

GRASSLAND TO WOODLAND TRANSITIONS: INTEGRATING CHANGES IN LANDSCAPE STRUCTURE AND BIOGEOCHEMISTRY

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Abstract. In many of the world's drylands, human-induced alteration of grazing and fire regimes over the past century has promoted the replacement of grasses by woody vegetation. Here, we evaluate the magnitude of changes in plant and soil carbon and nitrogen pools in a subtropical landscape undergoing succession from grassland to thorn woodland in southern Texas. Our approach involved linking a process-based ecosystem model to a transition matrix model. Grass and forest production submodels of CENTURY were parameterized with field data collected from herbaceous and wooded landscape elements broadly representative of habitats in global savanna systems. The Markov (transition matrix) model simulated the displacement of grassland communities under land use practices typical of many modern grasslands and savannas (heavy livestock grazing; no fire) and climate events. The modeled landscape was initialized for pre-Anglo-European settlement grassland conditions and then subjected to heavy, continuous livestock grazing and elimination of fire beginning in the mid-1800s. Rates of woody plant encroachment were directed by the Markov model, and the consequences for net primary production and plant and soil C and N pools were tracked by CENTURY.

Modeled output of plant and soil organic C were in good agreement with those quantified for present-day patch types, suggesting our reconstructions were reasonable. Results indicated that, in the absence of woody plant encroachment, heavy grazing and fire suppression would have reduced soil organic carbon mass in southern Texas grasslands 17% (clay loam lowlands) to 18% (sandy loam uplands) by the 1990s. Soil and plant carbon stocks in current (mid-1900s) *Prosopis* woodlands are estimated to exceed those of the pristine grasslands they have replaced by 1.3× and 10×, respectively. Our reconstructions thus suggest that an initial degradation phase induced by heavy livestock grazing was followed by a woody-plant-induced aggradation phase that is still in progress. Under climatic/atmospheric conditions of the past 100 years, future landscapes would equilibrate at soil and plant C densities that would be 3× and 15–24× that of the pristine, presettlement grasslands they have replaced. Replacement of grasslands and savannas by woodlands in this bioclimatic region has thus resulted in significant and ongoing increases in landscape-scale ecosystem carbon stocks in a relatively short (~100 years) period of time.

Key words: biogeochemistry; carbon sequestration; ecosystem models; grazing; landscape carbon accumulation; land use; *Prosopis glandulosa*; savannas; thorn woodlands; transition matrix models; vegetation change; woody plant encroachment.

INTRODUCTION

Over successional and longer time frames, the response of biogeochemical cycles and their subsequent feedbacks to vegetation structure have been identified as important components of global change (Pastor and Post 1988, Schimel et al. 1991, 1994). Within this framework, it is the dynamics of plant populations and

communities that regulate the rates of terrestrial biogeochemical change (VEMAP 1995, Schimel et al. 1997). One approach for integrating vegetation dynamics and biogeochemistry involves linking models of ecosystem function (biogeochemistry) with those that predict ecosystem structure (biogeography) (e.g., Haxeltine and Prentice 1996, Friend et al. 1997). Other models utilize “modular” logic, whereby biophysical, ecophysiological, and successional processes are linked in a single model (Foley et al. 1996). Although these models incorporate plant functional changes forced by altered climate, atmospheric CO₂ concentration, or disturbance, they do not track changes with regard to age states, or the successional dynamics of disturbance frequencies coupled with new and preexisting cohorts over time. Additionally, dynamic vegetation models are primarily designed to simulate at the

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global scale with spatial resolution, or pixel sizes on the order of 0.5 – 1.0°. As a result, they cannot represent successional processes and variability at landscape scales.

Representation of plant succession at landscape scales is critical, since changes in disturbance regimes and land use typically produce dramatic and transient changes in vegetation stature, cover, and composition over decadal timescales (Asner et al. 2003). Changes in vegetation composition in turn, may feed back to affect the soil nutrient pools and fluxes to promote or constrain future changes (Chapin 1993, Hooper and Vitousek 1997, Tilman et al. 1997). As a result, it is important to quantitatively track the biogeochemical changes that occur subsequent to changes in vegetation. Intensification of domestic livestock grazing and the concomitant reduction in fire has caused substantial vegetation change on dry land landscapes since Anglo-European settlement in the 1800s. Notable among these changes has been the replacement of grasslands and savannas by shrublands and woodlands. Although this physiognomic conversion has been widely reported (Archer 1994, Van Auken 2000, Archer et al. 2001) little is known of their rates and dynamics nor their consequences for biogeochemistry or land surface-atmosphere interactions. Here, we link a dynamic biogeochemistry model and a plant succession model with the goal of ascertaining how a change from grass to woody plant domination might affect landscape-scale pools of carbon and nitrogen.

Our objectives were to use linked biogeochemical-succession models to: (a) assess pre-Anglo-European settlement plant and soil carbon stocks on a grassland landscape; (b) estimate how plant and soil C and N pools might have changed with the advent of heavy, continuous livestock grazing in the mid-1800s; and (c) quantify how plant and soil C pools would subsequently change with and without woody plant encroachment. We addressed these objectives at a subtropical site in southern Texas by (1) parameterizing an ecosystem model, CENTURY, for herbaceous and woody patch types on a landscape with contrasting soil types; (2) simulating historical soil organic C and total N, plant biomass C, and net primary productivity (NPP) for grasslands subjected to varying combinations of fire and grazing; (3) using a transition matrix model to project changes in the abundance of woody plant age states and patch types subsequent to livestock grazing and fire suppression; and (4) integrating CENTURY with the transition matrix model to assess changes in landscape plant and soil organic C storage, which have occurred since Anglo-European settlement. We reasoned that if our current understanding and representation of retrogression and succession associated with grazing and woody plant encroachment is correct (Archer 1995a), and if changes in soil C and N accompanying changes in vegetation physiognomy and production are reasonably estimated by CENTURY, then

we should be able to generate estimates of plant and soil C and N that approximate those observed on present-day landscapes known to have undergone vegetation change. The successful reconstruction of historical disturbance scenarios and the associated changes in successional and ecosystem processes that characterize present-day landscapes is an important step (McGuire et al. 2001) in credibly projecting future changes in landscape C and N pools.

METHODS

Study site

Data for the modeling exercise were from the La Copita Research Area (27°40' N; 98°12' W; elevation 75–90 m above sea level) situated in the northeastern portion of the North American Tamaulipan Biotic Province (Blair 1950) in the Rio Grande Plains Major Land Resource Area (USDA/SCS 1981) of southern Texas. Climate of the region is subtropical (mean annual temperature = 22.4°C) with warm, moist winters and hot, dry summers. Long-term (1912–1993) mean annual rainfall is 650 mm (median = 620 mm) and highly variable (cv = 35%). The potential natural vegetation of this region has been classified as *Prosopis-Acacia-Andropogon-Setaria* savanna (Küchler 1964). However, the contemporary vegetation is subtropical thorn woodland (McLendon 1991) that occupies ~12 × 10⁶ ha in Texas alone (Jones 1975).

Current vegetation at the La Copita site, which has been grazed by domestic livestock since the mid-1800s, consists of savanna parklands on sandy loam uplands that gradually grade (1–3% slopes) into closed-canopy woodlands on clay loam intermittent drainages. Upland soils are underlain by a laterally continuous argillic (clay-rich) horizon at 0.4–0.6 m depth with cambic (nonargillic) inclusions (Loomis 1989). Upland vegetation consists of an herbaceous matrix dotted with discrete shrub cluster age states. Where the argillic horizon is poorly expressed, groves of numerous, large trees occur (Archer 1995a). *Prosopis glandulosa* var. *glandulosa* (honey mesquite), an arborescent legume, dominates the overstory of discrete clusters, groves and woodlands. The understory consists of numerous evergreen and deciduous shrubs whose size and composition vary with the size and age of the *Prosopis* plant. Woody plant cover on La Copita has increased from 10% in 1941 to 40% in 1983. The successional processes involved in woody plant community development and topographic controls over spatial patterns of tree/shrub expansion have been summarized by Archer et al. (1988) and Archer (1995a).

Model descriptions

CENTURY.—CENTURY (version 3.0) is an ecosystem model that simulates the elemental flux of carbon, nitrogen, water, and phosphorus through the plant-soil system (Parton et al. 1987, 1988, 1993). Plant produc-

tion submodels within CENTURY include grassland, forests, and crops. Disturbance regimes, including fire and grazing, forest harvest, and fertilization, can be imposed on the grassland, forest, and crop submodels, respectively.

CENTURY divides plant residues into metabolic (0.1–1 yr turnover time) and structural (2–5 yr turnover time) pools based on lignin-to-nitrogen ratios. The decay rate of the structural plant material is also a function of its lignin content. On-site determinations of foliar and wood nitrogen data were available for *Prosopis* (Schimel et al. 1996) along with lignin concentrations for roots and litter (S. R. Archer and T. W. Boutton, unpublished data).

Site input parameters included soil texture, bulk density, monthly precipitation, and maximum/minimum monthly temperature (Parton et al. 1987). Patch-specific soil texture and bulk density parameters were obtained from field sampling (Hibbard et al. 2001). Climate files were developed from National Weather Service records dating from 1912 from a station in Alice, Texas, ~15 km northeast of the study site. Climate files for simulations initiated between 1890 and 1993 were constructed by consecutively selecting rainfall and temperature data for the required number of missing years starting with 1912.

Forest submodels used for clusters and groves in uplands and woodland lowlands were parameterized to reflect measured and assumed differences in monthly litterfall, carbon allocation to roots, leaves, and woody stems, and soil N-fixation rates. CENTURY assumes a linear relationship between annual soil N-fixation and precipitation.

Transition matrix model.—Succession from grassland to woodland was represented using a Markov model that simulated the probability of various woody and herbaceous patch types replacing each other on landscapes subjected to heavy grazing and the concomitant elimination of fire. The development and application of this model is described in detail by Scanlan and Archer (1991). A brief summary is given here. Probabilities of change between vegetation states were based on transition matrices derived from analysis of aerial photographs encompassing a period of extended drought (1941–1960) and a subsequent period of normal to above-normal annual rainfall (1960–1983) (Fig. 1). At each time step (10 yr), the vegetation state matrix was multiplied by either the “wet” or the “dry” transition matrix to generate a new state matrix. Scanlan and Archer (1991) conducted a series of model runs whereby the frequency of time steps using the wet matrix ranged from 0 (dry matrix applied at each time step) to 1 (wet matrix used at each time step). They present arguments that model runs employing the wet matrix in 30–40% of the time steps best approximated historical rainfall records. We therefore used those vegetation change projections in our analysis.

General approach

Simulations of C and N dynamics accompanying vegetation changes were initiated on a hypothetical 100-ha landscape partitioned to represent an actual La Copita landscape consisting of 54 ha of sandy loam uplands and 46 ha of clay loam lowlands. Previous studies at the La Copita site have shown that soil C:N ratios were highly consistent across woody patch types and age states (C:N = 12–13; 1 SE = 0.2–0.7; Hibbard et al. 2001). We therefore focus on total organic carbon pools and present only select nitrogen data. Initial vegetation of the hypothetical landscape was dominated by grasses. This initial structure was ascribed on the basis of: (a) $\delta^{13}\text{C}$ analyses, which indicated that soils supporting present-day C_3 woody plants in uplands and lowlands were once dominated by C_4 grasses (Tieszen and Archer 1990, Boutton et al. 1998); (b) a woody plant growth model (Archer 1989) and tree-ring analysis (Boutton et al. 1998), which indicated the majority of woody plants in uplands and lowlands to be <100 yr of age; and (c) historical observations of early settlers and explorers (Inglis 1964, Lehman 1969).

Pre- and postsettlement herbaceous production and soil C and N pools (0–0.2 m depth) were estimated by running the grass production submodel of CENTURY for upland and lowland soil types with three levels of grazing (none, moderate, and heavy) and three fire frequencies (no fire; fire every 5 yr; fire every 10 yr) under modern (1912–1993) climate conditions (from National Weather Service records for Alice, Texas). While increases in atmospheric CO_2 may have facilitated increases in woody plant abundance over the past century (Johnson et al. 1993), mechanisms of shrubland expansion can be primarily attributed to heavy grazing and fire suppression (Archer et al. 1995, Archer 1995b). Historical increases in atmospheric CO_2 were therefore not treated as a variable in this analysis. Incorporation of changes in atmospheric chemistry may, however, become increasingly important for understanding future changes.

We began by initializing CENTURY with soil organic carbon (SOC; 0–0.2 m depth) values observed in present-day upland herbaceous patches (~2100 g/m²; Hibbard et al. 2001) and simulated plant and SOC levels that would occur under no or light grazing for the soils and climate of the study site. These were then assumed to represent the levels of plant and soil C present at the time of Anglo-European settlement and served as the baseline against which changes in C and N associated with the advent of heavy continuous livestock grazing and woody plant encroachment were evaluated. Increases in woody plant abundance were dictated by the transition matrix model, which represented changes in the proportionate cover of herbaceous patches, discrete shrub cluster age states (juvenile through mature), groves, and closed-canopy woodlands (Fig. 1).

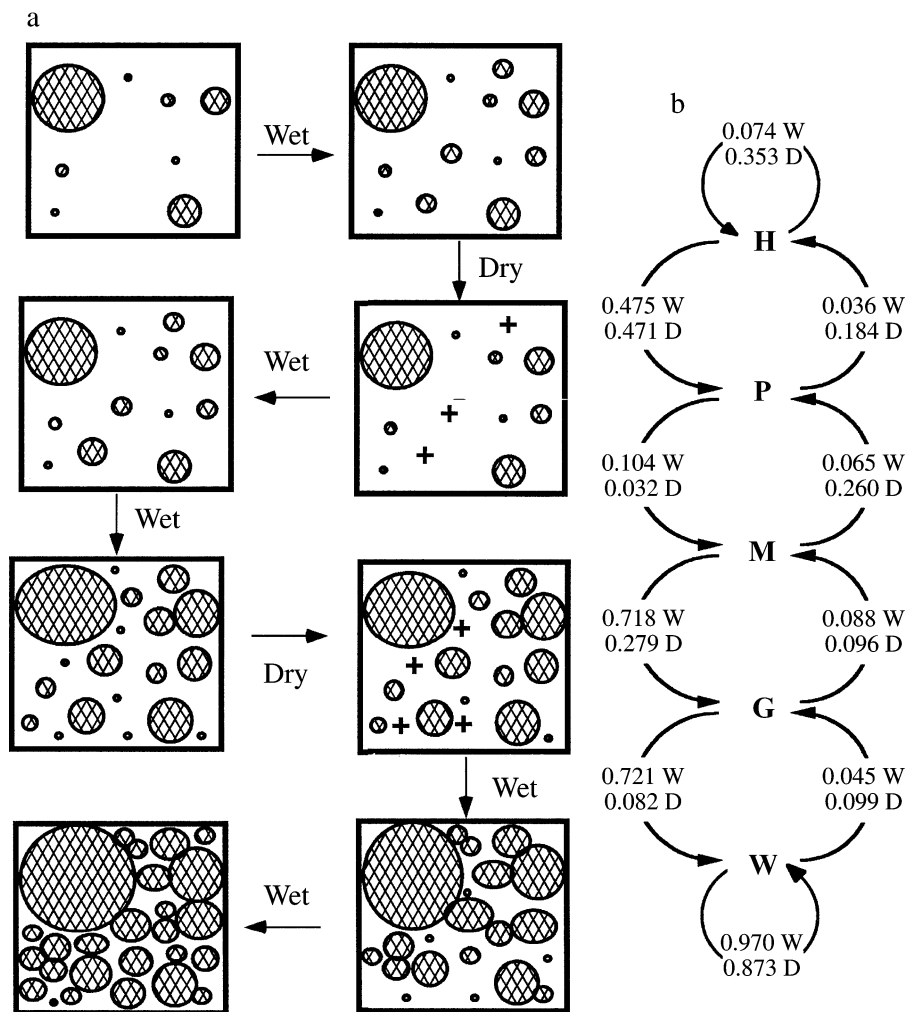


FIG. 1. Probabilities of transition among herbaceous and selected woody states during relatively dry (D; 1941–1960) and wet (W; 1960–1983) periods [panel (b) excerpted from Scanlan and Archer 1991]. Abbreviations are: **H**, herbaceous; **P**, small, pioneer woody cluster; **M**, large, mature woody cluster; **G**, groves of coalesced clusters; **W**, continuous canopy woodlands. For clarity of presentation, only a subset of possible transitions is shown; hence, probabilities out of a given state do not sum to 1.0. The rate and extent of woody plant encroachment in the conceptual sketch [panel (a)] is a function of the proportion of time steps employing wet vs. dry transitions (cross-hatched areas, woody [P, M, G, or W] patches; white areas, herbaceous matrix; “+” denotes transitions from woody to herbaceous). Changes in woody vs. herbaceous cover states used to assess changes in plant and soil C and N with CENTURY were based on wet/dry transition proportions deemed to represent climate at the study site over the past 100 years.

To track changes in plant and soil nutrient status associated with the advent of livestock grazing and woody plant encroachment, we employed a “time for space” approach by incorporating the proportion of landscape in woody and herbaceous patches generated from the transition matrix model (Fig. 1) into the appropriate CENTURY plant submodel. Estimation of changes in landscape-level nutrient mass accompanying succession from grassland to woodland required knowledge of the cumulative contribution of all age states of each woody patch type on the landscape. Changes in the area occupied by each of the patch types were output from the Markov model at 10-yr intervals. Woody patches appearing in any given time step were

subsequently tracked by CENTURY to generate age-specific estimates. At every time step, CENTURY outputs of plant and soil organic C and N density for age states of a given patch type were multiplied by the area associated with those age states. These were then summed to estimate plant and soil organic C and N mass for each patch type on the landscape. Plant and soil C and N masses were then summed across all patch types to estimate landscape-scale changes.

CENTURY parameterization

The impact of grazing in herbaceous patches was manipulated with three input parameters (Parton et al. 1993): (1) the effect of grazing on productivity was a

TABLE 1. Mean above- and belowground observed foliar and woody biomass and annual net primary productivity (NPP) for woody patch types used to set the carbon allocations in CENTURY (top six rows); and foliar litterfall, metrics of overstory *Prosopis* plants, and soil C and N density in cluster, grove, and woodland patches.

Variable	Woody patch type					
	Standing crop biomass (g C/m ²)			NPP (g C·m ⁻² ·yr ⁻¹)		
	Cluster	Grove	Woodland	Cluster	Grove	Woodland
Initialization parameters for CENTURY						
Peak foliar†	53	224	183	141	149	183
Fine root (<2 mm)‡	441	322	309§	294	215	309
Fine branch (<10 cm)‡	732	1274	1819¶	73	61	82
Large wood (>10 cm)‡	1359	2365	1820	48	41	55
Large root (>2 mm)‡	859	418	418#	48	41	55
Total	3444	4603	4549	604	507	684
Foliar litterfall (g·m ⁻² ·yr ⁻¹)§	247	288	381			
Traits of overstory <i>Prosopis</i> §						
Basal diameter (cm)	18	27	32			
Height (m)	3.3	4.9	5.2			
Mean age (yr)	50	58	77			
Range of ages (yr)	38–61	37–72	51–132			
Soil carbon (g/m ²)§	2035	1624	2551			
Soil nitrogen (g/m ²)§	180	137	220			

Notes: Estimates of annual foliar NPP were derived from the ratio of peak biomass : annual litterfall with turnover rates of 0.4, 1.5, and 1.0 years for discrete clusters, groves, and woodlands, respectively. Fine root turnover rates were set to 1.5 years for discrete clusters and groves. Turnover rates for fine and coarse woody biomass were estimated to be 10 years and 50 years, respectively.

† From June 1992 peak foliar biomass harvests (S. R. Archer and D. S. Schimel, *unpublished data*).

‡ Averaged from (Watts 1993) and peak standing crop (Hibbard et al. 2001).

§ Data from Hibbard et al. (2001).

|| Fine root turnover in woodlands was set equal to foliar turnover (1.0 year).

¶ Total woody biomass in woodlands is assumed to equal that of groves; fine branch and large wood received equal allocations in woodlands.

Large root biomass in woodlands is set equal to that of groves (based on their similar fine root biomass).

scalar ranging from minimal to moderate to maximum; (2) the month(s) of grazing; and (3) the fraction of live plant shoots removed by grazing. “Light” grazing, such as that assumed to have occurred prior to European settlement, included two months (March and April) of nominal grass shoot removal (12%), having a moderate effect on productivity. “Heavy” grazing, such as that presumed to have occurred with the introduction of large numbers and high concentrations of domestic livestock (Lehman 1969), consisted of high shoot removal rates (30%) in every month (January–December), and a maximum effect on productivity.

Soil N-fixation was based on relative N-uptake/fixation rates. The linear slope in CENTURY was set to 0.00 g N·m⁻²·yr⁻¹ (flat) and the intercept held constant at 2.5 g N·m⁻²·yr⁻¹ for discrete clusters; 1.5 g N·m⁻²·yr⁻¹ for grove and woodland patches (based on site-specific data from Boutton et al. 1992). N₂-fixation in the herbaceous submodel was kept constant at the standard CENTURY grassland parameterization (intercept = -1.32 g N·m⁻²·yr⁻¹; slope = 0.033 g N·m⁻²·yr⁻¹).

Carbon allocations in CENTURY were based on data summarized in Table 1. CENTURY initializes plant allocation to various plant pools (litterfall, leaf, stem,

root) on a monthly basis based on proportions and not a unit mass basis. CENTURY initialization parameters for soil pools and plant allocation were therefore derived from on-site field studies (Hibbard et al. 2001) by converting biomass or mass per unit area into proportions. Annual foliar net primary productivity (NPP) for grassland patches was calculated after Knapp et al. (1993). Annual foliar turnover rates of 0.4 (discrete clusters), 1.5 (groves), and 1.0 (woodlands) were estimated from the ratio of peak foliar biomass to total annual foliar litterfall using on-site data from Angerer (1991) and Hibbard et al. (2001). We had no litterfall data for immature woody patches, thus precluding comparisons of observed vs. simulated foliar litterfall for immature age states. Carbon allocation to woody plant foliage was estimated from peak foliar biomass harvests in 1992 (S. R. Archer and D. S. Schimel, *unpublished data*). Total above- and belowground woody biomass and carbon content of mature discrete clusters and groves, woody plant rooting depth, and root/shoot ratios were based on Watts (1993). Field data were not available for aboveground biomass in clay loam woodland habitats; these were therefore set equal to upland groves, which were qualitatively similar in terms of

TABLE 2. Output from a 10-yr run (1983–1993) of CENTURY's grassland production submodel compared to field measurements of upland soil carbon (0.2 m), annual N_{\min} (0–0.1 m), and productivity variables.

Data type	Soil carbon	Annual N_{\min} (g N/m ²)	ANPP	Peak live biomass		Precipitation (cm/yr)
				Above-ground	Below-ground	
Observed	2087 [†]	1–9 [†]	87–153 [‡]	43–56 [§]	186 –320 [†]	55–80
Simulated¶						
1991	2122	6	44	27	255	58
1992	2089	9	99	54	307	80
1993	2075	7	59	37	325	55

Notes: Contemporary simulation conditions included continuous heavy grazing and no fire (see *Results: Reconstruction*). All data are reported in g C/m² unless otherwise noted.

[†] From Hibbard (1995) to 0.2 m.

[‡] ANPP, aboveground net primary productivity (1986, 1987) from Vega (1991).

[§] Aboveground data measured from peak biomass harvests (S. R. Archer and D. S. Schimel, *unpublished data*); 1991, 1992, 1993.

|| From S. R. Archer and T. W. Boutton (*unpublished data*) to 0.2 m.

¶ Simulated years were chosen to reflect ranges of annual precipitation in observed data.

aboveground plant size (Hibbard et al. 2001). Carbon allocation to fine branches was estimated as 60% of total (Northup et al. 1995, 1996). Rooting depth for the herbaceous and discrete cluster submodels was set to 0.6 m; grove and woodland rooting depths were set to 1.0 m. Peak standing crop (0–0.2 m) of fine roots in woodlands (Hibbard et al. 2001) was similar to that measured in groves by Watts (1993). Therefore, fine and coarse roots in woodlands were set equal to those observed in groves. CENTURY's default monthly turnover settings were used for fine roots (0.10), fine branches (0.0083), coarse roots and coarse wood (0.0017). Output from CENTURY is expressed in terms of C and N mass·m⁻²·mo⁻¹; therefore, field biomass data utilized for model evaluation was converted to C mass by multiplying by 0.45, a conversion which has been substantiated for plants at this (S. R. Archer and T. W. Boutton, *unpublished data*) and other (Scholes and Walker 1993) savanna sites.

Evaluation of linked model output

Output from the grassland submodel for uplands was compared to field measurements of soil C and N_{\min} made in 1992–1993 (Hibbard et al. 2001), above- and belowground biomass harvests in 1991–1993 (S. R. Archer and D. S. Schimel, *unpublished data*), and aboveground NPP measured in 1986–1987 (Vega 1991). Observations used for model verification were obtained from studies independent of those used to parameterize the model. There were no lowland grassland patches, owing to the nearly continuous woody canopy cover on this portion of the landscape. As a result, we could not compare model predictions of present-day SOC in heavily grazed lowland grasslands to actual values. In lieu of this, we compared modeled SOC values to those obtained from soils sampled at the margins of *Prosopis* plant canopies (S. R. Archer and T. W. Boutton, *unpublished data*), and thus minimally impacted by woody plants. Estimates of presettlement

steady state upland and lowland grassland NPP were compared to “potential” NPP derived from protected relict sites in the county where the study site was located (USDA 1979). As an independent test of landscape-scale predictions from the linked CENTURY-succession model, we compared carbon densities predicted by the models to those estimated from field/aerial photo assessments (Archer et al. 2001). The latter consisted of quantifying aboveground plant carbon density in cluster, grove, and woodland patches at the La Copita site using allometric relationships and belt-transect surveys (Northup et al. 1996). Plant carbon density for a given patch type was then multiplied by patch area on aerial photographs from 1950, 1976, and 1990. The contributions of each patch type were then summed to obtain landscape scale estimates of aboveground C density for the three dates and compared to model predictions for those same dates.

RESULTS

Model performance

Herbaceous vegetation on relict, protected grasslands in the region, which presumably represent the vegetation of presettlement conditions, are characterized by mid- to tall statured perennial grasses. Peak standing crop from such sites (~600 g/m²; USDA 1979) compared well with those predicted from CENTURY equilibrium runs (~700 g/m²; *data not shown*). Present-day herbaceous vegetation at the La Copita is dominated by ephemeral dicots and short-statured, weakly perennial grasses; ground cover is low. CENTURY's grassland submodel, run for 10 years using climate years 1983–1993 generated estimates of productivity, biomass, and net nitrogen mineralization (N_{\min}) within ranges reported in various field studies at the site (Table 2).

Results from CENTURY's simulation of the contrasting woody patch types were assessed by comparing

TABLE 3. Comparison of CENTURY's forest submodel output with field measurements of soil carbon, N_{\min} , and productivity.

Patch type	Estimated age (yr)†	Soil carbon (g C/m ²)	N_{\min} (g N/m ²)	Live biomass (g C/m ²)	
				Peak foliar	Total
Discrete cluster					
Observed	50 (3)	1424–5010 (3385)†	13–32 (21)†	23–96 (53)‡	2241–4635 (3444)
Simulated	60	3197	18	78	3062
Grove					
Observed	58 (3)	1393–4168 (2466)†	8–27 (16)†	111–278 (224)‡	4127–6197 (4603)
Simulated	60	2548	11	100	3443
Woodland					
Observed	77 (6)	2401–6568 (4856)†	1–36 (14)†	80–341 (182)‡	NA§
Simulated	80	3394	14	106	5058

Notes: Key woody submodel parameters for mature discrete clusters, groves, and woodlands, respectively, included soil N_2 -fixation intercepts of 2.5, 1.5, and 1.5 $g\cdot m^{-2}\cdot yr^{-1}$ and a time to end of simulation of 60, 60, and 80 years. Time to end of simulation was based on average estimated *Prosopis* plant ages from Hibbard et al. (2001). Observed age data are presented as mean (SE); all other data are presented as range (mean). All simulations ended in 1993.

† From Hibbard et al. (2001).

‡ Data measured from peak biomass harvests, 1992 (S. R. Archer and D. S. Schimel, unpublished data).

§ No woody biomass harvests for this landscape element exist to date.

the output for modeled patch age states to those generated from field studies of patch age states. In general, CENTURY predicted annual N_{\min} , soil C, and peak foliar biomass within ranges observed in each woody patch type (Table 3, Fig. 2a–c). Differences in soil C pools between woody and herbaceous patches predicted by CENTURY were also comparable to those reported from other field studies at this site (McCulley 1998, Gill and Burke 1999). Total soil N (Fig. 2e–g) and peak and total foliar biomass (Table 3) were generally underestimated in all woody patch types; and foliar litterfall was underestimated in grove and woodland patches (*data not shown*). Aboveground carbon density estimated using field surveys and aerial photos of three landscapes “inventoried” in 1950, 1976, and 1990 averaged (\pm SE; $n = 3$ landscapes) 2.3 ± 0.3 , 2.8 ± 0.1 , and 3.3 ± 0.1 kg C/m², respectively (Archer et al. 2001). Carbon densities predicted by the linked CENTURY-succession model for these same dates (2.6, 3.1, and 3.2 kg C/m²) were within 13%, 10%, and 3% of these independent estimates.

Reconstruction of presettlement grassland carbon

Prior to the mid-1800s, grasslands of southern Texas would have been grazed by native herbivores (e.g., pronghorn, bison), and feral livestock (cattle and horses introduced by Spaniards in the 1500s). We assume that with herbivore migration, population fluctuation, predation, and other factors, presettlement grazing impacts would have been minimal. Historical fire frequencies for pristine grasslands of level to gently rolling topography, such as that of the La Copita site, have been estimated at 5–10 years (Wright and Bailey 1982, Scifres and Hamilton 1993). For these reasons, to evaluate changes in SOC with vegetation change, we used equi-

librium SOC levels generated from light grazing and fire every 10 yr (2520 and 3270 g/m² in upland and lowland soils, respectively) as our starting point to model the impacts of intensive grazing (Fig. 3).

Beginning in 1850, approximately coincident with the advent of large-scale, unregulated, heavy and continuous livestock grazing in southern Texas (e.g., Inglis 1964, Lehman 1969) and other regions of the western United States (e.g., Madany and West 1983), grazing levels in CENTURY were increased to 30% utilization on a 12-month basis. Heavy, continuous grazing typically has the effect of reducing fine fuel loads and can greatly reduce and even eliminate fire from grassland and savanna systems (Madany and West 1983, Baison and Swetnam 1990, Savage and Swetnam 1990), a consequence noted by Lehman (1969) for southern Texas. Fire in the heavy grazing simulations were therefore set to “none.” Under these conditions, by 1993, SOC decreased by 17% and 18% in lowland and upland landscape positions, respectively (Fig. 4). Changes on both soil types were rapid during the first 40 years of heavy grazing, then stabilized at SOC levels approximating those measured in present-day grassland communities (2060 vs. 2087 g/m² in uplands; 2700 vs. 3081 g/m² in lowlands). The 14% disparity between observed and predicted lowland grassland values likely was due, in part, to the fact that observed values were from soils at woody plant canopy margins (see *Methods: Evaluation*), which would have been somewhat influenced by *Prosopis* and associated shrubs.

Carbon and nitrogen dynamics in developing woody patches

Based on the age structure of existing *Prosopis* dominated patches (Boutton et al. 1998), we initiated woody

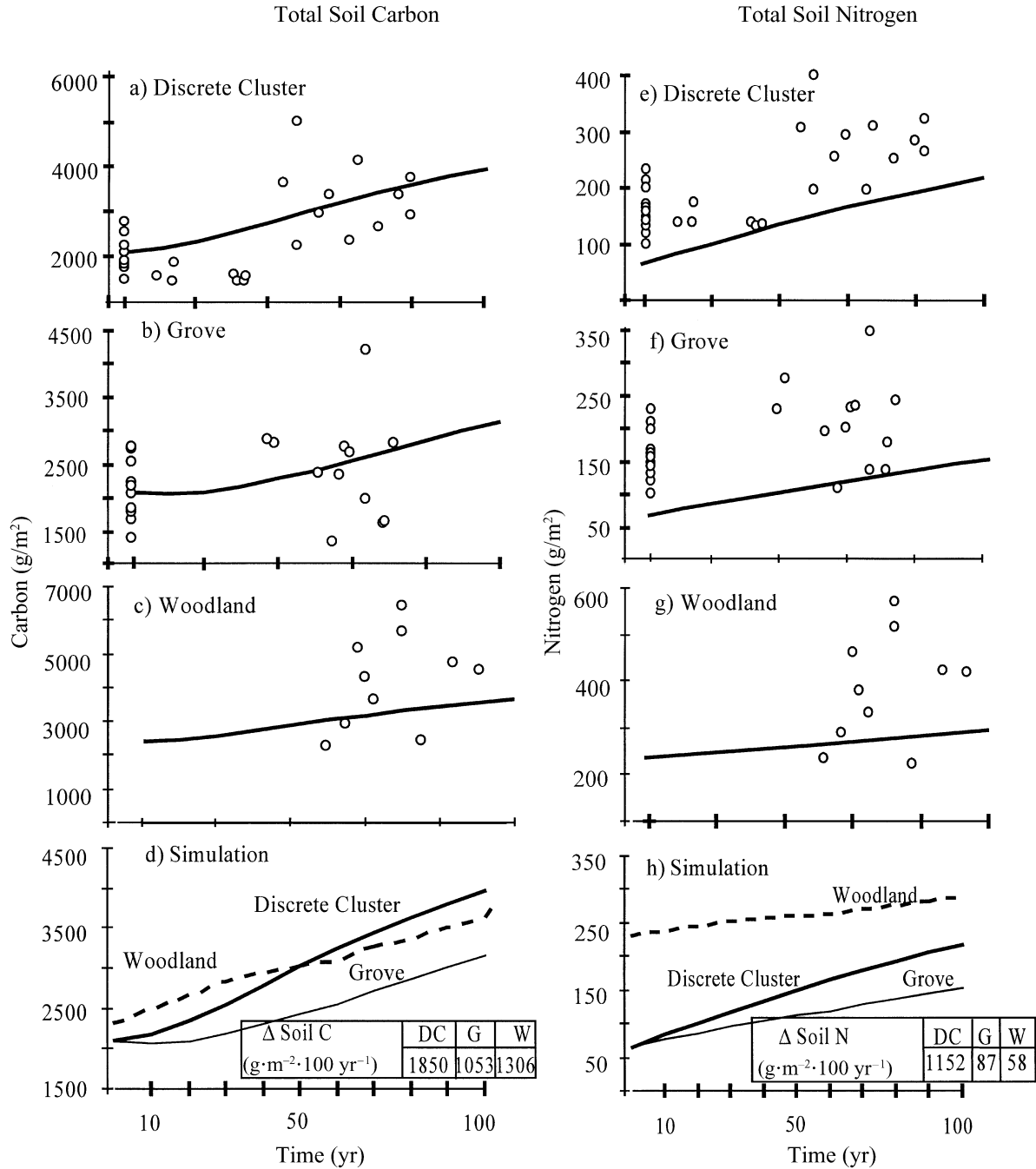


FIG. 2. Simulated (lines) and observed (open circles) changes in the mass of soil (0–0.2 m depth) organic carbon (left panels) and total nitrogen (right panels) accompanying the development of (a, e) discrete cluster, (b, f) grove, and (c, g) woodland patches. Values for herbaceous patches in 1992–1993 are shown at time = 0. CENTURY simulations for all woody patches are presented in (d) and (h) for comparison. Insets show rate of change (g/m^2) in soil organic carbon (d) and total nitrogen (h) over 100 years of woody patch development.

plant encroachment on livestock-impacted landscapes in 1890. Soil C and N pools and plant C pools increased with time in each woody patch type, the greatest accumulation rates occurring in upland cluster patches (Fig. 2d, h). Woodland patches on clay loam lowland soils accumulated soil C at a greater rate than groves

of sandy loam uplands; however, grove patches accumulated soil N at greater rates than woodland patches. Differences in aboveground C accumulation differed markedly among patch types (Woodland > Grove > Cluster) (Fig. 5b), but differences in total plant C (aboveground + belowground to 0.2 m) were much

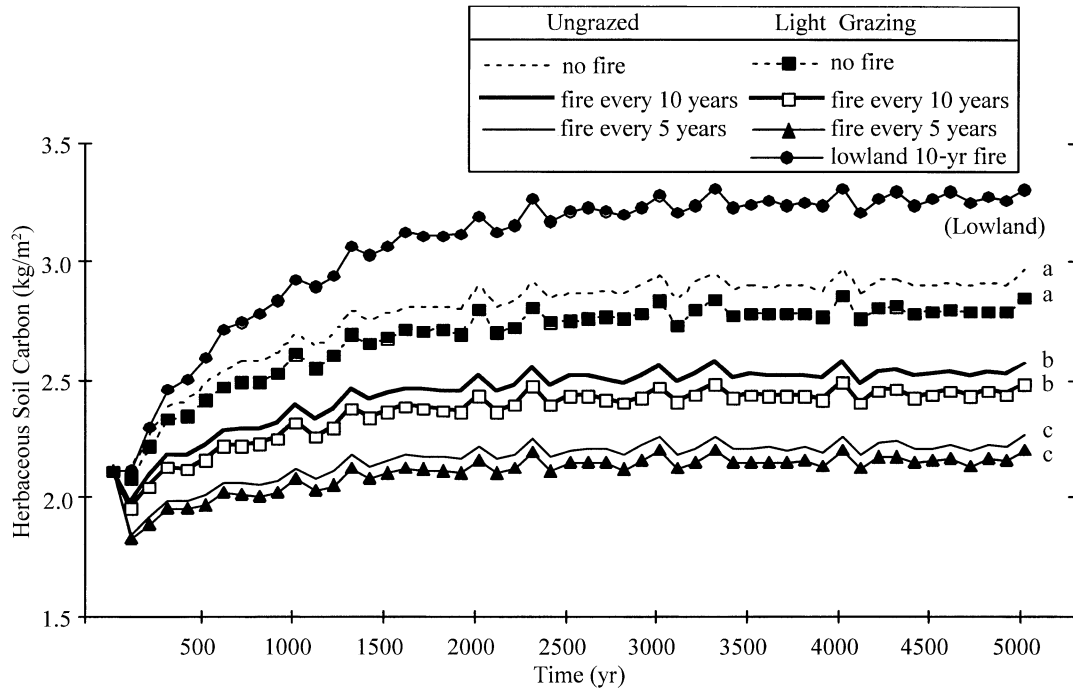


FIG. 3. CENTURY predictions of soil organic carbon mass (to 0.2 m depth) in ungrazed and lightly grazed sandy loam uplands experiencing no fire and fire at 5- and 10-yr intervals. Initial SOC values were from present-day (1992–1993) upland herbaceous patches. Results from a lightly grazed clay loam lowland grassland burned every 10 years are included for comparison. Different letters denote significant ($P < 0.05$) ANOVA and least significant differences among means at the end of the simulation period. Patterns in lowlands were similar to uplands, with carbon densities ranging from 2957 g C/m² (light grazing and fire every five years) to 3850 g C/m² (no grazing, no fire) (*data not shown*).

smaller (Fig. 5c). Net primary productivity varied in the order $W > C > G$ (Fig. 5d), with woodland patches having a relatively stable NPP, while that of groves and clusters steadily increased with patch age. In contrast to biomass estimations, CENTURY predicted higher NPP in clusters than in groves.

To ascertain if date of woody patch initiation might significantly affect plant biomass and soil carbon accumulation, patch “cohorts” were initiated on six different dates and allowed to develop under real-time climatic conditions for 50 years. Cohort initiation dates were chosen such that the last cohort reached 50 years

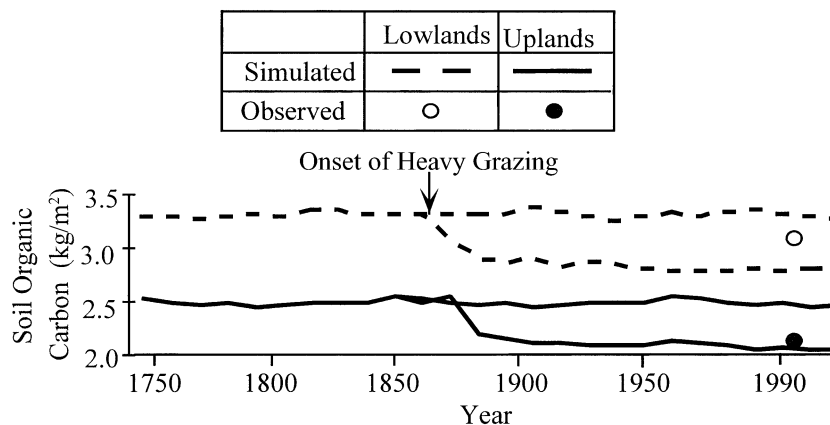


FIG. 4. Equilibrium runs (light grazing; fire at 10-yr intervals from Fig. 1) showing changes in grassland soil organic carbon (0–0.2 m) on two soil types (sandy loam upland, solid line and solid circle; clay loam lowland, dashed line and open circle) following the onset of heavy, continuous livestock grazing and cessation of fire in southern Texas. Data points in 1993 represent mean observed values for long-term heavily grazed sites (from Hibbard et al. [2001] and T. W. Boutton and S. R. Archer, *unpublished data*). Observed mean values for clay loam lowland grasslands, which are now dominated by woodlands, were from soils sampled at *Prosopis* canopy margins. Thus, these soils had been somewhat influenced by woody plants, though not to the extent of those occurring near *Prosopis* boles.

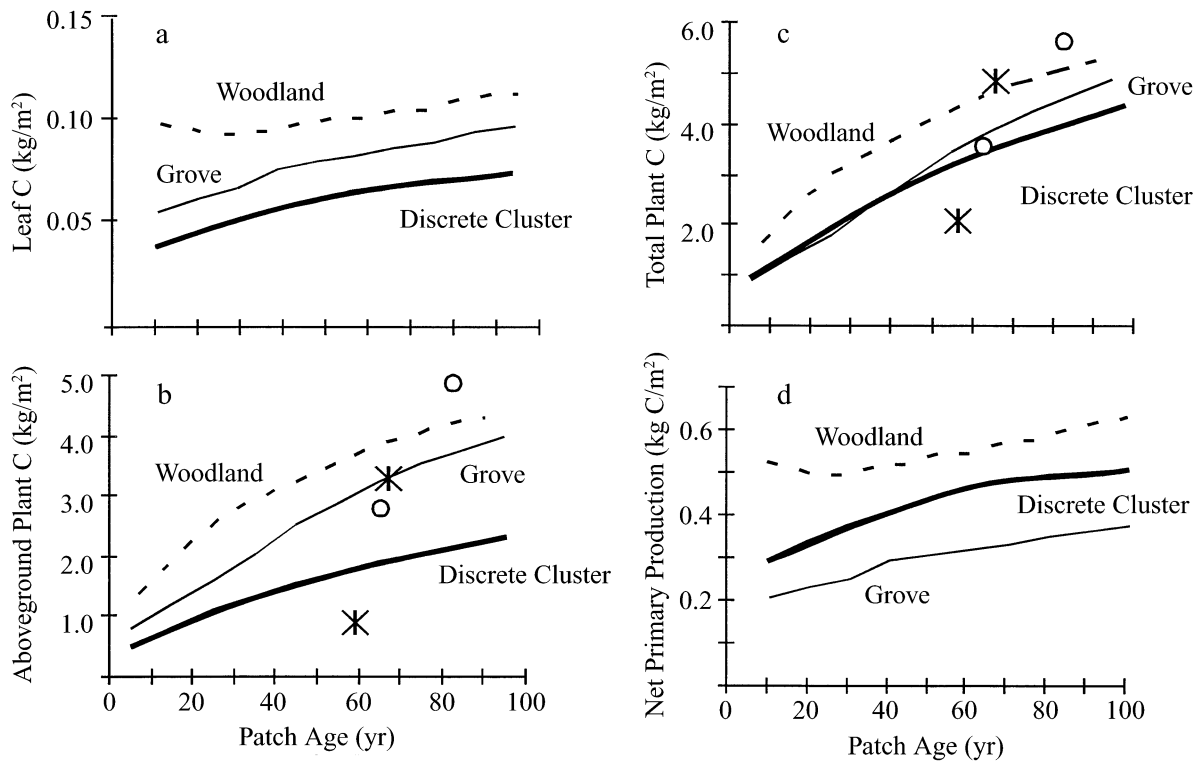


FIG. 5. Simulated accumulation (kg/m^2) of (a) foliar carbon, (b) total aboveground (foliar + woody) carbon, (c) total plant carbon (above ground + belowground to 0.2 m depth), and (d) annual net primary production in woody plant patch types in a southern Texas savanna parkland. Individual points in (b) and (c) represent discrete cluster (star) and grove (open circle) biomass data from Watts (1993).

of age in 1993, the ending date of the simulation period. The amount and variability of annual rainfall experienced by the six 50-yr-old cohorts was comparable, and patch initiation date had no significant effect on soil and plant C accumulation (*results not shown*).

Carbon stores in changing landscapes

Woody patches were initiated on the hypothetical heavily grazed landscape as directed by the transition matrix model (Scanlan and Archer 1991). Plant and soil C associated with age states of each patch type were then summed at each time step to ascertain the proportionate contribution of each patch type to overall landscape C pools. CENTURY results suggested that by 1900, total plant carbon on the La Copita landscape would have been $4\times$ greater than that of heavily grazed grasslands not undergoing woody plant encroachment and almost $3\times$ that of the presettlement grasslands present in the early 1800s (Fig. 6a). Between 1900 and 1950, plant C accumulated at a rate of $43\text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, then slowed and became asymptotic by 1970. By 1950, soil carbon levels across the heavily grazed landscape experiencing woody plant encroachment were approximately equal to those that would have occurred had the presettlement grasslands been maintained (Fig. 6b). By this time (1950), total plant carbon was $7\times$ that of presettlement conditions. Landscape soil C accumu-

lation between 1900 and 1990 averaged $9.3\text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. Long-term forward projections suggest the rate of carbon accumulation in woody plant biomass has nearly peaked and will begin to slow over the next 100 years, especially in discrete cluster patches (Fig. 7a). At 300 years after initiation, plant carbon in grove and woodland patches ($\sim 8600\text{ g}/\text{m}^2$) was about $1.3\times$ that of mature discrete cluster patches ($6400\text{ g}/\text{m}^2$). Accumulation of soil carbon lagged far behind that of plant carbon, with significant increases in mass projected to occur for another 100 (clusters) to 300 years (groves and woodlands) (Fig. 7b).

Woodland patch types dominated total landscape soil carbon stocks, their contribution increasing through time (48% of landscape soil C in 1900; 71% in 1993). This reflected both their extensive area (46% of landscape cover in 1900; 64% in 1993) and their high productivity (Fig. 5). In addition, woodland patches dominated the relative contribution ($>60\%$) of plant carbon accumulation over the entire simulation period (Fig. 6a). Developing clusters initially contributed 24% of the plant C stock, owing to their large numbers and high productivity. However, over time, their contribution to landscape C mass declined to 5% of the total. Groves and discrete clusters accumulated up to 16% and 3% of the total plant carbon, respectively. The relative contribution of the various vegetation patches

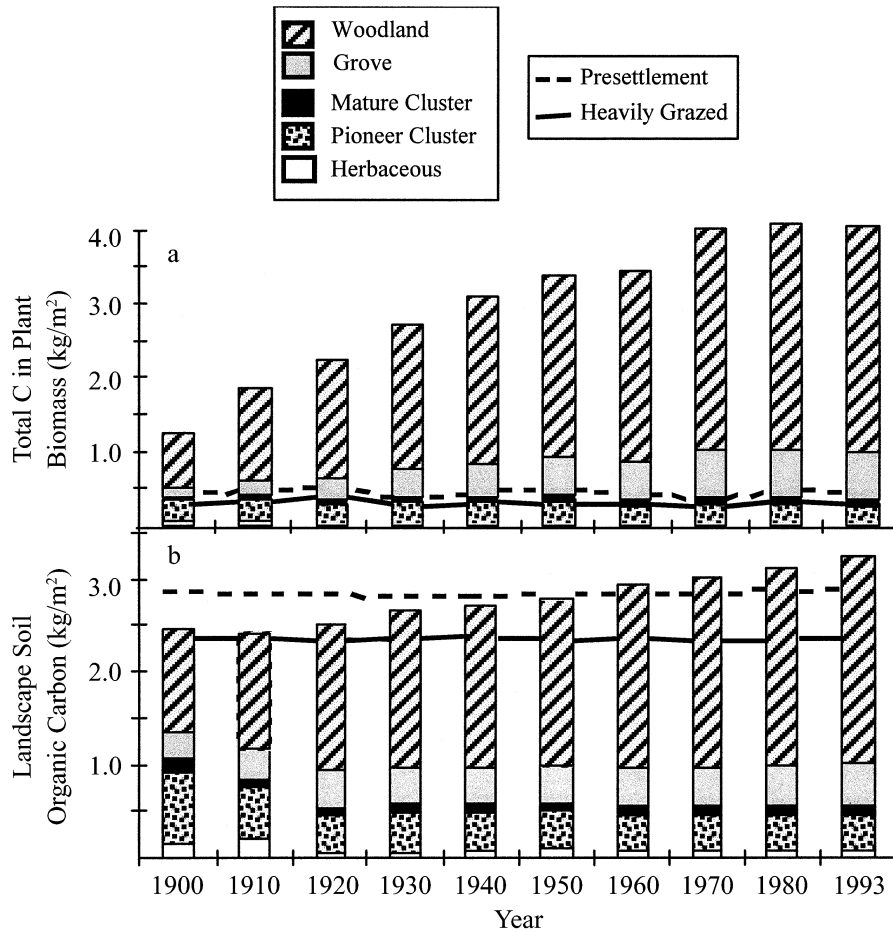


FIG. 6. CENTURY predictions (10-yr time intervals) of changes in landscape-scale carbon density in (a) plant aboveground + belowground (to 0.2 m) and (b) soil (0–0.2 m depth) pools associated with heavy, continuous livestock grazing, elimination of fire, and woody plant encroachment. Bars depict the proportionate contribution of woody patch types whose area changed in accordance with a transition matrix model (Fig. 1; Scanlan and Archer 1991). The solid line depicts carbon density on a heavily grazed landscape without woody plant encroachment; the dashed line depicts the C density that would be expected if the grasslands present at the time of settlement had been maintained (from Fig. 4).

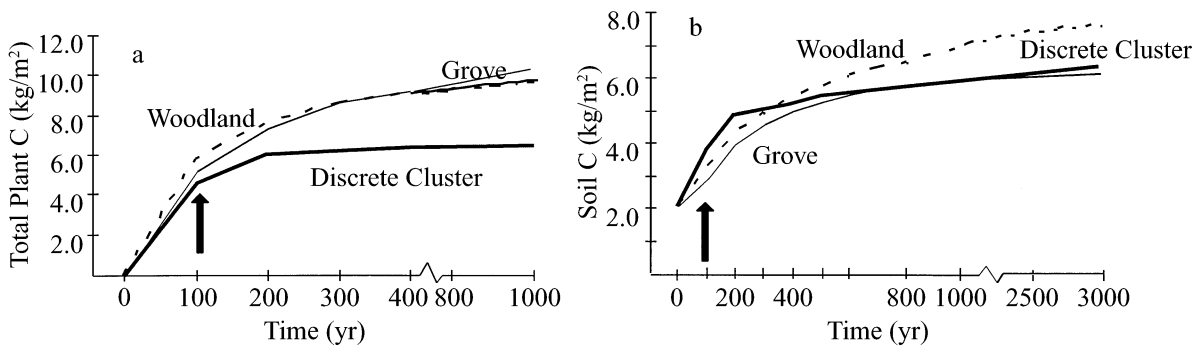


FIG. 7. Changes predicted by CENTURY in (a) total plant (aboveground \times belowground to 0.2 m) and (b) soil (to 0.2 m) C density accompanying the long-term development of upland shrub (cluster, grove) and lowland woodland patch types in southern Texas. Note differences in time to equilibrium between (a) and (b). Arrows point to present-day (1992–1993) values.

to total soil carbon was similar to that observed for plant carbon pools (Fig. 6b).

DISCUSSION

Reconstruction of grazing effects on grassland soil carbon

Effects of grazing on soil C storage may be positive, neutral, or negative (Milchunas and Lauenroth 1993). Our modeling exercise predicted declines in SOC (Fig. 4) of a magnitude similar to that which has been reported in comparisons of lightly vs. heavily grazed grasslands (Bauer et al. 1987, Frank et al. 1995). CENTURY 3.0 does not simulate spatial relationships within or across landscapes. Hence, model output did not explicitly include potential soil C and N erosion losses. The fact that simulated historical changes in SOC closely approximated those currently observed at the site without incorporating erosion suggests that such losses may have been minimal. This inference seems reasonable, since the La Copita landscapes have little topographic relief (1–3% slopes) and show no obvious physical signs of erosion (pedestals, rills, gullies). Elevated C and N pools in soils of developing woody communities (see *Discussion: Carbon dynamics*) thus appear to be primarily the result of in situ accumulations induced by trees and shrubs rather than erosional losses from grazed grasslands.

Carbon dynamics in contemporary woody plant patches

Our results suggest that subsequent to the establishment of woody plants in grazed patches, soil carbon has accumulated at rates of 11–19 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (Fig. 2d). The fact that the simulated patch initiation date had little or no effect on the size of plant and soil C pools over a 50-yr period (*data not shown*) suggests these accumulation rate estimates are robust and are not strongly influenced by the timing or sequencing of rainfall or other climate variables. Patch-scale accumulation rates (~ 0 in herbaceous and 11–19 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in woody patches) were higher than total landscape-scale accumulation rates (9.3 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), illustrating the importance of appropriately weighting patch specific estimates when extrapolating over heterogeneous areas.

NPP in drylands is strongly influenced by interactions between topographic and climatic variables. At the La Copita, patches representing sandy loam upland and clay loam lowland woody plant communities differed with respect to patterns of NPP and C accumulation. In relatively mesic systems, clayey soils support a higher NPP than sandy soils receiving the same rainfall; the reverse is true in more arid areas. This cross-over occurs at an annual rainfall of ~ 500 mm (Noy-Meir 1973). CENTURY's predictions that woody communities on fine-textured soils at the La Copita (mean annual rainfall = 650 mm) would have a greater NPP than those on coarse-textured upland soils (groves and

discrete clusters) (Fig. 5d) were consistent with this generalization.

Our model results suggest that an accounting of belowground root biomass is critical to assessing changes in the carbon cycle resulting from woody plant encroachment. From an aboveground plant C standpoint, woodland and grove patches accumulated $\sim 200\%$ more C than did discrete cluster patches (Fig. 5b). However, when the belowground plant component was factored in, differences between these communities were only $\sim 25\%$ (Fig. 5c). Studies documenting only the aboveground component would thus greatly overestimate the importance of some woody communities (woodlands and groves in this case) relative to others (discrete clusters). Field studies at this site also indicate that fluctuations in monthly woody plant root biomass in upper 0.2 m of the soil exceeded monthly foliar litter inputs by one to two orders of magnitude (Hibbard et al. 2001). This suggests that root rather than leaf/stem inputs of organic matter may drive changes in soil physical and chemical properties subsequent to woody plant establishment in grasslands.

The fact that CENTURY consistently underestimated soil N (Fig. 2e–h) suggests our estimates of woody plant root turnover and N inputs from biological fixation or decomposition (based on limited field data and treated as a function of residue lignin:N ratios in CENTURY), may have been conservative. There is a relative lack of information on N-fixation and its relationship to net primary production (Vitousek and Field 1999), and this remains a potentially important problem toward understanding ecosystem processes and function. The rates and magnitudes of N-fixation and its relationship to carbon stores and fluxes may be the least understood problem in these kinds of ecosystems. In addition, lignin:N indices useful in predicting litter decay rates in many systems, may be less so in systems such as the La Copita, which are dominated by plants with high concentrations of secondary compounds (Palm and Sanchez 1990). A more comprehensive documentation of woody plant leaf and root turnover and decomposition kinetics are thus an important next step toward improving our understanding of how shifts in plant life form composition might affect carbon pools in subtropical savanna and woodland systems via feedbacks through nutrient cycling and primary production.

CENTURY generated patch-specific differences in grove, discrete cluster, and woodland community biomass and nutrient stocks based on a few soil properties in the 0–0.2 m depth (texture, bulk density) and coarse plant growth attributes (litterfall, root/shoot allocation). Differences in woody patch function were also successfully simulated without explicitly incorporating, runoff/run-on, competition among woody species comprising the patch types (typically 8–12 species representing 4–5 functional types [Archer 1995a, Nelson et al. 2002] with contrasting rooting patterns and leaf phenology) or feedbacks between soil nutrient status

and plant composition. The robust performance of CENTURY in this structurally complex savanna grassland/parkland/woodland landscape suggests that regional assessments of ecosystem C and N stocks via linked biogeochemistry model–remote sensing approaches (e.g., Asner et al. 1998, DeFries et al. 1999) may be reasonably achieved with a fairly minimal knowledge of plant characteristics and soil properties.

Carbon stocks in changing landscapes

Although woody plant encroachment has long been a concern of land managers in dry lands (Fisher 1950), research on this phenomenon has been primarily focused on its consequences for herbaceous composition or production and the development of range management practices to reduce the abundance of trees and shrubs. Relatively little is known of the rates and dynamics of this lifeform transformation or its impact on biogeochemistry and biodiversity. Assessments based on historical aerial photography (Archer et al. 1988), growth rate (Archer 1989) and transition matrix (Scanlan and Archer 1991) models, dendrochronology and stable isotope assessments (Boutton et al. 1998) all indicate a transformation of the La Copita landscapes from grass to woody-plant domination over the past 150 years. Our results, using a linked biogeochemistry–succession model, suggest that this transformation would have included an initial 50-yr grazing-induced degradation phase characterized by a net loss of ecosystem carbon (Fig. 4). This was then followed by an aggradation phase, whereby plant and soil carbon stocks recovered to and eventually exceeded that of the original ecosystem (Fig. 6). These results are likely conservative in that they take into account only the root biomass and SOC in the upper 0.2 m of the soil profile. Woody plants in this system are deeply rooted (*P. glandulosa* roots have been encountered at depths up to 9 m [S. R. Archer and T. W. Boutton, unpublished data]) and woody plant patches developing on former C₄ grasslands contain 2× (drainage woodlands) to 4× (groves) more biomass to 1.3 m depth than remnant grassland patches (Boutton et al. 1998). Given the deeper rooting of woody plants relative to grasses (Jackson et al. 1996), we would expect that when grasses are replaced by woody plants, substantially more plant C would be translocated to soil depths where rates of decomposition would be very slow.

Aggradation of landscape plant and soil C pools, driven by woody plant colonization and community development, were still in progress at the time of this study. Plant C pools accumulated rapidly over the first 100 years of woody plant encroachment, but appear to have slowed markedly since 1970 (Fig. 6a). Reductions in rates of accumulation reflect the fact that woody cover on the landscape is approaching its maximum and that established trees and shrubs are reaching maturity. *P. glandulosa* clearly dominates the aboveground cover (Archer et al. 1988, Boutton et al. 1998)

and belowground biomass (Watts 1993) in all La Copita landscape elements. Future trends in plant carbon stocks may thus depend on the future growth and longevity of the central *Prosopis* plant. The maximum age of *P. glandulosa* stems sampled at the La Copita is 109 years (Boutton et al. 1998); the maximum longevity for this species in this region is unknown. When *P. glandulosa* plants begin to succumb to age-related mortality, several outcomes are possible based on succession scenarios elaborated in Archer (1995a): (a) plant carbon pools decline and stabilize at a level commensurate with the realized growth potential of remaining woody plants; (b) no net change in plant C pools if the loss of *P. glandulosa* is compensated by an increased growth of the remaining shrubs; or (c) a degradation phase is initiated, whereby the productivity and persistence of associated woody species are adversely affected by the changes in microclimate and loss of N-inputs from the N₂-fixing *P. glandulosa*. This would result in a substantial decline in plant C pools relative to present. Available data from short-term *Prosopis* removal experiments suggest (c) is unlikely (Barnes and Archer 1996, 1998). Loss of *Prosopis* may also cause declines in SOC within 10–15 years (Tiedemann and Klemmedson 1986). Projections of future trends in plant succession and productivity may thus need to account for changes in overstory–understory interactions and feedbacks between soil nutrient status and plant composition/performance along with plant responses to elevated [CO₂] (Polley 1997), N-deposition (Holland et al. 1999, Köchy and Wilson 2001), and climate/land use change.

The potential for carbon sequestration in savannas

Savannas, grasslands, and shrublands contribute ~36% of the total global annual land NPP (Field et al. 1998). Hence, when grasslands are transformed into savannas and savannas into woodlands, the potential to substantially alter local-, regional-, and global-scale C sequestration and dynamics is great. This transition from herbaceous to woody vegetation increases the residence time for carbon in these ecosystems and expands the capacity of biomass pools, especially if woody plants translocate substantial carbon deep into the soil. In the most recent USA carbon budget assessments, “thickening” of woody vegetation in dryland and montane forest ecosystems has emerged as a significant but highly uncertain modern sink (Houghton et al. 1999, Schimel et al. 2000, Pacala et al. 2001).

Assessments of present-day carbon sinks are the reflection of changes in carbon pools over the past several decades to centuries. Many ecosystem models are capable of “reproducing” general trends leading to present-day conditions (Schimel et al. 1997, 2000, McGuire et al. 2001, Prentice et al. 2001). Reconstruction of contemporary conditions in these analyses, however, has been over large spatial scales (0.5° latitude × longitude) and/or generated from averaged cli-

matic conditions that were recycled until the models reached equilibrium. Such large scale modeling experiments are not directly verifiable in the field. In addition, none of these analyses considered anthropogenic activities (e.g., grazing, fire suppression) to reconstruct historical carbon stocks. Our experiment to determine whether date of woody patch initiation and rainfall variability over the past hundred years influenced ecosystem carbon pools suggested that climate was not an overriding factor driving carbon accumulation. In contrast, manipulating fire frequency and grazing intensity significantly impacted carbon dynamics (Figs. 4 and 6). Finally, analyses based on Schimel et al. (1997, 2000) and CENTURY simulations suggest that changing climate/atmospheric CO₂ effects on plant productivity may be third order relative to human manipulation. Indeed, recent analyses by Asner et al. (2003) show that land management practices can alter the magnitude and even the sign of changes in plant and soil carbon pools. Therefore, we emphasized land management (fire, grazing) rather than changes in atmospheric CO₂ concentrations or climate manipulations in our analyses. However, it is important to remain cognizant of the fact that infrequent, extreme climatic events can also have dramatic effects on woody plant carbon pools (e.g., Allen and Breshears 1998). One area that requires more understanding is how semiarid landscapes undergoing vegetation changes would function under different climatic conditions. This is important for projecting into the future under climate change scenarios and extrapolating spatially into other climate regimes.

CONCLUSIONS

Nonforested regions experiencing woody plant proliferation are a potentially significant but highly uncertain component of the North American terrestrial carbon sink (Pacala et al. 2001). Modeled rates of plant carbon accumulation at the La Copita site ($\sim 36 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) over 100 years were comparable to those estimated for semiarid woodlands in Queensland ($\sim 42 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$; Gifford and Howden 2001). Our modeled rates of plant + soil C accumulation at the semiarid, subtropical La Copita site ($\sim 48 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) over 100 years were substantially lower than those estimated in mesic temperate savannas experiencing increases in woody plant abundance over a 35–40 yr period (149 [Johnston et al. 1996] and 180 [Tilman et al. 2000] $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$). Rates of accumulation in temperate savannas in turn, are substantially lower than those reported for humid tropical grasslands undergoing succession from grassland to forest in Venezuela ($285 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$; San Jose et al. 1998). Collectively, these studies indicate a positive relationship at regional scales between woody plant-induced increases in ecosystem C-sequestration potential and mean annual rainfall. This is counter to that proposed by Jackson et al. (2002) for SOC. These contrasting

perspectives point to the need for a better understanding of how ecosystem primary production and SOC pools change with replacement of grasses by woody plants (e.g., House et al. 2003). At regional scales, interactions between grazing, fire, and brush management occur against a backdrop of topoedaphic heterogeneity to affect woody plant abundance through time (Asner et al. 2003). Complex mosaics of plant/soil carbon pools and fluxes result and make it difficult to quantify carbon pools over time at large spatial scales. Approaches such as the one used here, which link remote sensing, field sampling, and ecosystem modeling, are emerging as plausible means for addressing this complexity (Wessman 1992, Asner et al. 1998, Akiyama and Koizumi 2002).

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