

BIOGEOCHEMICAL CHANGES ACCOMPANYING WOODY PLANT ENCROACHMENT IN A SUBTROPICAL SAVANNA

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Abstract. Ecosystem properties of surficial (0–10 cm) soils in remnant herbaceous patches were compared to those of contrasting woody plant patch types (upland discrete cluster, upland grove, and lowland woodland) where shifting land cover is known to have occurred over the past 50–77 yr. The purpose of this study was to evaluate and quantify the biogeochemical consequences and subsequent developmental rates of woody plant formation on sites formerly dominated by grasses.

Clay and water content of woodland soil patches was higher than that of soils associated with upland discrete cluster and grove patches. Even so, lowland woody patches were generally comparable to upland grove and discrete shrub cluster patches with respect to soil organic carbon (SOC), soil N, the ratio of annual N mineralization:total N, annual litterfall, and root biomass. The fact that finer soil texture, enhanced soil moisture, and the more advanced age of lowland woody patches did not translate into greater accumulations of SOC and N relative to upland grove and discrete cluster patches suggests that C and N losses might be higher in recently developed lowland woodland communities. Fluctuations in monthly root biomass standing crop (0–10 cm) far exceeded annual foliar litterfall in upland and lowland woody patch types, suggesting that belowground inputs of organic matter may drive changes in soil physical and chemical properties that occur subsequent to woody plant establishment.

The estimated annual mean rates of soil C accretion in the “islands of fertility” that developed subsequent to tree/shrub encroachment were variable and ranged from 8 to 23 g/m² (in groves and discrete clusters, respectively); N accretion ranged from 0.9 to 2.0 g/m² (in groves and discrete clusters, respectively), even though mean annual N mineralization rates were three- to fivefold greater than those measured in remnant herbaceous patches.

Woody plant proliferation in grasslands and savannas in recent history has been widely reported around the world. The causes for this shift in vegetation are controversial and center around changes in livestock grazing, fire, climate, and atmospheric CO₂. Our data, which are conservative in that they examine only the upper 10 cm of the soil profile, indicate that the rate and extent of soil C and N accumulation associated with this phenomenon can be rapid, substantial, and accompanied by increased N turnover. This geographically extensive vegetation change thus has important implications for understanding how the global carbon and nitrogen cycles may have been altered since Anglo-European settlement of arid and semiarid regions.

Key words: biogeochemistry; grass; grazing; landscape biogeochemistry; shrub; soil carbon; soil nitrogen; subtropical savanna; vegetation change; woody plant encroachment.

INTRODUCTION

Ecosystem biogeochemistry may be strongly influenced by plant species acting in concert with abiotic factors (Hobbie 1992). As a result, changes in vegetation composition can produce substantial changes in

carbon and nitrogen dynamics and accelerate or constrain future changes (Chapin 1993, Hooper and Vitousek 1997, Tilman et al. 1997). In arid and semiarid regions, trees and shrubs affect the spatial distribution and cycling of nutrients by altering soil structure, microbial biomass, soil moisture, and microclimate and by concentrating organic matter beneath their canopies (Binkley and Giardina 1998, Schlesinger and Pilmanis 1998). The result is the formation of “fertile islands” (but see Pauker and Seastedt [1996] for contrasting processes in alpine tree islands). This phenomenon has been widely described in cold desert scrub (e.g., Burke et al. 1989), hot desert scrub (Schlesinger et al. 1990, Kieft et al. 1998), temperate woodlands (Padien and Lajtha 1992), and tropical (Scholes and Archer 1997)

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and temperate (McPherson 1997) savannas. Soil properties in these fertile islands may be affected by species composition. Leguminous trees may enhance soil C and N in some cases but not in others (Abrams et al. 1990). In some instances, soil N pools in patches dominated by leguminous woody species may be greater than that of patches dominated by nonleguminous woody plants (Radwanski and Wickens 1967, Bernhard-Reversat 1982, Vitousek and Walker 1989). In other cases, N pools or mineralization rates may be comparable between legume and nonlegume woody patches (Garcia-Moya and McKell 1970, Belsky et al. 1993) and between deciduous tree legume and evergreen shrub patches (Mazzarino et al. 1991).

Although the biophysical characteristics of vegetative islands of fertility have been widely quantified, we know little of their rates of formation. An understanding of their developmental rates is of particular relevance in grassland and savanna systems, where woody plants have displaced grasses in recent history. How, to what extent, and at what rate do soil properties change when woody plants establish on sites formerly dominated by grasses? Answers to such questions are required if we are to effectively evaluate the biogeochemical consequences of woody plant encroachment, a widespread phenomenon in arid and semiarid grasslands and savannas over the past century (Grover and Musick 1990, Archer 1994, Archer et al. 2001).

The Rio Grande Plains of southern Texas and northern Mexico are a case in point. Historical accounts describe extensive grasslands and open savannas in this region at the time of Anglo-European settlement (Inglis 1964), and plant geographers have classified the potential natural vegetation as *Prosopis-Acacia-Andropogon-Setaria* savanna (Küchler 1964). However, the present-day vegetation is characterized by thorn scrub and thorn woodland (McMahan et al. 1984). This apparent transformation of grasslands and open savannas into thorn woodlands has been the focus of a series of coordinated investigations at the La Copita Research Area in southern Texas. The $\delta^{13}\text{C}$ of soil organic carbon indicates that tree/shrub patches on upland and lowland landscapes at this site occupy soils once dominated by C_4 grasses (Tieszen and Archer 1990, Boutton et al. 1998, Gill and Burke 1999). Historical aerial photography (Archer et al. 1988), plant growth models (Archer 1989), landscape-scale patch transition models (Scanlan and Archer 1991), and tree ring records (Boutton et al. 1998) all substantiate that tree and shrub abundance at this site has increased markedly over the past 100 yr.

The formation of woody patches at the La Copita site begins when the tree legume *Prosopis glandulosa* (honey mesquite) establishes in grassland patches and subsequently modifies soils and microclimate to facilitate the ingress and establishment of diverse assemblages of evergreen and deciduous shrubs beneath its canopy (Archer et al. 1988). As new shrub clusters are

initiated and existing clusters enlarge, coalescence occurs and closed-canopy woodlands develop. This process appears to have progressed to completion on more mesic portions of the landscape (clay loam intermittent drainages). On drier sandy loam uplands, this process appears to be in progress and mediated by variations in subsurface clay content. Where claypan horizons (B_t) are well developed (starting at ~ 40 cm depth), small, discrete clusters of woody plants are dispersed throughout a grassy matrix. Where the claypan horizon is absent, extensive *Prosopis* groves have developed. The *Prosopis* plants in these groves are larger, produce more seeds, and occur at higher densities than *Prosopis* plants growing where the argillic horizon is well developed (Archer 1995). Spatial variation in the development of this horizon, which is a significant barrier to root penetration and water percolation (cf. McAuliffe 1994), has therefore influenced above- and below-ground biomass (Watts 1993), hydrology (Loomis 1989), and patterns of woody plant development (Stokes 1999) across the landscape. The rate and extent of biogeochemical changes caused by woody plant encroachment in these contrasting topoedaphic settings (uplands with argillic horizon vs. uplands without argillic horizon vs. lowlands) is unknown.

The expansion of N-fixing species such as *Prosopis glandulosa* into nutrient-poor sites can have profound effects on landscape-level biogeochemistry (Tiedemann and Klemmedson 1973a, b, Virginia 1986, Vitousek 1986, 1990, Vitousek and Walker 1989). Here we compare and contrast soil properties associated with remnant grassland patches to that of *Prosopis*-dominated discrete cluster, grove, and woodland patches that have recently developed in sandy loam uplands (clusters and groves) and clay loam lowlands (woodlands). From this, we infer how and to what extent landscape biogeochemistry has changed with the establishment of woody plants on a former grassland landscape. We hypothesized that (1) soil C, N, and N mineralization (N_{min}) would be lowest in remnant herbaceous patches and greatest in woody patches, and (2) among upland woody patches, the surface soils of groves (argillic horizon absent) would have a greater soil C, N, and N_{min} than their discrete cluster counterparts (argillic horizon present). Given that soil clay content is positively correlated with N_{min} and retention of C and N (Jones 1973, Oades 1988, Buyanovsky et al. 1994), that clay loam intermittent drainages receive runoff from sandy loam uplands, and that lowland woodland patches are potentially more advanced than upland groves or upland discrete clusters in terms of their successional development, we hypothesized that (3) the extent of soil C and N accumulation and enhancement of N_{min} in lowland woodland patches would exceed that of upland discrete cluster and upland grove patch types.

STUDY SITE

Our field site was the La Copita Research Area (LCRA) located on the Rio Grande Plains in the eastern

portion of the Tamaulipan Biotic Province, 24 km southwest of Alice, Texas (27°40' N, 98°12' W). The climate of this region is semiarid and subtropical, with hot, dry summers and mild winters. Winter and summer temperatures average 14°C and 28°C, respectively. Long-term annual average precipitation (720 mm) is bimodally distributed, with maxima in late spring and early autumn (USDA 1979).

Current vegetation of the region is subtropical thorn woodland (Blair 1950, McMahan et al. 1984, McLendon 1991). Landscapes of the LCRA are characterized by a polygonal structure consisting of convex sandy loam uplands that grade (1–3% slopes) into surrounding clay loam intermittent drainages. Vegetation of uplands consists of small, discrete clusters (3–10 m diameter) and larger groves (10 to >20 m diameter) of woody vegetation embedded in a herbaceous matrix. The site has a long history of heavy, continuous livestock grazing. Hence, herbaceous patches consisted primarily of C₃ forbs and early seral rhizomatous and weakly caespitose C₄ grasses with relatively uniform cover. Discrete clusters and herbaceous zones are associated with soils having a well-developed argillic (B_t) horizon (Typic Argiustoll); in contrast, groves occur on inclusions with minimally developed B_t horizons (Typic Ustochrepts; Archer 1995). Lowlands (Pachic Argiustolls), which receive runoff from the sandy loam uplands and have intermittent water flow in high rainfall periods, are characterized by closed-canopy woodlands. *Prosopis glandulosa* var. *glandulosa* (Torr.) (honey mesquite; plant nomenclature follows Correll and Johnston [1979]) typically dominates the overstory of discrete clusters, groves, and woodlands. Understory shrubs are ubiquitously distributed among discrete cluster, grove, and woodlands and consist of evergreen, deciduous, and drought-deciduous growth forms. *Prosopis* is an N-fixing woody plant (potentially) as are some of the associated Rhamnaceae shrubs (*Condalia*, *Ziziphus*, *Karwinskia*). However, available evidence suggests symbiotic N fixation by the understory shrubs at this site is minimal (Zitzer et al. 1996). See Scifres and Koerth (1987), Archer (1995), and Boutton et al. (1998) for additional details on soils, vegetation, and climate.

METHODS

Sampling protocol

Plant and soil characteristics of herbaceous, discrete cluster, and grove patches in uplands were quantified and compared to those of closed-canopy woodlands in lowlands. To minimize variability associated with potential age-state differences within woody patch types, we restricted our sampling to undisturbed patches deemed “mature” as indicated by *Prosopis* size and understory richness (Archer 1995). Six patches of each type were sampled on each of two landscapes. Remnant grass-dominated patches were used as a baseline

against which to gauge changes in soil C and N density subsequent to woody plant encroachment. Rates of C and N accumulation (in grams per square meter per year) were calculated by subtracting the mean baseline value from the measured level in a patch and dividing that value by patch age.

Remnant grassland patches occurred only in sandy loam uplands. We therefore used a process-based ecosystem model (CENTURY; Parton et al. 1987, 1993) to estimate what soil C density would have been when woody plants began establishing on clay loam portions of the landscape. Soil carbon in lowlands were initialized in CENTURY with current upland values. Pre-settlement grazing and fire regimes were estimated as light grazing from native herbivores and fire every 10 yr. The grassland submodel of CENTURY was then run for 5000 yr with equilibrium reached at ~2500 yr. Next, equilibrium soil C values were used to initialize a simulation that took into account soil texture and climate under conditions of heavy, continuous grazing and no fire since the mid-1800s, yielding a baseline estimate of 1400 g C/m² in lowland grasslands. Soils at the edge of *Prosopis* canopies in lowland woodlands had organic carbon values ranging from 1210 to 1590 g C/m² (T. W. Boutton and S. Archer, unpublished data). These values for soils collected from areas minimally influenced by overstory woody plants bracketed the CENTURY predictions. In addition, a similar parameterization of CENTURY for sandy loam uplands at the La Copita site yielded estimates of soil organic carbon (SOC) within 3% those observed in remnant sandy loam grass patches and comparable to those which have been reported in the literature (see Hibbard 1995 for details). We took these as (1) support for our assumption that remnant upland grasslands were a reasonable baseline for gauging changes in soil C and N subsequent to woody plant colonization and (2) evidence that model-derived estimates of the soil C and N baseline in clay loam intermittent drainage grasslands were reasonable.

Vegetation and soil characterization

Species composition, height of the shrub understory, and height of the *Prosopis* overstory were determined in woody patches. Basal diameter of *Prosopis* was measured and stem age was estimated from patch-specific annual ring count–bole diameter regressions ($R^2 > 0.78$; Flinn et al. 1994, Stoker and Archer 1996). In March 1992, duplicate soil cores (0–10 cm) were collected from each patch. The extent to which soil properties might change along gradients from the *Prosopis* bole to canopy edge is unknown. We therefore standardized sampling in woody patches to the area ~1 m from the *Prosopis* bole. The typical distance from the bole to the canopy dripline was 3–6 m depending on patch type, hence we were consistently well within the zone where soils would have experienced prolonged woody plant influence. Soils sampled in herbaceous

patches were obtained well beyond (≥ 3 m) the canopies of woody plant patches. The site had neither large caespitose bunchgrasses nor heterogeneous mats of sod-forming grasses. As a result, we had no a priori reason to stratify sampling under vs. away from grass plants as has been done in other systems (cf. Burke et al. 1998). Because individual grass plants were small in terms of basal area, the soil in a typical core sample would be partially occupied by a grass plant and partially by "bare ground." As a result, a reasonably integrated assessment of C, N, and N_{\min} in the herbaceous portions of the uplands was obtained.

For logistical reasons we restricted our sampling to the upper 10 cm of soil, where the majority of microbial activity (Schimel et al. 1985a) and root biomass (Jackson et al. 1996) occur. Previous studies at the La Copita site have substantiated these generalizations for root biomass in woody and herbaceous patches (Watts 1993, Boutton et al. 1998, 1999) and showed that plant effects on soil C and N concentrations were most pronounced in the upper 15 cm of the soil profile (Archer 1995). Although upland grove and discrete woody cluster patch types differ with respect to subsurface soil features (e.g., expression of argillic horizon at 40–100 cm) it was beyond the scope of this study to characterize C and N pool and N_{\min} at these greater depths. Rather, and as a first approximation, we sought to ascertain whether these differences in subsoil properties might be manifested in near surface C and N pools and N_{\min} via integrated effects on above- and belowground biomass (see Watts 1993), species composition, hydrology (see Loomis 1989), microclimate, etc. Quantification of whole-profile C and N mass has been addressed in a companion study (Boutton et al. 1998, 1999; T. W. Boutton and S. Archer, *unpublished manuscript*).

Soil samples were pooled, dried at 60°C for 48 h, ground to pass through a 0.1-mm sieve, and analyzed for soil texture (Gee and Bauder 1986). Total organic C and N were determined using an automated C/N analyzer (Carlo Erba Instruments, Saddle Brook, New Jersey, USA). Soil pH was measured with a glass electrode (1 : 1, soil : H₂O). Bulk density (Blake and Hartge 1986) was determined on a random sample of one-third of the cores from each patch type. Water-holding capacity at -0.3 and -1.5 MPa was determined on subsamples dried at 100°C (Klute 1986).

Net nitrogen mineralization

Monthly N_{\min} was determined using the resin-core method (Di Stefano and Gholz 1986) for an annual cycle (May 1992–April 1993). At the beginning of each month, aluminum sleeves (2 cm diameter, 10 cm deep) were used to extract soils in each patch. Sleeves containing the extracted soils were then fitted with resin bags at each end and reinserted flush with the soil surface (and within 1 m of the bole of the *Prosopis* plant in woody patches). Resin bags placed at the top of the sample sleeve intercepted dry- and wet-deposition nu-

trients; resin bags at the bottom of the sleeve collected nutrients mineralized and leached from soils within the sleeve. Another core (2 × 10 cm) was extracted nearby, sealed in a sterile plastic bag, placed in an insulated cooler with chemical ice, and transported to the laboratory where it was stored at 4°C. At the end of each month, the soils and resin bags in the sleeves were similarly collected and stored. Gravimetric soil water content was determined on subsamples obtained at the time cores were collected.

Coarse roots were removed by hand and soils were then sieved through a 2-mm screen to remove finer roots and organic debris. Inorganic N (ammonium [NH₄⁺], nitrate [NO₃⁻], and nitrite [NO₂⁻]) was extracted from bottom resin bags and root-free soils with 2 mol/L KCl as described by Binkley (1984) and Schimel et al. (1985a). Phenylmercuricacetate (PMA; 5 μg/g) was used to inhibit microbial activity during extract storage. Extractions were analyzed (TRAACS 800 Autoanalyzer, Chicago, Illinois, USA) for NH₄⁺ (Bran and Luebbe 1987a) and NO₃⁻/NO₂⁻ (Bran and Luebbe 1987b). Bags containing resins from the batch used in field trials ($n = 5$) were prepared each month and extracted along with resins collected from field bags, thus serving as resin controls. Net nitrogen mineralization (N_{\min}) was calculated as the sum of incubated soil and resin-bag nitrogen minus the N concentrations present in soils collected the month previously.

Above- and belowground biomass

Aboveground biomass in herbaceous zones at locations ≥ 3 m beyond woody plant canopies was estimated by clipping randomly located 0.25 × 0.25 m plots every other month during 1992–1993. Biomass was sorted into forb and grass, green and nongreen tissue, oven-dried at 50°C for 48 h, and weighed. Litter deposition in wooded patches was collected monthly from 50 × 30 × 6 cm traps (2 trays per patch), oven-dried at 50°C for 48 h, and weighed. A subsample (25% by mass) of total litterfall biomass was sorted into foliage + fruit + flower (by species), duff (unrecognizable litter), and woody stem categories. This subsample was then used to estimate the composition of the total sample.

Coarse root biomass (in grams per square meter) in soil cores (2 cm diameter; 10 cm depth) was estimated by removing root segments >1 mm diameter by hand. We did not feel confident in distinguishing live from dead roots based on visual or tactile criteria, hence we report total root mass. Soils were then passed through a 250-mm mesh screen and stirred into a saturated NaCl solution (density ~1.2 g/cm³). Fine roots that floated to the surface of the saturated solution were suctioned off. The solution was stirred a second time, and fine root removal by suctioning was repeated. Preliminary trials indicated that these two mixing–floating bouts yielded 90% of the recoverable fine root biomass. Roots were dried at 50°C for 48 h and weighed. Samples from

June 1993 were ashed at 700°C, and a correction factor for soil contamination and ash content of fine root samples was developed:

$$\text{Light Fraction SOM} = 0.115 + [0.369 \times \text{floated biomass}]. \quad (1)$$

This correction factor ($r^2 = 0.90$, $P < 0.001$) was applied to the fine root mass extracted for all sample dates.

Statistical analyses

For logistical reasons, rather than randomly sample among patch types each month, we followed the same woody and herbaceous patches through time. Differences in monthly values of root biomass, litterfall, soil moisture, NH_4^+ , NO_3^- , and N_{\min} between patch types over an annual cycle were therefore tested using repeated-measures ANOVA with a randomized block design. Patch type differences in annual N_{\min} , annual litterfall, and vegetation and soil properties were assessed by standard ANOVA. Multiple mean comparisons were performed using the Bonferroni method as sample sizes were small (<50 ; Johnson and Wichern 1992). Single and stepwise multiple regression analyses were performed to assess the proportion of variance in seasonal and annual N_{\min} explained by edaphic (percentage of carbon, nitrogen, texture, pH, bulk density, and percentage of soil moisture), climatic (monthly precipitation, average air temperature), and biotic (foliar litterfall) variables. All analyses were conducted using SYSTAT version 5.2 for the Macintosh (SYSTAT 1992). Unless otherwise noted, differences were regarded as significant when $P \leq 0.05$.

RESULTS

Contrasts between woody patches

Overstory *Prosopis* plants in mature grove and woodland patches were comparable in size and larger than those in mature discrete clusters (Table 1). However, height and species richness of understory shrubs were similar among these woody patch types. The age of *Prosopis* plants in mature woodland patches (77 yr) was, on average, greater than that of *Prosopis* plants in mature discrete cluster (50 yr) and grove (58 yr) patches.

Soil carbon and nitrogen content (in percentages and in grams per square meter) and bulk density were statistically comparable between the different woody patch types (Table 2) as were C/N ratios (11.6–12.2). Upland woody patch types (groves and clusters) were similar in soil texture and had lower proportions of clay and higher proportions of sand than lowland woody patches. Soils associated with lowland woodlands had the greatest water holding capacity (Table 2) and seasonal gravimetric soil moisture content (Fig. 1a). Regression analysis indicated basal diameter of the overstory *Prosopis* plant explained 30% of the variance

TABLE 1. Structural characteristics of woody patches at the La Capita Research Area, 24 km southwest of Alice, Texas, USA.

Attributes	Uplands		Lowlands
	Clusters	Groves	Woodlands
<i>Prosopis</i>			
Basal diameter (cm)	17.8 (1.1) ^a	27.3 (1.8) ^b	32.1 (3.0) ^b
Height (m)	3.3 (0.2) ^a	4.9 (0.2) ^b	5.2 (0.2) ^b
Estimated age†	50 (3) ^a	58 (3) ^a	77 (6) ^b
Understory			
Height (m)	2.4 (0.2) ^a	2.6 (0.1) ^a	2.7 (0.2) ^a
No. woody spp.	7 (0.4) ^a	6 (0.4) ^a	6 (0.5) ^a
Annual litterfall (g·m ⁻² ·yr ⁻¹)			
<i>Prosopis</i> foliage	10 (4) ^a	61 (4) ^b	64 (9) ^b
Total foliar	247 (17) ^a	288 (22) ^{a,b}	381 (44) ^b
Foliar + duff	293 (35) ^a	353 (27) ^{a,b}	465 (53) ^b
Stems	184 (35) ^a	161 (26) ^a	134 (23) ^a

Notes: Means (1 SE) within a row followed by different letters were significantly different. The sample size was 12 for all woody patches unless otherwise noted.

† Based on size–age relationships from Stoker and Archer (1996).

in annual foliar litterfall. However, understory shrubs dominated annual litterfall in woody patches, with the overstory leguminous *Prosopis* plants contributing $<20\%$ of the total foliar input (Table 2). Annual foliar litter input was greatest in woodlands (381 ± 44 g·m⁻²·yr⁻¹, means ± 1 SE) and lowest in discrete clusters (247 ± 17 g·m⁻²·yr⁻¹); annual stem litterfall was comparable among woody patches.

Foliar litter deposition was generally steady and continuous at ~ 20 – 40 g·m⁻²·mo⁻¹ in summer (May–September) and continuous but lower (~ 5 – 15 g·m⁻²·mo⁻¹) during winter (November–April; Figs. 1b and 2a). Discrete, patch-specific pulses of foliar and stem litter input contributed to a significant patch type \times time interaction ($P < 0.001$). The large leaf-fall spike observed in July in woodland patches appears to have been in conjunction with an intense 220-mm rainfall event (Fig. 1b). Stem litterfall was typically <15 g·m⁻²·mo⁻¹ and did not vary significantly among patch types (data not shown; see Hibbard 1995).

Monthly coarse and fine root biomass (live + dead) ranged from ~ 100 to >1100 g/m² (Fig. 2b, c), whereas monthly foliar litterfall ranged from 10 to 110 g/m² (Fig. 2a). Root biomass varied significantly between patch types and with time ($P < 0.001$), but the patch type \times time interaction was not significant. Coarse root biomass for discrete clusters consistently exceeded that of other patch types and peaked in July and August.

Among woody patches, N_{\min} rates were typically highest in upland discrete clusters and lowest and most variable in lowland woodlands (Table 2, Fig. 3a). Even so, the proportion of total N mineralized was comparable in cluster, grove, and woodland patches (12–13%). Seasonal trends in monthly N_{\min} were not apparent (Fig. 3a). The interaction between patch type and time was highly significant, indicating that factors

TABLE 2. Soil characteristics (0–10 cm) for herbaceous patches and discrete cluster, grove, and woodland patches occupying former grassland.

Characteristic	Uplands			Lowlands
	Herbaceous	Clusters	Groves	Woodlands
Bulk density (g/cm ³)	1.4 (0.01) ^a	1.1 (0.04) ^b	1.1 (0.03) ^b	1.1 (0.03) ^b
pH	6.7 (0.2) ^a	6.8 (0.2) ^a	5.8 (0.2) ^b	6.2 (0.2) ^{a,b}
Clay (%)	20 (0.7) ^a	20 (1.0) ^a	18 (0.7) ^a	31 (1.5) ^b
Sand (%)	69 (0.8) ^a	66 (1.3) ^a	69 (1.0) ^a	54 (1.8) ^b
Carbon (%)	0.84 (0.05) ^a	2.2 (0.23) ^b	1.4 (0.2) ^{a,b}	2.3 (0.5) ^b
Nitrogen (%)	0.07 (0.00) ^a	0.18 (0.02) ^b	0.12 (0.01) ^{a,b}	0.20 (0.05) ^b
Carbon (g/m ²)	1165 (67) ^a	2352 (276) ^b	1623 (185) ^b	2551 (480) ^b
Nitrogen (g/m ²)	91 (6) ^a	192 (20) ^b	137 (16) ^b	220 (51) ^b
Accumulation rate [†]				
Carbon (g C·m ⁻² ·yr ⁻¹)	na [‡]	23 (7) ^a	8 (3) ^a	14 (5) ^a
Nitrogen (g N·m ⁻² ·yr ⁻¹)	na	2.0 (0.5) ^a	0.9 (0.3) ^b	na
Leached N (μg·g ⁻¹ ·yr ⁻¹)	19 (4) ^a	41 (5) ^b	44 (7) ^b	55 (12) ^b
N _{min} (g·m ⁻² ·yr ⁻¹)	6 (1) ^a	22 (2) ^b	16 (2) ^b	14 (3) ^{a,b}
N _{min} (μg·g ⁻¹ ·yr ⁻¹)	42 (5) ^a	200 (18) ^b	137 (16) ^{b,c}	127 (29) ^c
Range	3–68	109–331	66–235	102–363
CV (%)	41	30	40	80
Percentage of N mineralized	7 (1) ^a	12 (2) ^b	12 (2) ^b	13 (5) ^b
Potential water holding capacity (% volumetric)				
–0.3 MPa	12 (1) ^a	13 (2) ^a	13 (2) ^a	20 (2) ^b
–1.5 MPa	8 (1) ^a	10 (1) ^a	8 (1) ^a	15 (1) ^b
Contribution to landscape (%) [§]				
SOC	10	2	14	74
Total N	9	3	10	78
N _{min}	9	5	17	69

Notes: Means (1 SE) within a row followed by different letters were significantly different ($n = 12$).

[†] Values are means of present-day remnant herbaceous patches used as a baseline in upland grove and cluster patches; CENTURY simulations were used to estimate the soil organic C (SOC) baseline in woodland patches (1400 g/m²).

[‡] Data not available.

[§] Area of each patch type (as determined on 1983 aerial photos [Scanlan and Archer 1991]) was multiplied by its C and N density and annual N_{min}. These were then summed to give landscape-scale estimates. The proportion contributed by each patch type to the landscape total is presented here.

influencing N_{min} were behaving differently in the contrasting patch types. Monthly N_{min} in discrete clusters and groves of uplands generally tracked each other fairly closely. N_{min} rates in lowland woody patch types were consistently lower than N_{min} rates in upland woody patches from October to February, when mean monthly temperatures were <15°C (Fig. 1a).

Total nitrogen leached into resin bags generally followed precipitation (data not shown). Mean annual losses of mineralized nitrogen into resin bags ranged from 41 to 55 μg·g⁻¹·yr⁻¹ and were statistically comparable among woodland, grove, and discrete cluster patches (Table 2). Nitrogen leached on a monthly basis ranged from 0.1 to 11.4 μg/g and varied significantly with respect to time, patch type, and their interaction ($P < 0.001$; data not shown). Initial and mineralized nitrate (NO₃⁻) concentrations were comparable to total N_{min} (Fig. 3) and were generally twice the levels of initial and mineralized NH₄⁺ (data not shown; see Hibbard 1995). Exclusion of root uptake in sample cores eliminated nitrifiers' competition for NH₄⁺ and possibly enhanced nitrate production. However, the initial high NO₃⁻ concentrations in all patches suggests that nitrification was occurring even in the presence of plant roots.

Simple and multiple regression analyses failed to reveal significant relationships between annual N_{min} and climatic (mean monthly temperature and precipitation) or edaphic (percentage of C, percentage of N, texture, bulk density, pH, and gravimetric moisture content) variables. Correlations between N_{min} and *Prosopis* basal diameter ($r = -0.37$), foliar litterfall ($r = -0.18$), and total evergreen (*Zanthoxylum fagara* + *Mahonia trifoliata*) litterfall ($r = 0.26$) were significant, but low. The proportion of total litterfall contributed by shrubs classified as "evergreen" in woody patches ranged from 0% to 82%, but accounted for only 4% of the variation in N_{min}.

Contrasts between woody and herbaceous patches

Relative to near surface (0–10 cm) soils of remnant grass-dominated patches, soils associated with woody plant patches had lower bulk densities (1.1 vs. 1.4 g/cm³; Table 2) and consistently higher fine and coarse root biomass (Fig. 2b, c). Soils associated with woody patches also had higher SOC (0.8% vs. 1.4–2.3%), N (0.07% vs. 0.12–0.20%; Table 2), and NO₃⁻ (Fig. 3b, c) concentrations than herbaceous patches. We estimated the mean rates of annual C and N accretion in these fertile islands that have developed subsequent to

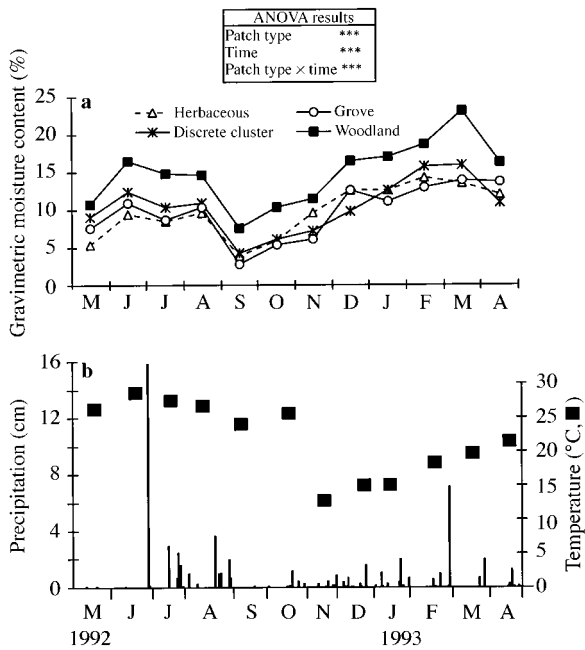


FIG. 1. (a) Mean gravimetric soil moisture content (0–10 cm depth; $n = 12$) of herbaceous and woody patches and (b) daily precipitation and average monthly temperature for the La Copita Research Area, 24 km southwest of Alice, Texas, USA, during the study period. ANOVA contrasts between patch type, time, and their interaction are shown in the inset (***) $P < 0.001$.

tree/shrub establishment in grass patches to have ranged from 8 to 23 g C/m² and 0.9 and 2.0 g N/m² (in groves and in clusters, respectively; Table 2).

Accumulation of C and N in surface soils influenced by woody plants occurred even though mean annual N_{min} rates in soils of tree/shrub patches (127–200 $\mu\text{g}\cdot\text{g}^{-1}\cdot\text{yr}^{-1}$) were three- to fivefold greater than those measured in herbaceous patches (42 $\mu\text{g}\cdot\text{g}^{-1}\cdot\text{yr}^{-1}$; Table 2). Monthly N_{min} rates in herbaceous patches never exceeded 10 $\mu\text{g}/\text{g}$ (Fig. 3a). In contrast, peak monthly N_{min} in mature woody patches was 35 $\mu\text{g}/\text{g}$. Annual resin bag N was lowest in grassland patches ($19 \pm 4 \mu\text{g}\cdot\text{g}^{-1}\cdot\text{yr}^{-1}$; range = 0.1–6.1 $\mu\text{g}\cdot\text{g}^{-1}\cdot\text{mo}^{-1}$) and highest in woody patches (41–55 $\mu\text{g}\cdot\text{g}^{-1}\cdot\text{yr}^{-1}$; range = 0.1–11.4 $\mu\text{g}\cdot\text{g}^{-1}\cdot\text{mo}^{-1}$; Table 2). The fraction of total annual mineralized N in leached into resin bags was greatest in grassland (45%) and woodland (43%) soils, followed by grove (32%) and discrete cluster (21%) soils. Although C/N ratios differed only slightly between herbaceous (12.8) and woody (11.6–12.2) patches, the proportion of total N mineralized in tree/shrub patches (12–13%) was significantly higher than that mineralized in grass patches (7%).

On an area-weighted basis, upland herbaceous patches accounted for only 9–10% of the organic carbon, total N, and annual N_{min} in the upper 10 cm of soils on the La Copita landscape (Table 2). Lowland woodlands clearly dominated, accounting for 74% of the land-

scape-scale SOC, 78% of total soil N, and 69% of the annual N_{min} .

DISCUSSION

C, N, and N_{min} in contrasting woody patches

C and N pools and rates of N_{min} in soils associated with woody and herbaceous patches at the La Copita savanna parkland/woodland site fell within ranges reported for other semiarid savannas, shrublands, and grasslands (e.g., Bernhard-Reversat 1982, 1988, Burke et al. 1989, Mazzarino et al. 1991, Virginia et al. 1992, Belsky et al. 1993, Fenn et al. 1993, Ruess and Seagle 1994). Woody plant patches in sandy loam uplands (clusters and groves) were structurally different from each other and from woody patches in clay loam intermittent drainages. *Prosopis* trees in upland groves, which have developed where the argillic horizon is

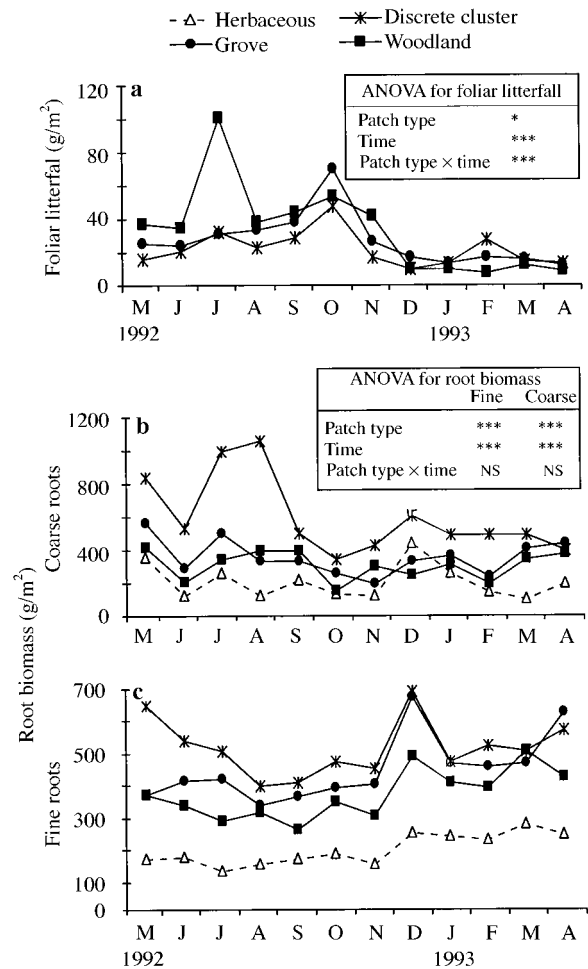


FIG. 2. (a) Mean foliar and stem litterfall biomass from woody patches and (b) coarse and (c) fine root biomass (0–10 cm) from herbaceous and woody patches ($n = 12$). Note that the root biomass estimates include live and dead roots. ANOVA contrasts between patch type, time, and their interaction are shown in the insets (* $P < 0.05$, *** $P < 0.001$, NS = nonsignificant at $P > 0.05$).

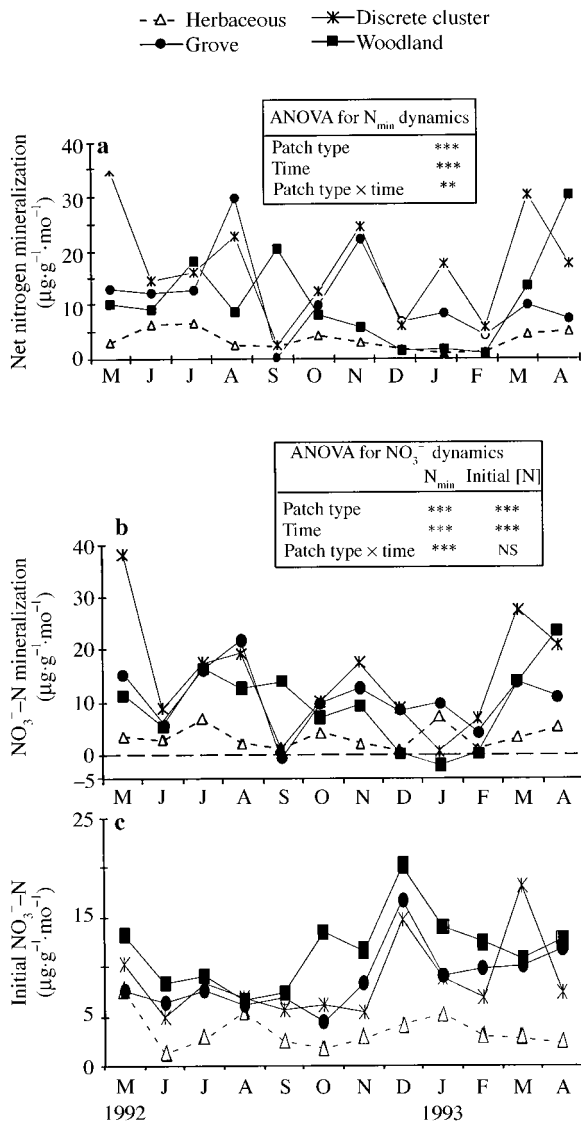


FIG. 3. Mean values for (a) net nitrogen mineralization, (b) nitrate mineralization, and (c) initial nitrate concentrations in herbaceous and woody patches ($n = 12$). ANOVA contrasts between patch type, time, and their interaction are shown in the insets (** $P < 0.01$, *** $P < 0.001$, NS = nonsignificant at $P > 0.05$). See Table 2 for detailed mean comparisons between woody and herbaceous patch types.

poorly expressed, were larger than *Prosopis* plants in discrete clusters underlain by a well-developed argillic horizon (Table 1). We therefore hypothesized that soils associated with groves would have greater levels of soil C and N and higher rates of N_{\min} than soils associated with discrete clusters. This was not the case (Table 2). In fact, although soil C and N and N_{\min} were statistically comparable, there was a consistent tendency for mean values in discrete clusters to exceed that of groves. Grove and discrete cluster patches were similar with respect to their mean ages (50 vs. 58 yr) and with respect to soil physical features that might be

expected to influence C and N accumulation or turnover (bulk density, texture, water holding capacity, and water content; Table 2, Fig. 1a). Greater foliar litter input from the larger *Prosopis* plants in groves was nearly negated by higher inputs from understory shrubs in clusters. The slightly higher seasonal aboveground litter inputs in groves may have been offset by the slightly higher seasonal root production in discrete clusters (Fig. 2). The net result was that soil C and N pools, accumulation rates, and N_{\min} rates were statistically comparable in contrasting upland woody patches.

Past studies have demonstrated that the presence/absence of the argillic horizon in uplands has a dramatic affect on total woody plant biomass (groves \gg clusters) and on biomass allocation above- and below-ground. (Groves have greater aboveground biomass supported by less belowground biomass to 1.5 m depth; root biomass in clusters is skewed to the upper 40 cm, whereas grove plants have a larger fraction of root mass below 40 cm [Watts 1993].) Even so, we saw little manifestation of these striking subsoil contrasts in surficial soils (Fig. 3, Table 2). Above- and belowground biomass (to >1.5 m) is currently being quantified (T. W. Boutton and S. Archer, *unpublished manuscript*). These "whole profile" perspectives will likely shed more light on cluster-grove-woodland contrasts and will provide a more comprehensive assessment of C and N stocks.

Clay content of soils is often positively correlated with high retention of soil organic C and N (Jones 1973, Schimel et al. 1985a, b, Oades 1988, Buyanovsky et al. 1994) and high C and N mineralization rates (Has-sink 1992). As a result, N_{\min} and nutrient concentrations typically increase from upland to lowland positions along catena gradients (Pastor et al. 1984, Schimel et al. 1985a, b, Gosz and White 1986, Burke et al. 1989, 1995). We therefore hypothesized soil C and N pools and N_{\min} rates would be lowest in upland discrete cluster and grove patches developing on coarse-textured surface soils and highest in woodland patches developing in clay loam intermittent drainages. As expected, soils of intermittent drainages had a higher clay content (31% vs. 18–21%; Table 2), a higher soil water holding capacity (Table 2), and a higher seasonal water content (Fig. 1a) than soils of uplands. In addition, time of woody plant occupancy in lowlands (77 yr) exceeded that for uplands (50–58 yr; Table 1). Even so, annual N_{\min} , soil C and N levels, and rates of C and N accumulation in lowland woody patches were not statistically elevated relative to upland woody patches (Table 2). In fact, N_{\min} expressed on a mass basis was actually higher in discrete clusters. Foliar litter inputs (Table 1, Fig. 2a) and root biomass (Fig. 2b, c) were also statistically comparable among upland and lowland patches, as were soil respiration rates measured over an annual cycle in a separate study (McCulley 1998). Summertime in situ NO emissions from woodland soils (10.6 ± 3.0 ng \cdot cm $^{-2}\cdot$ h $^{-1}$) exceeded those from upland

grove ($2.8 \pm 0.3 \text{ ng}\cdot\text{cm}^{-2}\cdot\text{h}^{-1}$) and herbaceous patch soils ($0.2 \text{ ng}\cdot\text{cm}^{-2}\cdot\text{h}^{-1}$; Cole et al. 1996), suggesting denitrification losses in woodland soils were offsetting accumulations that might otherwise be expected (Paul and Van Veen 1978, Brubaker et al. 1993).

Variability in N_{\min} of semiarid shrub (Burke et al. 1989), forest (Reich et al. 1997), and savanna systems (Bernhard-Reversat 1982, Ruess and Seagle 1994) has been attributed to various combinations of climatic (temperature and precipitation), edaphic (texture, total N, C : P, electrical conductivity, soil moisture, and water holding capacity), and biotic (litterfall N, net primary production, and plant growth form) factors. However, for this subtropical savanna parkland/woodland system, neither single nor multiple combinations of patch age, climatic variables, litterfall mass, root mass, or surficial soil characteristics explained a significant amount of variation in annual or seasonal net N_{\min} . It therefore appears that various climatic, topoeadaphic, and biotic factors interacted in nonlinear or offsetting ways to affect the nitrogen dynamics in tree/shrub patches on this site. A more detailed accounting of species or growth-form leaf and root litter chemistry and decomposition kinetics may be required to explain the observed variation in C and N dynamics in contrasting tree/shrub patch types in this subtropical system (e.g., Hooper and Vitousek 1997).

Contrasts between woody and herbaceous patches

Past research at the La Copita site has demonstrated that discrete clusters, groves, and woodlands have developed on former grasslands over the past 100 yr (Archer 1995, Boutton et al. 1998). Compared to soils of remnant herbaceous patches, the soils associated with these tree/shrub patches had higher rates of N_{\min} , a lower bulk density, greater pools of soil C and N, and a greater mineralized N pool fraction (Table 2). The extent to which the high C and N soil pools in woody patches represents net gains associated with woody plant occupation vs. net losses from remnant herbaceous patches is open to debate. The site has a history of heavy, continuous livestock grazing dating back to the early to mid-1800s. A low cover of ephemeral dicots and short-statured, weakly perennial grasses dominates the present-day herbaceous patches at the La Copita site. In contrast, herbaceous patches on relict, protected grasslands in the region are characterized by mid- to tall-statured perennial grasses whose potential productivity ($500\text{--}600 \text{ g}/\text{m}^2$; USDA 1979) is two to three times that recorded on the La Copita site ($210 \text{ g}/\text{m}^2$ [Vega 1991]; $269 \text{ g}/\text{m}^2$ [this study, data not shown]) and whose peak standing dead biomass is four times that recorded in this study ($125 \text{ g}/\text{m}^2$). Thus, it is reasonable to expect that soil C and N levels have declined in herbaceous patches over the past century on this site, the combined result of changes in herbaceous composition and microclimate, reductions in biomass pro-

duction, and wind and water erosion associated with heavy, continuous livestock grazing.

CENTURY simulations indicate that declines in SOC of upland and lowland herbaceous communities associated with grazing and elimination of fire had stabilized by the early 1900s on the La Copita site and have changed little since that time (Hibbard 1995). Thus, the elevated soil C and N pools in woody patches initiated since 1900 would appear to indicate accumulations associated with woody plant occupancy rather than declines in herbaceous patches. A companion study which quantified soil C and N across woody patch ages ranging from 10 to 110 yr indicated a linear increase in these variables with time (T. W. Boutton and S. Archer, *unpublished manuscript*), further suggesting that differences between herbaceous and woody patch soil C and N are attributable to the direct and indirect influences of trees and shrubs.

The relative contributions of aboveground inputs (foliar litter fall and leaching, dry deposition, stemflow, and throughfall [cf. Virginia 1986]) and belowground inputs (root exudation and turnover) to observed increases in surficial soil C and N stocks and elevated N_{\min} accompanying woody plant encroachment into grassland is not clear. We were surprised by the magnitude of root biomass in surficial soils of woody patches, which greatly exceeded that of herbaceous patches and which greatly exceeded that of foliar litter inputs (Fig. 2). In addition, fluctuations in root mass pools were also greater in woody than in herbaceous patches, suggesting more rapid turnover. This runs counter to the widespread assumption that root turnover is high in grasslands (<1 yr) and slow in woody systems. However, some studies indicate root turnover in grasslands may in fact be slow (on the order of 2–8 yr; Weaver and Zink 1946, Milchunas and Lauenroth 1992, Reich et al. 2001), whereas fine root turnover in woody-dominated communities may be <1 yr (Eissenstat and Yanai 1997, Hendrick and Pregitzer 1997). The role of belowground inputs in fueling changes in surficial soil C and N stocks and mineralization rates accompanying shifts from grass to woody plant domination may therefore be more substantial than previously appreciated. Lack of information on the nutrient concentration, productivity, turnover, and decomposition of shallow woody plant roots is likely a primary limitation to understanding C and N cycling in this savanna parkland/woodland system (cf. Kelly et al. 1996).

La Copita is a mosaic of herbaceous, discrete cluster, grove, and woodland patches. Estimates from 1983 aerial photography (Scanlan and Archer 1991) indicated that woodlands were the dominant patch type in terms of areal extent (64% of landscape) followed by groves (14%), herbaceous clearings (19%), and discrete clusters (3%). An area weighting of C and N density in these contrasting patch types revealed that these recently established woody plant patches clearly dominate the current 0–10 cm soil C and N stocks, ac-

counting for >90% of the landscape total (Table 2). In the same vein, $\sim 500 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ is mineralized from woody patches on the landscape, compared to $60 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in herbaceous patches. Differences in nutrient density and fluxes between woody and herbaceous patches, when coupled with increases in the areal extent of woody vegetation, have thus combined to have a major influence on the biogeochemistry of this subtropical savanna site. (See Hibbard [1995] and Archer et al. [2001] for more detailed treatments of the historical [decadal] changes in landscape-scale plant and soil C and N stocks.)

The contrasts between woody and herbaceous patches reported here are conservative in that they do not include an assessment of whole plant C and N stocks (woody biomass aboveground; root biomass with depth belowground). Past studies have shown that root biomass in woody upland patches is substantial to depths of 1.5 m (Watts 1993). Accordingly, recent studies have shown greater soil C concentrations at deeper depths in woody patches (particularly in lowland woodlands) than in herbaceous patches (Boutton et al. 1998) and greater C mass to depths of 1 m (Gill and Burke 1999) to 4 m (Boutton et al. 1999) in upland woody vs. upland herbaceous patches. These increases in deep soil C are particularly noteworthy, given the longer turnover times that occur lower in the soil profile (Trumbore et al. 1995, Van Dam et al. 1997). With respect to aboveground C stocks, simulations with a linked plant succession–biogeochemistry model (Hibbard 1995) substantiated by field measurements (Archer et al. 2001) indicate plant C mass has increased tenfold with the conversion of grassland to savanna woodland over the past 100 yr.

Rates of fertile island development

Island of fertility studies typically contrast soil properties under vs. away from woody plant canopies without regard for time of woody plant occupancy. Available data suggest that when time has been considered, trees and shrubs in dryland systems can change soil C and N stocks over decadal time scales. For example, Bernhard-Reversat (1982) found a strong positive correlation between soil total C and N and tree girth in Senegal savannas. Correlations between woody plant age and various soil properties have been reported for piñon pine (Barth and Klemmedson 1978), *Retama* sp. (Pugnaire et al. 1996), and chaparral and pine (Quideau et al. 1998). Agroforestry studies with *Prosopis* spp. have indicated significant N soil accretion within 7 yr of planting and significant differences in rates of N accumulation among the species examined (Abrams et al. 1990). Our results quantified soil C and N on multispecies woody patches ranging from 50 to 77 yr of age (Table 1) and indicate that soil nutrient pools have changed rapidly and markedly since the encroachment of woody plant vegetation into grasslands at the subtropical La Copita site (Table 2). Our estimates as-

sumed linear accumulations for both C and N. Sampling of a greater number and broader range of woody patch age-states (T. W. Boutton and S. Archer, *unpublished manuscript*) has validated this assumption.

CONCLUSIONS

Woody plants in this subtropical savanna parkland/thorn woodland system have markedly increased the near-surface (0–10 cm) soil C and N pools in the five to seven decades since their establishment in heavily grazed grasslands. The rate and extent of change was statistically comparable for three woody habitat types that differed with respect to soils, topography, and vegetation structure. The net accumulation of soil C and N in woody patches was accompanied by, and occurred in spite of, increased N fluxes. Biomass data suggest inputs via tree/shrub roots were more important than foliar litter inputs in driving the observed C and N accumulation. More information on the nutrient concentration, productivity, turnover, and decomposition of shallow woody plant roots is needed to fully quantify C and N cycling in this developing savanna parkland/woodland system.

Woody plant expansion into drylands has been geographically widespread over the past century (see Archer 1994 for review). Although this phenomenon has been widely studied with respect to its implications for livestock production and wildlife management, relatively little is known of the biogeochemical consequences of this physiognomic change. This case study documents significant and rapid rates of soil C and N sequestration accompanying the shift from grass to woody plant domination. Given that 40% of the terrestrial biosphere consists of arid and semiarid savanna, shrubland, and grassland ecosystems, this type of vegetation change may be of significance to the global C and N cycle. At present, we lack comprehensive information on the historic or modern rate, areal extent, and pattern of woody plant expansion in the world's drylands. As a result, it is difficult to objectively and quantitatively assess implications for regional and global C and N cycling. Recent advances in remote sensing show promise for quantifying grass vs. woody plant biomass in drylands (Asner et al. 1998b) and, when used in conjunction with ecosystem simulation modeling (Asner et al. 1998a), should help to reduce these uncertainties.

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