pm 0.08		9.6 \pm 2.2		0.07 \pm 0.03		2.5 \pm 1.0	
SC14	0.27 \pm 0.10		6.9 \pm 2.8		0.08 \pm 0.03		2.7 \pm 1.0	
SC15	0.61 \pm 0.15		16.5 \pm 4.3		0.17 \pm 0.03		5.4 \pm 1.1	
SC18	0.96 \pm 0.14	1.26 \pm 0.18	25.4 \pm 3.3	34.7 \pm 4.9	0.26 \pm 0.08	0.48 \pm 0.10	8.6 \pm 2.7	* 22 \pm 4.6
SC20	0.79 \pm 0.17	0.80 \pm 0.11	20.2 \pm 4.7	21.8 \pm 2.7	0.14 \pm 0.02	* 0.48 \pm 0.10	4.7 \pm 0.8	* 22 \pm 4.4
SC27	1.25 \pm 0.14*	* 2.00 \pm 0.30	30.5 \pm 3.0	* 52.3 \pm 8.3	0.74 \pm 0.18	* 1.53 \pm 0.15	24.5 \pm 6.0	* 69 \pm 7.0
CL19	1.07 \pm 0.17		27.9 \pm 4.3		0.22 \pm 0.06		7.2 \pm 2.1	
CL20a	1.38 \pm 0.27		33.8 \pm 7.7		0.50 \pm 0.11		16.5 \pm 3.8	
CL20b	1.27 \pm 0.30		29.9 \pm 6.9		0.37 \pm 0.08		12.3 \pm 2.6	
CL20c	1.01 \pm 0.33		24.1 \pm 7.6		0.17 \pm 0.04		5.7 \pm 1.3	
CL21a	1.91 \pm 0.22		46.0 \pm 5.8		0.47 \pm 0.09		15.6 \pm 2.8	
CL21b	1.34 \pm 0.18	1.46 \pm 0.17	32.0 \pm 4.6	36.5 \pm 4.2	0.54 \pm 0.08	* 1.25 \pm 0.15	17.7 \pm 2.6	* 56 \pm 6.9
CL23a	1.08 \pm 0.26		25.3 \pm 5.8		0.65 \pm 0.15		21.4 \pm 4.8	
CL24a	1.64 \pm 0.15		34.6 \pm 3.8		1.68 \pm 0.25		55.3 \pm 8.2	
CL24b	1.42 \pm 0.12	1.60 \pm 0.10	32.1 \pm 3.1	40.0 \pm 2.8	0.96 \pm 0.18	1.34 \pm 0.22	31.8 \pm 6.1	* 60 \pm 10.1
CL24c	1.26 \pm 0.23	1.10 \pm 0.10	26.3 \pm 4.6	26.5 \pm 6.9	1.00 \pm 0.19	* 1.79 \pm 0.22	32.8 \pm 6.2	* 81 \pm 9.7
CL27	1.11 \pm 0.13	1.30 \pm 0.12	25.5 \pm 2.9	32.5 \pm 3.0	0.68 \pm 0.14	1.27 \pm 0.24	22.3 \pm 4.6	* 57 \pm 11.1
CL30	0.95 \pm 0.14	1.30 \pm 0.22	24.0 \pm 3.5	33.8 \pm 5.8	0.43 \pm 0.09	* 0.94 \pm 0.13	14.1 \pm 2.9	* 42 \pm 5.9
CL33	0.64 \pm 0.07	0.69 \pm 0.07	14.5 \pm 1.7	16.8 \pm 1.4	0.54 \pm 0.07	* 1.48 \pm 0.26	17.9 \pm 2.4	* 67 \pm 11.9
CL35	0.66 \pm 0.10	0.67 \pm 0.07	14.7 \pm 2.1	16.3 \pm 1.6	0.63 \pm 0.14	* 1.49 \pm 0.32	20.6 \pm 4.7	* 64 \pm 13.2
CL68	0.51 \pm 0.18	0.27 \pm 0.08	13.3 \pm 5.0	6.3 \pm 1.9	1.03 \pm 0.19	* 1.90 \pm 0.27	34.0 \pm 6.1	* 86 \pm 12.2

C and N pools were estimated by multiplying biomass values by the appropriate concentration values in Table 4. An asterisk denotes a significant difference between locations 'under' and 'away' from *Prosopis* canopies, as determined from two-tailed *t*-tests assuming unequal variance ($P < 0.05$).

SC, shallow clay; CL, clay loam.