

SOIL RESPIRATION AND NUTRIENT CYCLING IN WOODED COMMUNITIES DEVELOPING IN GRASSLAND

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Abstract. Grasslands and savannas worldwide are experiencing increases in woody plant abundance. In the subtropical Rio Grande Plains of southern Texas and northern Mexico, this change in physiognomy typically results in soil C and N accumulation. The extent to which this accumulation is the result of increased C and N inputs vs. decreased losses is not known. To address this issue, we compared soil C and N pools, soil respiration, soil microbial biomass, and potential C and N mineralization and nitrification rates in remnant grassland communities and adjacent woody plant communities known to have developed on grassland within the past 100 years. Mean soil organic C (SOC) and total N pools in the upper 20 cm of the profile were 2× larger in wooded communities (3382 and 273 g/m² for C and N, respectively) than in remnant grasslands (1737 and 150 g/m²). The larger pool sizes in the wooded communities supported higher annual soil respiration (SR; 745 vs. 611 g C·m⁻²·yr⁻¹ for woodlands and grasslands, respectively) and greater soil microbial biomass C (444 vs. 311 mg C/kg soil), potential rates of N mineralization (0.9 vs. 0.6 mg N·kg⁻¹·d⁻¹) and nitrification (0.9 vs. 0.4 mg N·kg⁻¹·d⁻¹). However, despite higher SR rates, mean residence time of near-surface SOC in wooded communities (11 years) exceeded that of remnant grassland communities (6 years). The fact that increased fluxes of soil C and N were accompanied by increases in SOC and N pools and total SOC mean residence time suggests that shifts from grass to woody plant dominance have increased both labile and recalcitrant pools of SOC and total N, the latter to a greater extent than the former. Given the widespread increase in woody plant abundance in drylands in recent history, the observed net increase in soil C storage that potentially accompanies this change could have global implications for C and N cycling and the climate system.

Key words: microbial biomass; nitrification; potential mineralization; *Prosopis glandulosa*; savanna; soil organic carbon and nitrogen; soil respiration; Texas, USA; thorn woodland; woody plant encroachment.

INTRODUCTION

Most of the major vegetation changes occurring around the world today involve alterations in the relative abundances of woody vs. herbaceous life forms (Jackson et al. 2000). As a case in point, the abundance of woody plants has increased in grasslands and savannas throughout the world in recent history (Archer et al. 2001). Causes for this shift from grass to shrub or tree domination are the subject of active debate, but appear to be the result of interactive changes in grazing, and climatic and fire regimes, augmented by changes in atmospheric CO₂ and N-deposition since the industrial revolution (Archer 1994, Köchy and Wilson 2000, Van Auken 2000).

The proliferation of woody plants in grasslands and savannas has long been of concern to range managers

because its adverse effects on herbaceous productivity and livestock handling threaten the sustainability of pastoral, subsistence, and commercial livestock grazing (Fisher 1950, 1977, Rappole et al. 1986). However, these dramatic changes in ecosystem structure also have the potential to profoundly influence hydrology, biogeochemistry, biodiversity, and future land use options in the affected areas. Studies demonstrating the biophysical (Asner 1998, Hoffman and Jackson 2000) and biogeochemical (Schlesinger et al. 1990, Scholes and Hall 1996, San Jose et al. 1998, Tilman et al. 2000, Archer et al. 2001, Jackson et al. 2002) consequences of herbaceous-to-woody life form transitions are accumulating. Given that grassland/savanna ecosystems conduct >35% of global terrestrial net primary production (Field et al. 1998) and store >30% of global soil organic carbon (Schlesinger 1997), alterations in the biogeochemistry of these regions have the potential to influence global carbon and nitrogen cycles and perhaps even the climate system (Schimel et al. 1990, Schlesinger et al. 1990, Scholes and Hall 1996). Indeed, recent estimates suggest woody plant proliferation in drylands comprises a significant, but highly uncertain

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fraction of the North American C sink (Houghton et al. 1999, Pacala et al. 2001, Houghton 2003).

Effects of woody plants on soil nutrient pools and fluxes are difficult to predict owing to strong interactions between biotic (e.g., effects of contrasting growth forms on organic matter quality and quantity) and abiotic (e.g., soil moisture, temperature, and texture) factors (Binkley and Giardina 1998). Woody plants establishing in herbaceous communities may promote soil C and N accumulation in some systems via "island of fertility" effects (Virginia 1986, Vetaas 1992), but cause no net change or declines in others (Kieft et al. 1998, Schlesinger and Pilmanis 1998, Gill and Burke 1999, Scott et al. 1999, Jackson et al. 2002).

Contrasting effects of woody plants on soil nutrient pools are the result of differences in the relative importance of C and N accumulation and loss pathways. Factors promoting soil C and N accumulation subsequent to woody plant establishment in grasslands may be partially or fully offset by factors that promote increased losses. The generally lower C:N ratio of woody plant foliage compared to that of grasses may stimulate soil microbial biomass and activity (soil respiration, mineralization) and combine with lower root biomass to limit C and N accumulation in near-surface soils. Alternatively, woody plants may promote C and N accumulation if they have greater productivity and produce lower quality litter (foliage with secondary compounds; lignified woody tissue) than the grasses they replace. However, shifts from bacterial to fungal populations may accompany shifts from herbaceous to woody domination (e.g., Imberger and Chiu 2001, Purohit et al. 2002), enabling the microbial biomass to effectively deal with lower litter quality, and thus maintain or increase soil respiration and mineralization. Shading, stem flow, or hydraulic lift by woody plants may increase soil moisture and enhance microbial activity and hence soil respiration and mineralization, thus slowing or preventing C and N accumulation; but, reductions in soil temperatures from shading may counter these effects.

At the landscape scale, woody plant encroachment occurs across topoedaphically diverse conditions that may alter the processes controlling soil C and N accumulation. For example, lowland run-on sites experiencing woody plant encroachment may accumulate C and N more rapidly than adjoining run-off sites owing to potentially greater primary production and finer soil texture; however, these effects may be wholly or partially offset by increases in respiration, nitrification, and/or denitrification. Understanding the mechanisms responsible for changes in soil C and N pools following woody plant encroachment therefore requires a landscape-level assessment of the extent to which C and N inputs and outputs differ between herbaceous and woody community types and across contrasting topoedaphic settings.

To better understand the processes controlling changes in soil C and N pools accompanying woody plant encroachment and how those processes vary across the landscape, we quantified rates of soil C and N cycling and loss via measurements of soil respiration and soil microbial biomass and activity (potential C and N mineralization and nitrification) in grassland communities and in upland vs. lowland woody plant communities known to have displaced grasslands during the past century. By comparing these nutrient cycling parameters in contrasting communities, we sought to ascertain the specific mechanisms within the diverse array of interacting factors that determine the extent of change in soil C and N pools accompanying woody plant encroachment.

METHODS

Site description

Research was conducted at the Texas Agricultural Experiment Station La Copita Research Area on the eastern edge of the Central Rio Grande Plains (27°40' N, 98°12' W). The climate is subtropical with a mean annual temperature of 22.4°C. Mean annual precipitation is 716 mm, with peaks in May–June and September. Topography consists of nearly level uplands that grade (1–3% slopes) into lower lying drainages and playas; elevation at the site ranges from 75 to 90 m. The site has been grazed by livestock since the late 1800s.

Upland soils are sandy loams (Typic and Pachic Argiustolls); lower lying intermittent drainages are clay loams (Pachic Argiustolls). Woody plant communities of uplands and lowlands are generally similar in composition and dominated by *Prosopis glandulosa* in the overstory, and by a diverse array of understory shrubs including *Zanthoxylum fagara*, *Condalia hookeri*, *Mahonia trifoliolata*, and *Diospyros texana*. *Prosopis glandulosa* forms root nodules capable of symbiotic N₂ fixation when grown in soils from this site (Zitzer et al. 1996). Remnant grasslands are dominated by *Chloris cucullata*, *Panicum hallii*, *Bouteloua hirsuta*, and *Tridens* spp. Additional details regarding the plant communities and soils are available elsewhere (Archer 1995, Boutton et al. 1998).

Potential vegetation of the area has been classified as *Prosopis–Acacia–Andropogon–Setaria* savanna (Küchler 1964), and historical accounts suggest that the region was once grassland and open savanna (Inglis 1964). Currently, much of the region is dominated by subtropical thorn woodland (McMahan et al. 1984). Our study assessed soil C and N pools and cycling rates in the dominant plant communities on a landscape consisting of upland grasslands interspersed with shrub clusters (where an argillic horizon is present) and *Prosopis* groves (where the argillic horizon is poorly expressed) that graded (1–3% slopes) into lowland drainage woodland communities (see Archer 1995 for de-

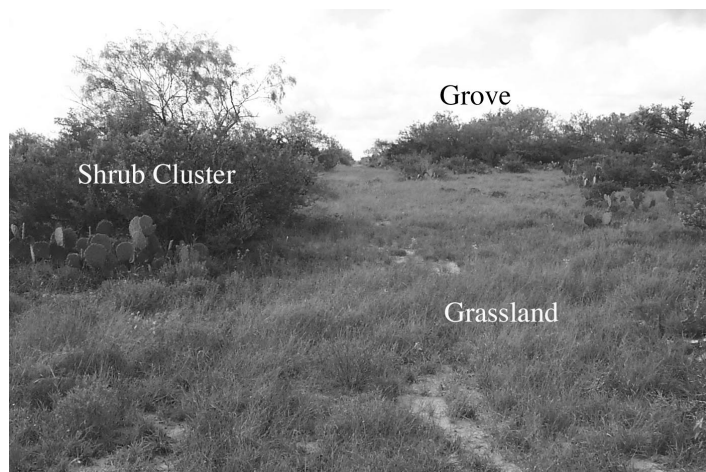


PLATE 1. Woody plant encroachment in the Rio Grande Plains of southern Texas, USA. Shrub cluster and grove communities have developed in areas previously supporting grassland. Photo credit: S. Archer.

tails; also see Plate 1). Isotopic analyses of plants and soils, tree ring analyses, and historical aerial photography all confirm that trees and shrubs in cluster, grove, and drainage woodland communities have replaced grasslands at the La Copita site over the past 100 years (Archer 1995, Boutton et al. 1999, Gill and Burke 1999).

Approach and experimental design

Soil C and N pools, C loss via soil respiration, soil microbial biomass, potential C and N mineralization rates, and soil N concentrations were quantified in upland grasslands, shrub clusters and groves, and in adjoining lowland drainage woodland communities from March 1996 through February 1997. Our objective was to assess the effects of woody plant encroachment on ecosystem processes by comparing these parameters in woody plant communities known to have developed on grasslands to those in a remnant grassland community. It should be recognized, however, that such comparisons are constrained by assumptions inherent in “space-for-time” substitution approaches and by surface and/or subsurface soil texture differences in the various communities that may influence soil processes independent of vegetation effects.

Replicate ($n = 6$) plots (4×5 m) representative of each community type were established within a 1-km² area. In plots representing woody community types (cluster, grove, and drainage woodland), all soil sampling and respiration measurements were conducted within 1.5 m of the bole of the largest *Prosopis* tree. This locational constraint was used to minimize potentially confounding effects that might occur if bole to canopy dripline gradients exist and to ensure that the soils sampled would have been maximally affected by woody vegetation (assumption: soils near the bole would have been influenced by woody plants longer than soils at the woody canopy dripline). Rainfall was recorded daily by an automated weather station situated near the center of our sampling area.

Plant community characterization

Age of woody community types was estimated from the basal diameter of the largest *Prosopis* stem in each plot using soil-specific equations (Stoker 1997). Woody plant litterfall was quantified by placing one $50 \times 25 \times 5$ cm plastic tray on the ground surface in each plot. Litter was collected monthly, sorted into woody and leaf components, dried, weighed, and pulverized. Monthly samples were then pooled across replicates and analyzed for C and N concentrations using a Carlo Erba NA-1500 elemental analyzer (CE Elantech, Lakewood, New Jersey, USA).

Soil respiration and mean residence times of soil organic carbon

Monthly measurements of soil respiration (SR) were made in the field using a LICOR-6000-09 (LICOR, Lincoln, Nebraska, USA) chamber attached to a LICOR-6200 infrared gas analyzer (IRGA; Norman et al. 1992). At each measurement period, PVC collars (10 cm diameter \times 7 cm tall; one per plot) were inserted in the soil to a depth of 2.5 cm in the evening, and SR rates were measured at 04:00, 09:00, 14:30, and 22:00 the following day. Plots were visited in the same sequence over the 24-hour period. Soil temperatures were recorded concurrent with SR measurements using a probe inserted 5 cm into the soil and interfaced with the LICOR unit. The IRGA was calibrated with a standard (501 ppm CO₂ in air) before every measurement period.

To derive a daily SR, the trapezoidal rule was used to calculate the area under the curve (AUC) produced by the diel instantaneous respiration rates (Stewart 1991):

$$\begin{aligned} \text{AUC} = & \text{mean}(\text{SR}_1, \text{SR}_2) \times (t_2 - t_1) \\ & + \text{mean}(\text{SR}_2, \text{SR}_3) \times (t_3 - t_2) \\ & + \text{mean}(\text{SR}_3, \text{SR}_4) \times (t_4 - t_3) \end{aligned} \quad (1)$$

where SR_1 , SR_2 , SR_3 , and SR_4 were the soil respiration rates measured at times t_1 , t_2 , t_3 , and t_4 (04:00, 09:00, 14:30, and 22:00, respectively). Daily respiration was then multiplied by the number of days in the month to calculate monthly SR. Annual SR was computed as the sum of the monthly rates.

The mean residence time (MRT) of soil organic C was estimated for each community type by dividing the mass of organic C in the top 20 cm of the soil profile by the heterotrophic respiration rate (total soil respiration minus root respiration). Since neither root respiration nor heterotrophic respiration were quantified separately, we estimated MRTs for scenarios in which root respiration comprised 30%, 50%, or 70% of total soil respiration (Raich and Schlesinger 1992, Hanson et al. 2000).

Soil collection and characterization

After completion of each monthly diel SR measurement, a soil core (5 × 20 cm) was extracted from each PVC collar and partitioned into 0–10 and 10–20 cm increments. Each depth increment was then sectioned longitudinally. One of the halves was sealed in a tin for gravimetric soil moisture analysis which was later converted to a volumetric basis. The other half was sealed in a ziploc bag, placed in a cooler, and analyzed later for microbial biomass, C, and N. When N-mineralization analyses were conducted (alternate months), a second soil sample located adjacent to the first was collected and partitioned (0–10 and 10–20 cm segments), sealed in a ziploc bag, and kept cool during transport. Soils were refrigerated at 4°C until analyses were performed.

Soil samples (0–10 and 10–20 cm) taken during July 1996 and January 1997 were analyzed for organic C and total N by combustion/gas chromatography using a Carlo-Erba NA-1500. Soils were sieved through a 2-mm screen to remove coarse roots, dried at 60°C, and finely ground in a centrifugal mill. Organic C and total N concentrations were determined according to methods described previously for calcareous soils/sediments (Nieuwenhuize et al. 1994).

Soil bulk density was measured in each community type by the core method (Blake and Hartge 1986). Soil texture was determined by the pipette method (Gee and Bauder 1986). Soil pH was determined on a 2:1 (water: soil) mixture (McLean 1982).

Soil microbial biomass and potential mineralization rates

Soil microbial biomass C and N were determined by chloroform fumigation-incubation (Horwath and Paul 1994). Approximately 25 g of field-moist soil (sieved to remove organic fragments >5 mm) was placed in 50-mL beakers, moistened to 90% field capacity, fumigated with ethanol-free chloroform, and incubated in 1-L gas-tight jars at 25°C for 10 d. Evolved CO₂ was captured in a vial containing 5 mL of 1 mol/L NaOH,

and the quantity of CO₂-C absorbed in the alkali was determined by titration with 1 mol/L HCl. Soil microbial biomass C (SMB-C) was calculated using a k_C value = 0.45 and the equations reported in Voroney and Paul (1984). SMB-C values were calculated without subtracting an unfumigated control (Paul and Voroney 1980, Franzluebbers et al. 1999). The ratio of SMB-C to soil organic C (C_{mic}/C_{org}) was computed as an index of the proportion of soil organic C that might be readily metabolized (Anderson and Domsch 1989). Potential C mineralization rates were determined on unfumigated soils incubated for 10 d using incubation methods identical to those described previously. The metabolic quotient (qCO_2 = ratio of microbial respiration to microbial biomass) was computed as an index of the efficiency with which microbes were converting available carbon into microbial biomass (Anderson and Domsch 1985, Wardle and Ghani 1995).

Inorganic N was extracted from initial soil samples before incubation, and from fumigated and unfumigated soil samples after the 10-d microbial biomass incubation. Soils were shaken for 30 min in 2 mol/L KCl (1:4, mass : volume), and the filtered extract was analyzed for NH₄⁺-N, NO₂⁻-N, and NO₃⁻-N concentrations using a Technicon autoanalyzer with salicylic acid modification of the indophenol blue method (Technicon Systems 1977a) and the cadmium reduction method (Technicon Systems 1977b). Soil microbial biomass N (SMB-N) was calculated according to the equations in Horwath and Paul (1994), with a k_N = 0.38 (Sparling et al. 1986). Potential N mineralization and nitrification rates were calculated from the difference between the unfumigated and initial soil samples in the concentrations of NH₄⁺-N and NO₃⁻-N (for mineralization) and NO₃⁻-N alone (for nitrification) over the 10-d incubation.

Statistical analyses

Statistical differences in pools and rates of C and N cycling between community types were assessed using SAS (1996). Although 0–10 and 10–20 cm depth increments were sampled and analyzed for all soil parameters, we present the average across depth increments for soil microbial parameters in order to simplify presentation of the data (see McCulley 1998 for depth-specific values). Using a general linear model, a repeated-measures analysis of variance (ANOVA) was used to test for differences in soil microbial variables, SR, and litter production attributable to time (month), community type, and their interaction. Pairwise modified Bonferroni means comparisons (Day and Quinn 1989) were performed on significant main effects from the repeated-measures tests. Univariate analysis of variance was used to test for differences between community types with respect to soil properties (separately on each depth fraction), abiotic variables, and mean residence times. Multiple linear regression (stepwise)

TABLE 1. Soil characteristics of the community types at the La Copita Research Area, Texas, USA.

Community type	Clay (%)		Bulk density (g/cm ³)		pH		Soil temperature (°C)		Soil moisture (cm ³ /cm ³)	
	0–10 cm	10–20 cm	0–10 cm	10–20 cm	0–10 cm	10–20 cm	Min., max.	Year avg.	0–10 cm	10–20 cm
Grassland†	12.5 ^b (±3.5)	13.8 ^b (±3.8)	1.47 ^a (±0.06)	1.51 ^a (±0.05)	7.4 ^a (±0.3)	7.4 ^a (±0.3)	6.2, 45.8	26.7 ^a (±7.6)	0.06 ^b (±0.04)	0.06 ^c (±0.03)
Cluster†	12.9 ^b (±2.2)	13.8 ^b (±3.3)	1.27 ^{ab} (±0.18)	1.51 ^a (±0.14)	6.7 ^b (±0.5)	6.7 ^b (±0.4)	7.7, 44.3	25.7 ^b (±7.1)	0.05 ^c (±0.03)	0.06 ^{bc} (±0.03)
Grove‡	12.4 ^b (±2.6)	13.7 ^b (±2.3)	1.09 ^b (±0.12)	1.45 ^a (±0.13)	7.1 ^a (±0.8)	7.2 ^a (±0.7)	9.5, 42.9	24.7 ^c (±6.3)	0.05 ^c (±0.03)	0.06 ^b (±0.02)
Drainage woodland§	22.2 ^a (±4.6)	23.3 ^a (±4.6)	1.13 ^b (±0.13)	1.33 ^a (±0.15)	7.2 ^a (±0.6)	7.2 ^a (±0.6)	10.9, 41.9	24.7 ^c (±6.6)	0.09 ^a (±0.04)	0.11 ^a (±0.04)

Notes: Numerical values are means (± 1 SD). Different letters represent significant differences between means within a column ($P \leq 0.05$). Soil taxonomy is from Boutton et al. (1998). Minimum and maximum soil temperatures (5 cm depth) measured throughout the year are presented, as well as the yearly average. Soil moisture values represent the yearly average for each depth fraction.

† Soil taxonomy and texture are Typic Argiustolls and fine sandy loam.

‡ Soil taxonomy and texture are Pachic Haplustolls and sandy loam.

§ Soil taxonomy and texture are Pachic Argiustolls and sandy clay loam.

was used to assess which abiotic variables were accounting for observed variation in daily SR.

RESULTS

Site characteristics

Clay content of soils in the upland community types (13% in grasslands, clusters, and groves) was significantly lower than that in the lowland drainage woodland community (23%; $P < 0.001$, Table 1). Soil pH in clusters (6.7) was more acidic than in other community types (7.1–7.4; $P < 0.01$). Bulk density at 0–10 cm in grasslands (1.47 g/cm³) was significantly higher than that in woody communities (1.09–1.27 g/cm³; $P < 0.05$), but did not differ between community types at 10–20 cm. The mean age of *Prosopis* trees in the woody community types was greater in groves (82 yr) and drainage woodlands (62 yr) than in clusters (40 yr; Table 2).

Soil temperature, rainfall, and soil moisture

Soil temperature was affected by month, community type, and the month \times community interaction ($P < 0.0001$ in all cases). Mean daily soil temperatures over the measurement period ranged from 16 to 35°C in drainage woodlands and from 15 to 38°C in grasslands, with maximum and minimum temperatures for all community types occurring in July 1996 and February 1997, respectively (Fig. 1). Mean soil temperatures over the study period were 1 to 2°C lower in woody community types (24.7–25.7°C) than in grasslands (26.7°C; Table 1).

Annual rainfall in 1996 (307 mm) was ~57% below the long-term (1951–1976) average (716 mm). Most of this deficit occurred from January through July, which received <50 mm of rainfall. This rainfall deficit was evident in the relatively low soil moisture values in all communities (Fig. 1, Table 1). Repeated-measures univariate tests on soil moisture at individual soil depth

increments indicated significant ($P < 0.001$) month, community type, and month \times community interactions. In general, mean annual volumetric moisture content was higher in drainage woodlands (0.10 cm³/cm³) than grasslands (0.06 cm³/cm³), but means comparison tests indicated the rank order of the other community types varied by soil depth (Table 1).

Soil organic carbon and total nitrogen

Concentrations (grams per kilogram, data not shown) and pools (grams per square meter) of soil organic C and total N (Table 3) were higher in woody community types than grasslands at both depths ($P < 0.001$). Means separation tests on C and N concentrations and pool sizes indicated a rank order of drainage woodlands \approx groves $>$ clusters $>$ grasslands. The C:N ratio of soil organic matter was comparable in upland plant communities (11–12 in grasslands, clusters, and groves) and significantly higher ($P < 0.001$) in drainage woodlands (13–15; Table 3).

Litterfall

Woody and leaf litterfall varied significantly over time (data not shown; “month” main effect, P value < 0.01 for each). A large pulse in leaf litterfall in June 1996 in groves was not evident in clusters or drainage woodlands and contributed to the significant month \times community interaction ($P < 0.001$; data not shown). Leaf litterfall did not differ significantly between woody community types, but woody litterfall and total annual litter production did (grove $>$ drainage woodland \approx cluster; $P < 0.001$; Table 2). Leaf litter had higher concentrations of N than woody litter, and litterfall C:N was generally higher but more variable in clusters (seasonal range of 18–40) than in groves or drainage woodlands (~20–36 for both; Table 2).

TABLE 2. Vegetation characteristics of three woody community types at the La Copita Research Area, Texas, USA.

Community type	Estimated patch age (yr)	Annual litter input (g·m ⁻² ·yr ⁻¹)			Leaf litter			Woody litter		
		Woody	Foliar	Total	%C	%N	Avg. C:N	%C	%N	Avg. C:N
Cluster	40.3 ^b (±6.8)	28 ^b (±14)	133 ^a (±49)	161 ^b (±41)	35.1–46.2	1.1–2.5	28.7	40.5–46.3	1.0–1.5	36.3
Grove	81.6 ^a (±38.1)	173 ^a (±118)	182 ^a (±35)	356 ^a (±105)	40.7–44.5	1.6–2.6	20.1	40.0–45.4	0.7–2.0	30.3
Drainage woodland	61.9 ^a (±13.6)	83 ^b (±48)	133 ^a (±50)	232 ^b (±96)	40.4–47.8	2.0–2.7	19.0	34.9–44.9	1.1–2.0	28.7

Notes: Numerical values are means (±1 SD). Different letters represent significant differences between means within a column ($P \leq 0.05$). The seasonal range of leaf and woody litter C and N concentrations are given, as well as the yearly average C:N ratio. Age of woody community types was estimated from the basal diameter of the largest *Prosopis* stem in each plot using soil-specific equations (Stoker 1997).

Soil respiration and mean residence times of soil organic carbon

Soil respiration (SR) generally tracked monthly precipitation in all community types (Fig. 2). Stepwise multiple linear regression models of daily SR from all community types indicated that soil temperature and precipitation accounted for the majority of the variability in the SR data ($R^2 = 70.3\%$, $P < 0.05$):

$$SR = -19615 + 1881(ST) - 34(ST)^2 + 10267(PPT)$$

where SR is daily soil respiration (mg CO₂·m⁻²·d⁻¹), ST is mean daily soil temperature, and PPT is total precipitation (mm) during the two weeks prior to the diurnal soil respiration measurement.

Maximum SR occurred in September and ranged from 655 in grasslands to 768 g CO₂·m⁻²·mo⁻¹ in groves. A significant month × community interaction indicated by repeated-measures ANOVA apparently reflects subtle, but unique differences in drainage woodland SR trends from November–February (data not shown). Annual SR in drainage woodlands and groves (771 and 780 g C·m⁻²·yr⁻¹, respectively) was significantly greater than that of grasslands (611 g C·m⁻²·yr⁻¹; $P < 0.01$; Table 3). Mean residence times (MRTs) for near-surface pools of soil organic C were significantly longer in the drainage woodlands (7.7–18.0 yr) and groves (6.6–15.5 yr) than in clusters (4.8–11.3 yr) and grasslands (4.1–9.6 yr; $P < 0.0001$; Table 3).

Soil microbial biomass

Woody communities had significantly higher soil microbial biomass carbon (SMB-C) than remnant grasslands ($P < 0.001$; Table 4, Fig. 3). The repeated-measures ANOVA month × community interaction was not significant, indicating that seasonal patterns of SMB-C were similar across community types. Troughs in SMB-C occurred in September and November in all communities. Grasslands had significantly higher C_{mic}/C_{org} than groves and drainage woodlands (Table 4). C_{mic}/C_{org} varied significantly with respect to month and community type, but not their interaction (Fig. 3). Seasonal variation in C_{mic}/C_{org} was more pronounced in the grasslands than in the woody community types. There was

a trend toward higher qCO₂ ratios in wooded areas (30–36 mg C·g⁻¹ SMB-C·d⁻¹) than in grasslands (28 mg C·g⁻¹ SMB-C·d⁻¹ Table 4), but there were no significant differences with respect to plant community type, time, or their interaction (Fig. 3).

Repeated-measures ANOVA indicated significant differences in soil microbial biomass nitrogen (SMB-N) between community types (Table 4), with woody communities generally having higher SMB-N than grasslands (Fig. 3). Seasonal variation in SMB-N was less pronounced than SMB-C for all community types.

Potential mineralization rates

Potential C and N mineralization rates (Fig. 4, Table 4) were greater in woody communities than in remnant grasslands ($P < 0.001$). Repeated-measures ANOVA indicated a significant effect of month on potential C mineralization rates, with seasonal lows occurring in September for both community types (Fig. 4). Potential

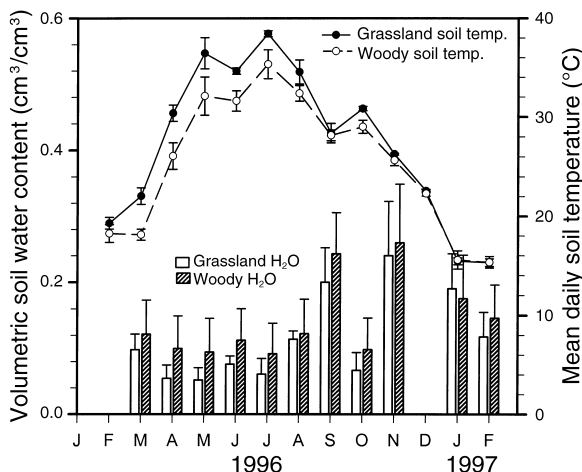


FIG. 1. Histogram bars depict mean (+1 SD) volumetric (0–20 cm depth) soil moisture, and lines depict mean (±1 SD) daily soil (5 cm depth) temperature for grassland and for pooled woody (cluster, grove, and woodland) communities. February and December 1996 soil moisture measurements are missing due to problems collecting data in the field. November soil moisture was elevated due to a 22-mm rainfall event the night before sampling.

TABLE 3. Soil organic C and total N pools, soil C:N ratios, total soil respiration rates, and estimated mean residence times (MRTs) for soil C.

Community type	Soil organic carbon (g C/m ²)			Soil total nitrogen (g N/m ²)		
	0–10 cm	10–20 cm	Total	0–10 cm	10–20 cm	Total
Grassland	987 ^c (±170)	749 ^d (±128)	1737 ^b (±250)	84 ^c (±16)	66 ^c (±13)	150 ^b (±24)
Cluster	1302 ^b (±414)	1010 ^c (±342)	2312 ^b (±709)	111 ^b (±36)	86 ^b (±31)	197 ^b (±63)
Grove	2151 ^a (±866)	1469 ^b (±431)	3642 ^a (±1064)	191 ^a (±64)	121 ^a (±38)	315 ^a (±87)
Drainage woodland	2230 ^a (±823)	2011 ^a (±633)	4193 ^a (±1325)	173 ^a (±76)	137 ^a (±47)	307 ^a (±114)

Notes: Numerical values are means (±1 SD). MRTs were obtained by dividing the total pool size (0–20 cm depth) of soil organic C by heterotrophic respiration. The percentage of total soil respiration attributable to root respiration was estimated at 30%, 50%, and 70% and subtracted from total respiration to estimate heterotrophic respiration. Different letters represent significant differences between means within a column ($P \leq 0.001$).

N-mineralization rates also varied significantly ($P < 0.001$) with respect to time. Rates in grasslands and woody communities were comparable in spring and summer, then diverged in the fall and winter (Fig. 4). Expressing potential mineralization rates on a per gram SOC or soil N basis gave similar results to the C_{mic}/C_{org} data (i.e., grasslands and clusters had greater mineralization rates per gram of organic matter than groves and drainage woodlands; data not shown).

Nitrification rates (Fig. 4, Table 4) were greater in drainage woodlands and groves than grasslands ($P < 0.01$). Peaks in nitrification occurred in May for woodland communities, and in March and September for grasslands, resulting in a significant month and month \times community type interaction.

Concentrations of soil inorganic nitrogen

Concentrations of both NH_4^+ and NO_3^- were generally 2–3 \times greater in groves and drainage woodlands than in grasslands and clusters (Table 4); however, only NO_3^- concentrations were significantly different across community types ($P < 0.01$). The NO_3^- fraction of the inorganic N pool was 72–75% in groves and drainage woodlands and 65% in grasslands and clusters. There was considerable temporal variation in both NH_4^+ and NO_3^- (Fig. 5). Distinct peaks in $[NH_4^+]$ occurred between April and July in woody communities, but seasonal changes in $[NH_4^+]$ were less pronounced in grasslands. Maximum NO_3^- concentrations typically occurred between September and January in woody communities and between July and January in grasslands.

DISCUSSION

C and N in contrasting woody communities

Soil respiration, potential C and N mineralization, nitrification, and soil microbial biomass C and N were similar in cluster, grove, and drainage woodland communities at this subtropical site and fell within ranges reported for other savanna ecosystems (Hao et al. 1988, Mazzarino et al. 1991, Scholes and Walker 1993, Ruess

and Seagle 1994, Zepp et al. 1996). We therefore postulate that differences in SOC and total N between the woody community types (clusters < groves ~ drainage woodlands; Table 3) reflect differences in stand ages and biomass input rather than differences in fluxes (i.e., mineralization and respiration) and microbial biomass. In support of this interpretation, we note that the mean age of drainage woodland (62 yr) and grove (81 yr) stands exceeded that of cluster stands (40 yr), thus allowing for 2–4 more decades of woody plant litter input. The expectation that differences in the period of woody litter input might be of significance is substantiated by results from another study on this site, which

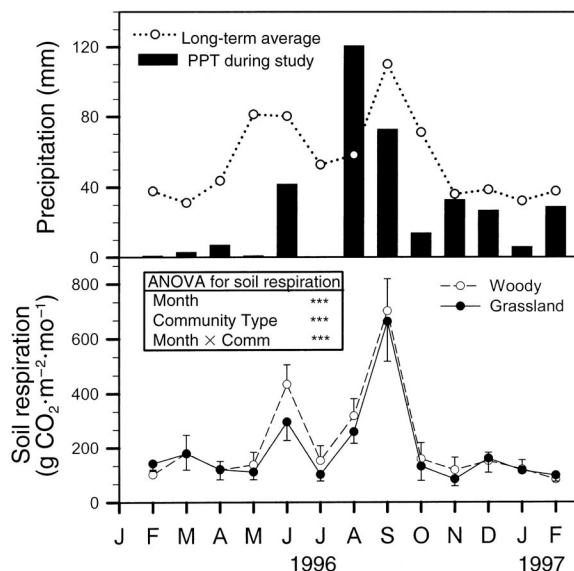


FIG. 2. The top panel shows precipitation (PPT) during the study period (bars) and the long-term (1911–1997) average (dotted line). The bottom panel depicts mean (± 1 SD) monthly soil respiration for grassland and pooled woody plant communities (see McCulley [1998] for seasonal cluster, grove, and drainage woodland values). Repeated-measures ANOVA results are shown in the inset (*** $P < 0.001$).

TABLE 3. Extended.

Soil C:N			Total soil respiration (g C·m ⁻² ·yr ⁻¹)	Mean residence time (yr)		
0–10 cm	10–20 cm	Total		30%	50%	70%
11.9 ^b (±0.9)	11.5 ^b (±1.4)	11.7 ^b (±1.0)	611 ^b (±83)	4.1 ^b	5.8 ^b	9.6 ^b
11.8 ^b (±0.9)	12.0 ^b (±1.6)	11.8 ^b (±1.0)	683 ^{ab} (±51)	4.8 ^b	6.8 ^b	11.3 ^b
11.3 ^b (±2.3)	12.2 ^b (±0.9)	11.7 ^b (±1.6)	780 ^a (±69)	6.6 ^a	9.3 ^a	15.5 ^a
13.2 ^a (±1.4)	14.9 ^a (±1.6)	13.9 ^a (±1.4)	771 ^a (±85)	7.7 ^a	10.8 ^a	18.0 ^a

found that upland grove and cluster communities of approximately similar ages (50 vs. 58 yr, respectively) had statistically comparable SOC and N levels (Hibbard et al. 2001).

Comparisons of upland cluster and grove communities to lowland woodland communities are potentially confounded by differences in surface soil texture between upland and lowland woody communities. Although the clay content of drainage woodland soils (22–23%) was substantially higher than that of grove soils (12–14%; Table 1), the two community types were statistically similar with respect to SOC and N pools (Table 3) and other nutrient cycling properties (Table 4). This lack of differences in grove vs. drainage woodland soil nutrient pools and cycling properties was surprising, given that fine textured soils of lowland landscape positions typically accumulate and retain more SOC and N than coarser textured upland soils (Schimel et al. 1985, Hook and Burke 2000). Drainage woodland and grove communities have plants of qualitatively similar stature, species composition (S. R. Archer, unpublished data), and growth rates (Miller et al. 2001), so there is no a priori reason to expect that differences in aboveground production might be overriding soil texture effects. If anything, long-term dynamic simulations suggest drainage woodland communities are typically more productive than grove communities (Hibbard et al. 2003), which should serve to magnify differences in C and N pools in upland vs. lowland soils. It could be argued that the older age of grove stands (81 yr) compared to drainage woodland stands (62 yr) might have compensated for differences that would otherwise be expected from differences in soil texture. However, Hibbard et al. (2001), working at this site, also failed to find differences in SOC and N pools and field N mineralization rates in fine textured drainage woodland communities that were 20–30 yr older than coarse textured grove communities. Our data cannot explain this conundrum, other than to suggest that the unexpected similarities in SOC and soil N pool sizes do not appear to be the result of offsetting differences in nutrient loss via soil respiration or C and N mineralization between the two woody plant community types.

Differences in soil C and N pools between cluster, grove, and drainage woodland plant communities may also reflect species effects. Species of woody plants at this site do in fact differ with respect to foliar decomposition rates (Boutton et al. 1998). However, at the stand level, the species composition of clusters, groves, and drainage woodlands is quantitatively similar, with the most common species being highly ubiquitous in their distribution (S. R. Archer, unpublished data). Thus, there is no a priori reason to expect that SOC and N differences between clusters, groves, and drainage woodlands would be the result of species effects (e.g., Hobbie 1992) per se. The woody communities do, however, differ with respect to the size and biomass of their woody components. Relative to woody plants in cluster communities, those in grove and drainage woodland communities are typically larger in terms of height, basal area, canopy area, and biomass (Watts 1993, Archer 1995, Hibbard et al. 2001). Though not strongly reflected in our litterfall data (collected in a year where annual rainfall was 57% below the long-term average), other studies on this site have observed that litter inputs (particularly foliage, fine branch, and coarse woody debris) are greater in grove and drainage woodland than in cluster communities (Hibbard et al. 2003). C:N ratios of leaf and woody litter were lower in grove and drainage woodland communities compared to cluster communities (Table 2), probably reflecting differences in N inputs by *Prosopis glandulosa* plants, the dominant, N₂-fixing (Zitzer et al. 1996) overstory tree in these community types. Although lower C:N ratios might be expected to accelerate decomposition in grove and drainage woodland communities, secondary compounds in these inputs (Solbrig et al. 1977) may reduce rather than enhance litter quality. The higher SOC and N pools in grove and drainage woodland communities relative to cluster communities may thus reflect greater litter inputs in the former community types more than differences in litter quality (Table 2).

Soil C and N in woody communities developing on grasslands

Field assessments of decadal-scale changes in soil properties occurring subsequent to woody plant estab-

TABLE 4. Mean (± 1 SD) soil microbial biomass (SMB) C and N and activity for the year of study averaged across both soil depth increments (0–10 and 10–20 cm).

Community type	SMB-C (mg C/kg soil)	SMB-N (mg N/kg soil)	C min (mg C·kg ⁻¹ ·d ⁻¹)	N min (mg N·kg ⁻¹ ·d ⁻¹)
Grasslands	328 ^b (± 130)	39 ^c (± 13)	8.0 ^b (± 4.7)	0.5 ^b (± 0.5)
Clusters	458 ^a (± 166)	51 ^b (± 26)	13.8 ^a (± 7.2)	1.0 ^a (± 0.9)
Groves	435 ^a (± 183)	59 ^{abc} (± 32)	14.9 ^a (± 7.6)	1.0 ^a (± 0.8)
Drainage woodland	592 ^a (± 212)	90 ^a (± 40)	16.9 ^a (± 8.8)	1.0 ^a (± 0.8)

Notes: C_{mic}/C_{org} is the ratio of SMB-C to soil organic C; qCO_2 is the ratio of C respired during the soil incubation to SMB-C. Different letters indicate significant differences (overall $P < 0.05$) between means for community types, as determined by repeated-measures ANOVA and pairwise modified Bonferroni means comparisons tests.

ishment in grasslands are potentially confounded by a variety of factors and cannot be readily assessed experimentally or in comparative studies. In this field study, we approximated woody plant effects on soils and nutrient cycling using a space-for-time approach. Our comparisons of woody vs. herbaceous communities are predicated on the assumption that the soil properties in present-day remnant grassland zones are a reasonable baseline from which to gauge direct (plant inputs) or indirect (changes associated with erosion or deposition) changes associated with woody plant en-

croachment. However, surface and subsurface soil texture differences between remnant grasslands and groves and drainage woodlands compromise the strength of this assumption. Ideally, we would have specifically quantified differences between groves and grassland communities lacking an argillic horizon starting at ~ 40 cm depth and differences between drainage woodlands and remnant grasslands on lowland clay loam soils. However, grassland communities on such sites were rare at the study area, thus precluding a more rigorous experimental design.

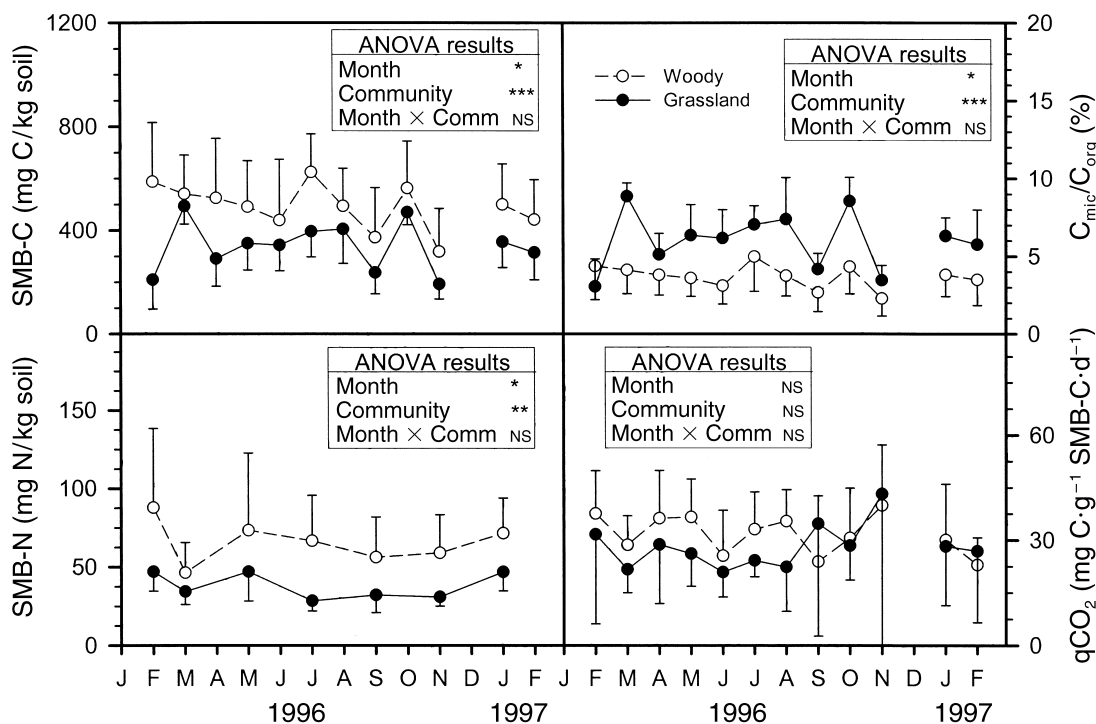


FIG. 3. Spatiotemporal variation in mean (± 1 SD) surface soil microbial biomass C (SMB-C) and N (SMB-N), the ratio of SMB-C to soil organic C (C_{mic}/C_{org}), and the qCO_2 (calculated as grams of carbon respired during incubations divided by g SMB-C) of grassland and pooled woody plant communities averaged across the two soil depth increments sampled (see McCulley [1998] for seasonal and depth-specific cluster, grove, and drainage woodland values). Repeated-measures ANOVA results are shown in the insets ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$; NS, not significant). SMB-C, C_{mic}/C_{org} , and qCO_2 were measured monthly; SMB-N was measured bimonthly, with the last collection occurring in January 1997. SMB-C samples were not collected in December 1997.

TABLE 4. Extended.

Nitrification (mg N·kg ⁻¹ ·d ⁻¹)	C _{mic} /C _{org} (%)	qCO ₂ (mg C·g ⁻¹ SMB-C·d ⁻¹)	Soil NH ₄ ⁺ -N (mg N/kg soil)	Soil NO ₃ ⁻ -N (mg N/kg soil)
0.4 ^b	6.0 ^a	28 ^a	4.1 ^a	6.3 ^b
(±0.4)	(±2.3)	(±21)	(±5.5)	(±4.4)
0.8 ^{ab}	4.7 ^{ab}	31 ^a	5.5 ^a	9.1 ^{ab}
(±0.8)	(±1.8)	(±13)	(±6.1)	(±5.7)
1.0 ^a	2.8 ^c	36 ^a	8.6 ^a	21.9 ^a
(±0.8)	(±1.1)	(±16)	(±8.8)	(±17.1)
1.0 ^a	3.5 ^{bc}	30 ^a	7.3 ^a	19.7 ^{ab}
(±0.7)	(±1.4)	(±12)	(±6.4)	(±15.5)

Soil $\delta^{13}\text{C}$ values indicate that cluster, grove, and drainage woodland communities have developed on former grasslands at this site (Boutton et al. 1998, Gill and Burke 1999). Historical aerial photographs (Archer et al. 1988), transition matrix (Scanlan and Archer 1991) and plant growth (Archer 1989) models indicate this transformation has been ongoing over the past 100 years. Comparisons of woody communities and remnant grassland communities (Table 3) suggest these increases in woody plant abundance have been accompanied by increases in SOC (0–20 cm) on the order of approximately $+1.3\times$ (cluster), $+1.5\times$ (drainage woodlands) and $+2.1\times$ (groves) (note: we do not have field data for remnant grasslands on the drainage woodland community soil type [clay loam], so we have used a value [2750 g C/m²] based on simulations by Hibbard et al. [2003]). This interpretation is supported by dynamic simulations, which indicate that although long-term, heavy grazing at this site did cause significant losses of SOC, those losses had stabilized at levels observed in the present, remnant grassland communities by the early 1900s (Hibbard et al. 2003), before the time the oldest trees in this study had established; and that woody plant proliferation has created elevated soil C levels above those present in the early 1800s. Furthermore, coupling the community-specific data reported here with changes in the relative cover of community-types quantified from sequential aerial photography, Archer et al. (2001) found that over time woody plants have increased landscape scale plant and soil C storage at this site. These results contrast with studies from more arid sites, where woody plants have been shown to alter the spatial distribution of C storage but cause little net change at the landscape scale (Kieft et al. 1998, Schlesinger and Pilmanis 1998). Although the data from this study are for surficial soils (0–20 cm only), the changes in SOC across the various community types are in agreement with other field studies at this site that quantified SOC to greater depths (1.5 m; $1.3\times$ more SOC in groves and $2\times$ more SOC in drainage woodlands than in remnant grasslands; Boutton et al. 1998; T. W. Boutton and S. R. Archer, *unpublished data*). All these assessments run counter to predictions from a regional woody plant encroachment study that suggests that at this site, with its mean annual

rainfall of 716 mm, woody plant encroachment should be accompanied by significant declines ($\sim 18\%$) in SOC (Jackson et al. 2002). Such discrepancies suggest that our understanding of woody plant effects on grassland biogeochemistry is rather limited and perhaps confounded by species, disturbance, and land use history effects.

It is noteworthy that significant woody plant-induced accumulations of SOC and N appear to have occurred even though woody communities generally supported a significantly larger soil microbial biomass, exhibited higher potential C and N mineralization rates and had higher concentrations of inorganic N than remnant grasslands. Field measurements indicate that soil respiration (Fig. 2), in situ net N mineralization (Hibbard et al. 2001), and N trace gas production (Cole et al. 1996) are also higher in soils associated with these woody communities, suggesting that the accelerated rates of C and N cycling and loss in woody vs. grassland communities observed under controlled laboratory conditions in this study (Table 4) are being realized in the field. The extent to which enhanced nutrient availability might feed back to influence species interactions and succession in these developing woody communities is not known. Higher concentrations of NH₄⁺ and NO₃⁻ could induce a shift in plant species dominance from N₂-fixing tree legumes important in early stages of woody community development (such as *Prosopis* and *Acacia* spp.) to other non-N₂-fixing species capable of responding to the greater availability of mineral N (Archer 1995).

The accumulation of SOC and total N in woody communities despite indicators of higher nutrient cycling and flux rates implies that woody plants have augmented inputs of organic matter to a greater extent than they have induced losses of C and N from these pools. Comparisons of field data from woody and grassland plant communities and CENTURY model predictions indicate aboveground net primary production in woody communities is $\sim 2\times$ that of remnant grasslands (Hibbard et al. 2003). In addition, woody communities at this site have significantly greater near-surface (0–10 cm) root biomass than remnant grasslands; and shallow root biomass inputs in woody communities greatly exceed those of foliar litter (Hibbard et al. 2001). We

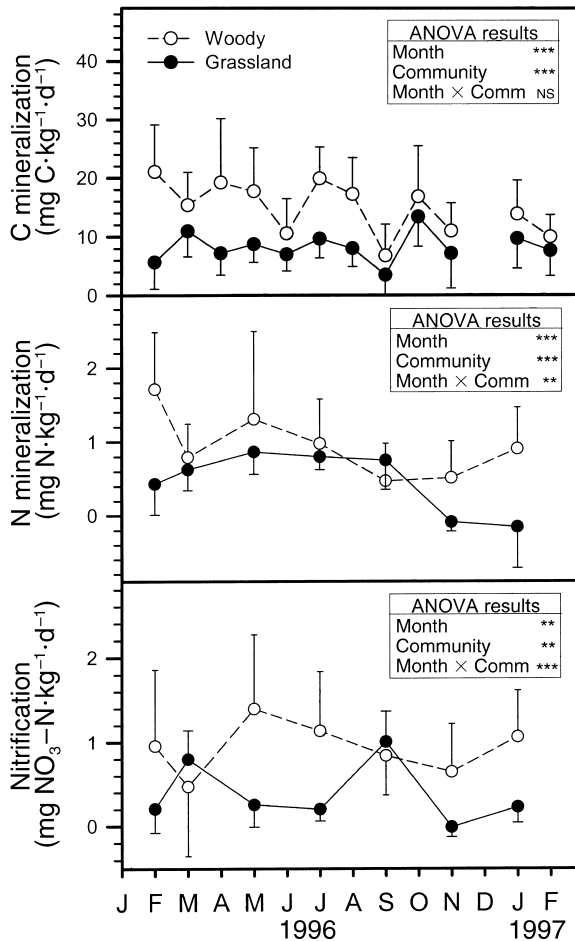


FIG. 4. Spatiotemporal variation in mean (± 1 SD) potential C mineralization, potential N mineralization, and nitrification rates averaged across the two soil depth increments sampled in the grassland and pooled woody plant communities (see McCulley [1998] for seasonal cluster, grove and woodland values). Repeated-measures ANOVA results are shown in the insets ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$; NS, not significant). Potential C mineralization was measured monthly, whereas potential N mineralization and nitrification were measured bimonthly.

postulate that these increases in organic matter input represent increases in both recalcitrant (e.g., lignified roots and stems; foliage with relatively high levels of secondary compounds) and labile fractions, with the former exceeding the latter. This would explain SOC and N accumulations despite larger soil microbial biomass pools and higher C and N mineralization rates observed in wooded communities. Higher rates of soil respiration in woody communities compared to remnant grasslands (Table 3) are also consistent with this explanation, and may reflect greater root respiration (a consequence of the greater shallow root biomass in woodland communities mentioned previously) along with greater microbial respiration.

The notion that recalcitrant inputs have increased to a greater extent than labile inputs is supported by $C_{mic}/$

C_{org} ratios, which indicate that less microbial biomass is supported per unit of SOC in woody communities than in remnant grasslands (Table 4; Anderson and Domsch 1989). Longer mean residence times of SOC in woody communities vs. remnant grasslands are also indicative of an overall decline in soil organic matter quality accompanying woody plant encroachment (Table 3). While all methods for estimating absolute mean residence times have limitations, the relative difference in MRTs between woody and grassland communities in Table 3 are consistent with results from long-term soil incubations indicating that the recalcitrant C fraction of the total SOC pool is 65% in remnant grasslands and 80–90% in woody communities (Boutton et al. 2002). Alternatively, the lower C_{mic}/C_{org} in wooded areas could imply that the microbial communities in those soils are less efficient at converting available carbon into microbial biomass. Although qCO_2 ratios were generally higher in wooded areas and suggested that microbial communities in those soils might be less carbon-use efficient than those in grasslands, this difference was not significant. Thus, the lower C_{mic}/C_{org} values in woody areas appear to be a consequence of a

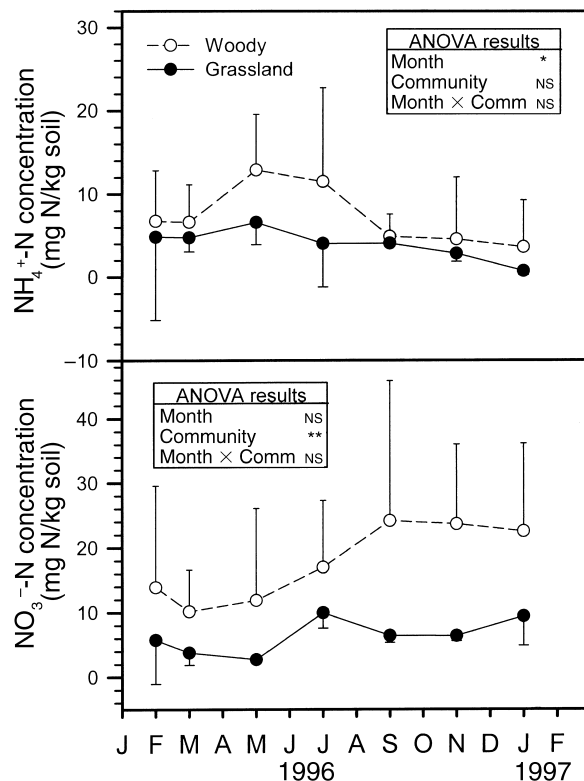


FIG. 5. Spatiotemporal variation in mean (± 1 SD) concentrations of NH_4^+ and NO_3^- averaged across the two soil depth increments sampled in grassland and pooled woody plant communities (see McCulley [1998] for seasonal cluster, grove, and woodland values). Repeated-measures ANOVA results are shown in the insets ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$; NS, not significant). Note the difference in scale between graphs of the N species.

more recalcitrant organic matter pool rather than a less efficient soil microbial biomass community.

CONCLUSIONS

Predicting ecosystem C and N storage consequences of woody plant encroachment into grasslands requires a process-level understanding of how nutrient inputs and losses are altered by vegetation change. At this subtropical site, conversion of grasslands to woody-dominated communities has increased pools of SOC and total soil N. Enhanced soil C and N pools in wooded areas sustain a larger and more active microbial biomass. Higher rates of soil respiration and C and N mineralization under both field and controlled environment settings indicate that at least a portion of the organic matter pool derived from woody plants was labile and available to the microbial community. However, $C_{\text{mic}}/C_{\text{org}}$ ratios indicated that less microbial biomass was supported per unit of SOC in woody communities than in remnant grasslands. This could mean that soil microbial populations in woody communities were less efficient at converting available carbon into biomass, and/or that there has been an overall increase in the recalcitrance of the soil carbon pool. While metabolic quotients ($q\text{CO}_2$) indicated that microbial carbon-use efficiency was comparable in wooded areas vs. grasslands, mean residence times of soil organic carbon were greater in woody plant communities. Overall, these results imply that, despite increases in microbial biomass and activity, the soil organic matter pool becomes more recalcitrant and turns over more slowly when woody communities replace grasslands.

The fact that woody plant encroachment into grasslands has been shown to increase, decrease, and/or cause no net change in ecosystem nutrient storage (Wessman et al., *in press*) indicates that the results reported here are not universal. Given the potentially significant, but highly uncertain recent estimates of C sequestration accompanying woody plant encroachment into grasslands (0.10–0.13 Pg C/yr or 20–40% of the present ecosystem sink strength in the USA; Houghton et al. 1999, Pacala et al. 2001, Houghton 2003), it is imperative that we gain a better understanding of how plant species, soil physical properties, prior disturbance, and land use history interact to alter biogeochemical processes to produce such a wide array of ecosystem nutrient storage outcomes.

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