

Carbon and Nitrogen Accumulation in a Savanna Landscape: Field and Modeling Perspectives

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Abstract. Indirect assessments suggest that increases in woody plants in the world's drylands during the past 100 y may have had a significant impact on carbon sequestration. However, these assessments are characterized by a high degree of uncertainty. A linked succession-biogeochemistry model has recently been used to estimate changes in ecosystem carbon and nitrogen pools accompanying the proliferation of woody plants over the past 150 y at a southern Great Plains site in North America. Here, we evaluate the validity of that modeling approach using historical aerial photos (1950, 1976, and 1990) and field data.

Field sampling indicated soil organic carbon (SOC) and total nitrogen (TN) pools on sites invaded by woody plants become enriched relative to remnant grassland communities, the extent being a linear function of woody patch age. However, woody patch age explained only 21–57% of the variance in SOC and 44–68% of the variance in TN, suggesting factors other than time of tree occupation are at play. Field-aerial photo assessment of changes in aboveground plant carbon pools from 1950–1990 were consistently lower (ca. 23 to 38%) than those predicted by the linked succession-biogeochemistry model. Some of the discrepancy likely reflects the fact that landscapes responded rather individually with regard to rates of C sequestration, whereas the modeling approach represents “an-average” landscape. The modeled long-term rate of aboveground plant C sequestration ($360 \text{ kg C ha}^{-1}\text{y}^{-1}$) fell well within the broad range of observed short-term (14 to 26 y) rates (32 to $933 \text{ kg C ha}^{-1}\text{y}^{-1}$) observed on three landscapes. Discrepancies between field- and model-based estimates of TN accumulation rates were much greater than those for SOC. In addition, the sign of the differences varied among the plant communities inventoried.

Our data suggest that predicting and understanding changes in SOC and TN following shifts in plant community life form composition cannot be reliably achieved using simple, empirical relationships. The linked succession-biogeochemistry model was able to generate estimates of plant and soil C storage consistent with field-based estimates, but did not generate changes in soil TN comparable to field-based assessments. Inclusion of species, topographic, and land use history effects on SOC and TN may be required to improve the performance of dynamic, mechanistic simulation models.

Keywords: biodiversity, land cover change, land use, *Prosopis glandulosa*, soil carbon, soil nitrogen, woody plant encroachment

INTRODUCTION

Grasslands and savannas cover approximately 40% of the terrestrial land surface (Bailey, 1996), account for 30–35% of terrestrial net primary productivity (Field *et al.*, 1998), contain 20% of the world's human population and support the majority of the world's livestock (Turner *et al.*, 1990). Given the multi-faceted importance of grassland and savanna ecosystems, their sustainability is of vital ecological and socioeconomic importance (Young and Solbrig, 1993). Among the most important threats to the conservation and sustainability of the world's grassland and savanna ecosystems is woody plant encroachment, which leads to the conversion of grasslands to savannas and of savannas to shrublands or woodlands. Woody encroachment has been widely documented in temperate and tropical systems in North America, South America, Australia, and Africa, (Archer *et al.*, 2001; Archer, 2004). In arid systems, this change in physiognomy may represent a form of desertification, as xerophytic shrubs displace mesophytic grasses; in semi-arid and subhumid bioclimatic zones, such transformations may reflect changes in resource availability or disturbance regimes that favor woody plants over herbaceous plants (Fig. 1).

Changes in land use practices, such as increased grazing pressure and decreased fire frequency, have been associated with shifts from grass to woody plant domination (Archer, 1994; Archer *et al.*, 1995; Van Auken, 2000). Other potentially important, interacting factors include climate change, introduction of exotic species, atmospheric N deposition (Köchy and Wilson, 2001), and atmospheric CO₂ enrichment (Polley *et al.*, 1997). Woody encroachment typically

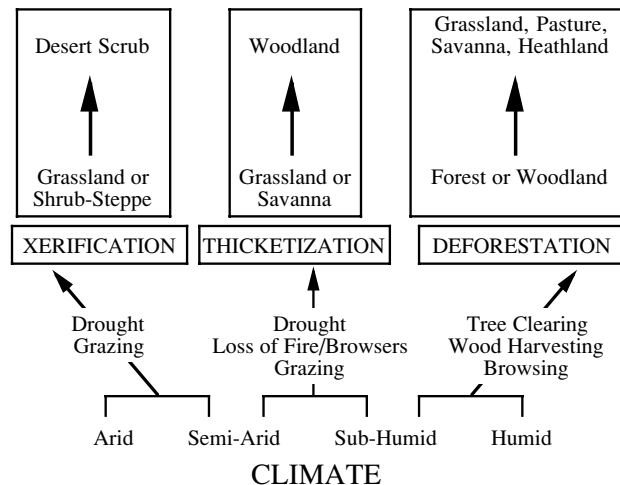


Fig. 1. The proliferation of shrubs represents a form of desertification and ecosystem degradation in arid and semi-arid systems (e.g., Schlesinger *et al.*, 1990); in more mesic systems it represents succession from grassland and open savanna to woodland or forest (adapted from Archer and Stokes (2000)). The proliferation of woody plants in drylands stands in a marked contrast to deforestation, which has received much more attention. Although increases in woody plant abundance in drylands have been geographically widespread, little is known of the ecological consequences of this vegetation change.

decreases grass productivity and has long been regarded as a major threat to sustainable livestock production in drylands of the United States and Australia (Fisher, 1942; Rappole *et al.*, 1986; Noble, 1997; Grant *et al.*, 1999). As a result, the majority of research on this phenomenon has had an “applied” focus with emphases on forage production, livestock yields, and woody plant control strategies (Scifres, 1980; Bovey, 2001). Our knowledge of the rates, patterns, and biogeochemical consequences of tree and shrub proliferation is limited. Even less well understood are the potential impacts on biological diversity (Fig. 2). In some cases, the proliferating woody plants are exotic invaders (e.g., *Tamarix* spp., *Sapium sebiferum*, *Eleagnus* and *Melaleuca* spp. in North America; *Acacia nilotica*, *Cryptostegia grandiflora*, *Mimosa pigra* and *Ziziphus mauritiana* in Australia (Grice and Brown, 1999)); but in many cases, the culprits are native trees and shrubs which have increased in stature and density within their historic ranges (e.g., *Prosopis*, *Larrea*, *Juniperus*, *Quercus*, *Pinus* and *Artemisia* spp. in North America; *Acacia*, *Cassia*, *Eremophila*, *Prosopis* and *Eucalyptus* spp. in Australia). Clearly, the proliferation of woody plants is a threat to the conservation of grassland and open savanna ecosystems and the plants and animals endemic to them.

Recent studies suggest increases in woody plant abundance in dryland ecosystems may alter biogeochemical processes and influence atmospheric

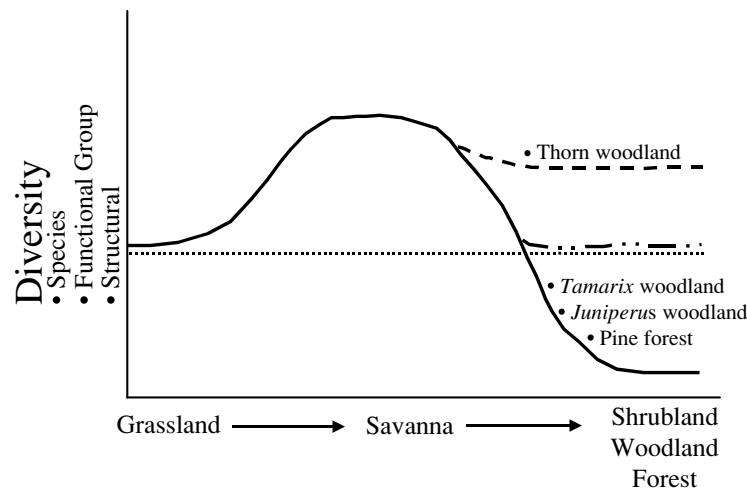


Fig. 2. Conceptual model of changes in ecosystem biodiversity (species, growthform or structural) that might accompany the proliferation of woody plants in grasslands. Maximum diversity might be expected during early stages of woody plant encroachment into grasslands, owing to the mixture of woody and herbaceous floral/faunal elements. As woody plant density increases, loss of grassland components occurs. In subtropical thorn woodland and dry forests with high woody plant species richness, a net increase in diversity may result. In other cases there may be no net change in diversity, only a change in physiognomy. Where woody plants form virtual monocultures with little or no understory, the loss of diversity may be profound. In all scenarios, regardless of the numerical changes in biodiversity, the existence of grassland and open savanna ecosystems and the plants and animals endemic to them is jeopardized.

chemistry and climate (Schlesinger *et al.*, 1990). Transitions between grass and woody plant-dominated ecosystems can affect hydrology (Boutton *et al.*, 1999; Wu *et al.*, 2001; Wilcox, 2002), regional precipitation patterns (Hoffman and Jackson, 2000), rates of soil respiration (Raich and Schlesinger, 1992), and the emissions of non-methane hydrocarbons (Klinger *et al.*, 1998; Guenther *et al.*, 1999) and NO_x (Martin *et al.*, 2003). Woody plants are often larger, more productive, more deeply rooted, longer-lived and slower to decompose than the grasses they have replaced. Consequently, marked increases in their distribution and abundance may represent a significant component of the carbon budget in the USA (Pacala *et al.*, 2001; Schimel *et al.*, 2001; Houghton, 2003) and Australia (Gifford and Howden, 2001; Burrows *et al.*, 2002), but these assessments are characterized by a high degree of uncertainty. In addition, soils associated with woody plants may accumulate more carbon than those associated with herbaceous vegetation, but here too, results are controversial (Jackson *et al.*, 2002).

Woody plant proliferation during the past century has been well documented in the subtropical regions of the southern Great Plains of North America. Assessments based on soil $\delta^{13}\text{C}$ indicate that C₃ trees and shrubs now dominate sites once occupied by C₄ grasses (Boutton *et al.*, 1998). Models based on woody plant growth rates and transition probabilities and substantiated by plant age estimates indicate this shift from grass to woody plant domination has occurred during the past 100 y (Archer, 1995). Dynamic simulations with a biogeochemical model (CENTURY; Parton *et al.*, 1993) have been linked to a woody plant cover change model (Scanlan and Archer, 1991) to reconstruct past changes and to project future changes in plant carbon pools accompanying succession from grassland to woodland (Hibbard *et al.*, 2003). However, the reconstructions and projections from that model have not yet been validated. Here, we reconstruct historic (1950–1990) changes in plant and soil C pools using field assessments and historical aerial photography and use these data to evaluate predictions obtained from the linked succession-biogeochemistry model.

APPROACH

Changes in plant C pools accompanying grassland-to-woodland succession were quantified on replicate landscapes at the Texas Agricultural Experiment Station La Copita Research Area (LCRA) 65 km west of Corpus Christi, Texas, USA (27°40' N; 98°12' W; elevation 75–90 m ASL). Contemporary vegetation of the region has been described by (McMahan *et al.*, 1984). The 1,103 ha LCRA is situated in the eastern Rio Grande Plains of the Tamaulipan Biotic Province. Climate of the area is subtropical (mean annual temp = 22.4°C) with warm winters, hot summers and a mean annual rainfall of 680 mm. Vegetation of the site, which has been grazed by cattle since the 1800s, consists of savanna parklands in sandy loam uplands that grade (1–3% slopes) into closed-canopy woodlands in clay loam lowland, intermittent drainages. Wooded communities are dominated by *Prosopis glandulosa* var. *glandulosa* (honey mesquite) in both uplands and lowlands. Associated understory shrubs consist of a diverse, ubiquitous

mixture of evergreen, winter- and summer-deciduous species. See Archer (1995) and Boutton *et al.* (1998) for additional details on climate, soils, vegetation history and succession.

Black and white aerial photos (nominal scale 1:20,000) from 1950, 1976 and 1990 were used to quantify woody cover change on each of three landscapes ranging from 4.40 to 11.16 to 12.3 ha in size. Positive transparencies of photographs were scanned and georeferenced (1 m resolution) using ERDAS Imagine (ERDAS, 1998). Lowland woodlands and upland savanna parkland landscape elements were manually delineated and digitized. Upland savanna parkland portions of landscapes were subjected to an unsupervised classification using Iterative Self-Organizing Data Analysis (ISODATA) (ERDAS, 1998). This classification initially grouped all pixels (4×4 m) into 40 classes based on reflectance value similarities. These 40 classes were subsequently collapsed into one of two categories: woody or non-woody. Based on previous field studies (Archer, 1995), pixels classified as “woody” were further classified as either “clusters” or “groves” based on their size and shape. The total area of cluster, grove, woodland and herbaceous communities was then computed for each photographic date.

Samples of leaves and different size classes of stems were collected by species and analyzed for carbon concentration by combustion/gas chromatography using a Carlo-Erba NA-1500 elemental analyzer (CE Elantech, Lakewood, NJ). Allometric relationships relating basal area, canopy area and height of aboveground biomass were determined for the common woody species (Northup *et al.*, 2004). Patches representing each community type were then randomly selected and plant structural attributes needed to estimate species-specific biomass were obtained within belt transects. Woody species biomass and C density (g m^{-2}) in transects was computed and summed to generate community-specific estimates of aboveground biomass and carbon density. Woody plant biomass and C density values of a given community type were then multiplied by the total area of that community on each of the three photographic dates. The area-weighted aboveground biomass and C pools of each community on a given date were then summed to estimate whole landscape pools.

To assess model predictions of rates of change in soil organic carbon, we sampled patches of different ages in each community type (cluster, grove and woodland). Soil cores (2.5 cm diameter \times 20 cm deep) were collected near the bole of *Prosopis* plants and *Prosopis* stem ages were subsequently determined by counting annual rings on cross-sections as described by (Flinn *et al.*, 1994). Cores were partitioned into 0–10 and 10–20 cm segments and dried at 60 C for five days. Coarse roots and organic fragments >2 mm were removed by sieving, and soils were then pulverized ($<5 \mu\text{m}$) in a centrifugal mill. Bulk density was determined on additional samples ($n = 12/\text{community type}$) using the clod method (Blake and Hartge, 1986). Organic carbon and total nitrogen concentrations were determined by combustion/gas-chromatography (Carlo Erba NA-1500 elemental analyzer; Nieuwenhuize *et al.*, 1994). Densities of organic carbon and total nitrogen were then determined by multiplying concentrations by bulk densities.

DECADAL TRENDS IN CARBON STORAGE

Woody plant cover increased on each of the three landscapes inventoried (e.g., Fig. 3), averaging (\pm SE; $n = 3$ landscapes) $41 \pm 6\%$ in 1950, $49 \pm 4\%$ in 1976 and $57 \pm 2\%$ in 1990. This represented a 39% increase over 40 y ($0.98\%/y$). Increases in woody plant cover were primarily the result of expansion of groves in uplands and upslope migration by lowland woodlands. Total cover of woody communities (clusters + groves + woodlands) on the three landscapes on the first inventory date (1950) ranged from 32% to 59%. These relatively large initial differences in woody cover may reflect differences in local disturbance regimes (e.g., landscape-to-landscape variation in livestock grazing pressure, fire history, etc.), differences in local precipitation patterns (spatial variation in rainfall on the LCRA is high) that affect woody plant community development or differences in catena-scale run-off/run-on patterns (Wu and Archer, 2004). By 1990, the range of woody cover values on the three landscapes (54 to 59%) had narrowed to only ca. 5%. This convergence suggests that the landscapes may be approaching the climatic carrying capacity for woody vegetation. If this is true, we would expect that in the absence of climatic events, disturbances or management actions that adversely affect woody plants, there may be little additional cover change in the

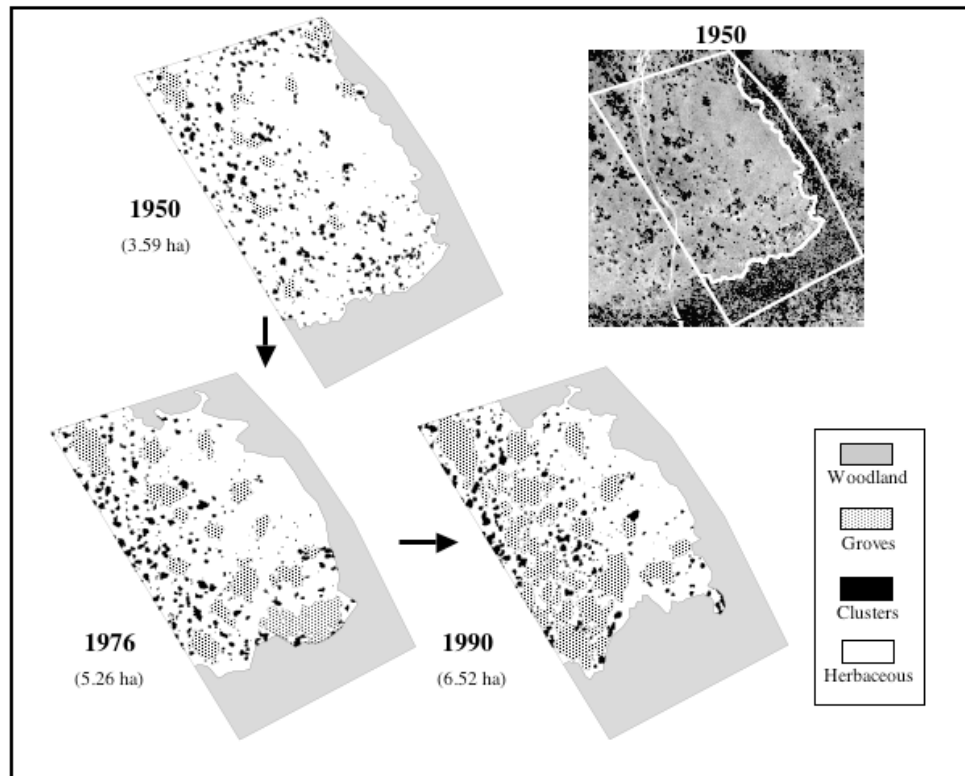


Fig. 3. Changes in upland (herbaceous, discrete cluster and grove) and lowland (woodland) plant community cover (1950–1990) on a single landscape in southern Texas, USA. Values given below dates are total hectares of woody cover (cluster + grove + woodland) for the 11.06 ha landscape outlined in the 1950 photograph (top right).

future. However, woody plant biomass may continue to increase as the plants present on the 1990 landscape increase in basal area.

Plant biomass and C density in upland grove (12.0 and 5.4 kg m⁻², respectively) and lowland woodland communities (10.6 and 4.8) were comparable, and greater than those in upland cluster communities (6.2 and 2.8) (Table 1). Species composition in cluster, grove and woodland communities is fairly comparable (McMurtry *et al.*, 2002), hence, differences in biomass and C density among the woody communities developing on former grasslands likely reflect differences in soils and topography. For example, the relatively low biomass and C density of upland clusters compared to upland groves is probably the result of a restrictive clay-pan horizon that is well-developed beneath clusters and poorly developed or absent in grove communities (Archer, 1995). Similarities in biomass and C density between grove communities on sandy loam uplands and woodland communities of clay loam intermittent drainages may be indicative of trade-offs in factors influencing woody plant productivity. Coarse-textured soils (such as in sandy loam uplands) are generally regarded as more favorable for woody plants in savannas (Johnson and Tothill, 1985); however run-on from uplands coupled with higher fertility of fine-textured soils may be enhancing the productivity of trees and shrubs in clay loam lowlands.

Area-weighting and summing of community-specific biomass and C density values revealed increases in aboveground woody plant C pools between 1950 and 1990 on each landscape (Fig. 4). Rates of plant carbon and biomass accumulation varied between the three landscapes and between the time intervals investigated (1950–1976 and 1976–1990) (Table 2). Our *a priori* expectation was that rates of accumulation between 1950 and 1976 would be lower than those from 1976–1990, owing to a major regional drought in the 1950s that had a significant impact on woody cover (Carter, 1964) and, by extension, biomass. This expectation was upheld on two of the three landscapes; but on the third landscape, the accumulation rate during the drought was 1.9× higher than during the post-drought period. To the best of our knowledge, each of the landscapes had a similar management history. Although we cannot account for the contrasting behaviors of these landscapes, the significant climate-landscape interactions indicate that caution must be exercised in generalizing or extrapolating carbon sequestration in plant biomass from one landscape to another.

Table 1. Mean (\pm SE) aboveground biomass and carbon density (kg m⁻²) within woody plant communities developing on former grasslands in uplands and lowlands. Different letters denote significant ($P < 0.05$) differences between communities.

| Topographic setting | Community | Biomass density | Carbon density |
|---------------------|-----------|-----------------------------|----------------------------|
| Upland | Cluster | 6.2 \pm 0.7 ^a | 2.8 \pm 0.3 ^a |
| Upland | Grove | 12.0 \pm 1.0 ^b | 5.4 \pm 0.4 ^b |
| Lowland | Woodland | 10.6 \pm 1.3 ^b | 4.8 \pm 0.6 ^b |

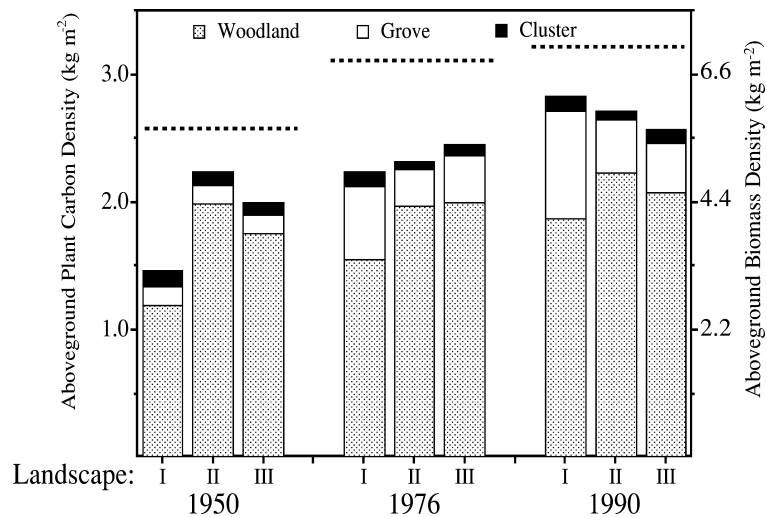


Fig. 4. Area-weighted woody plant carbon density in 1950, 1976 and 1990 on three subtropical savanna landscapes in southern Texas. Values were obtained by multiplying the area of woody plant communities (determined from aerial photos) by community-specific plant carbon density values determined from field sampling, then standardizing for differences in total landscape area. Dashed lines denote predictions from linked CENTURY-succession model for each of the aerial photo dates (Hibbard *et al.*, 2003). Note differences in the time intervals between consecutive dates.

What of changes in soil organic carbon (SOC) and total nitrogen (TN) pools accompanying woody plant encroachment? Little is known of the rate or direction of nutrient pool changes subsequent to woody plant establishment in grasslands. Most studies suggest soil nutrient pools should increase (the well-known “island of fertility” effect reviewed in Scholes and Archer (1997)). However, some studies suggest no net changes will occur (Smith and Johnson, 2003), and others suggest significant declines could result (Scott *et al.*, 1999; Jackson *et al.*, 2002). Our previous work at the La Copita site has demonstrated that the current woody communities have displaced grass-dominated communities during the past 100 y (Boutton *et al.*, 1998). Differences in nutrient pools between remnant herbaceous communities and present day woody communities should therefore indicate effects of woody plants on soil carbon and nitrogen. By aging the dominant plant woody communities, we can estimate accumulation rates of these changes. Field sampling of remnant herbaceous communities and woody community age-states indicated that SOC and TN pools in soils associated with woody plants are enriched relative to remnant grassland communities, the extent being a linear function of woody patch age (Fig. 5). Such enrichment has occurred despite larger soil microbial biomass pools and increased rates of microbial processes such as soil respiration and N-mineralization (McCulley, 1998; Hibbard *et al.*, 2001). Despite accelerated rates of soil C and N cycling, SOC and TN have increased, indicating that shifts from grass to woody plant dominance have increased both labile and recalcitrant pools of SOC and TN (the latter to a greater extent than the former). Tree size/age explained 21–57% of the variance in SOC and 44–68% of the variance in TN. These results mirror those from a broader geographic survey

Table 2. Whole-landscape rates of biomass ($\text{kg ha}^{-1}\text{y}^{-1}$) and carbon accumulation ($\text{kg C ha}^{-1}\text{y}^{-1}$) on three landscapes undergoing succession from grassland to woodland. Last two rows depict mean and SE for the three landscapes. Values are based on area-weighted totals for shrub clusters, groves and woodland communities in 1950, 1976 and 1990. The overall mean ($\pm\text{SE}$, $n = 6$) rate of carbon accumulation in aboveground biomass from 1950 to 1990 was $258 \pm 71 \text{ kg C ha}^{-1}\text{y}^{-1}$.

| Landscape | Biomass | | Carbon mass | |
|-----------|------------|------------|-------------|-----------|
| | 1950–1976 | 1976–1990 | 1950–1976 | 1976–1990 |
| 1 | 644 | 933 | 299 | 420 |
| 2 | 70 | 621 | 32 | 280 |
| 3 | <u>384</u> | <u>184</u> | <u>173</u> | <u>83</u> |
| Mean | 373 | 580 | 168 | 261 |
| SE | 210 | 266 | 95 | 120 |

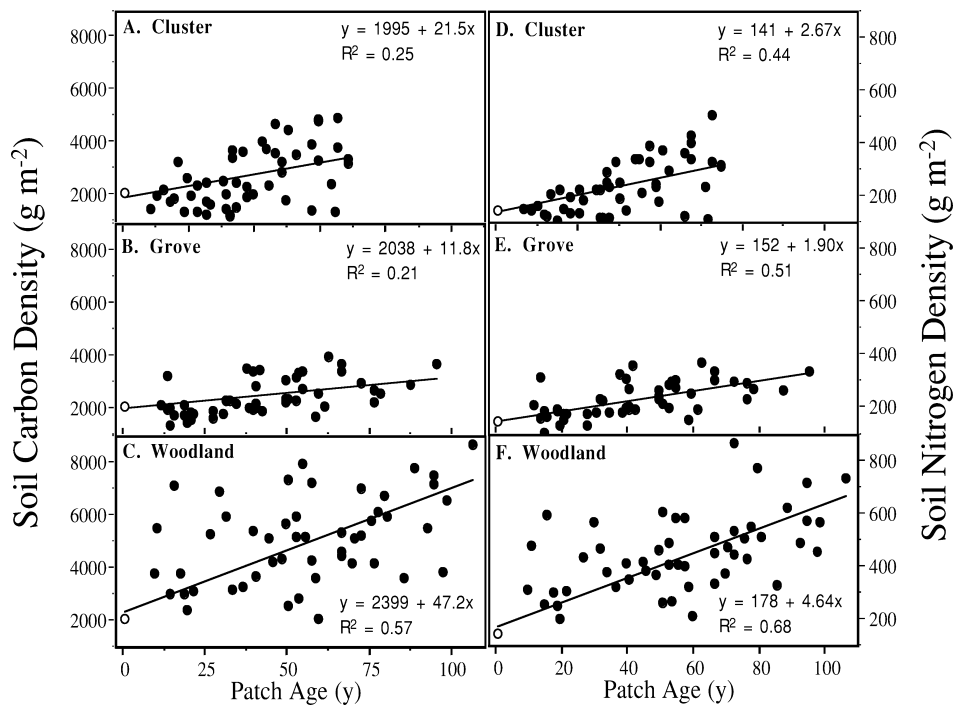


Fig. 5. Relationship between woody plant patch age (years; determined by annual ring counts on dominant *Prosopis* plants) and soil organic carbon and total nitrogen mass (g m^{-2} to 20 cm) in subtropical savanna undergoing succession from grassland to woodland. Values at patch age = 0 are those of remnant grasslands.

of our study region by Geesing *et al.* (2000) and suggest factors other than time of tree occupation are at play in influencing soil nutrient pools, particularly in upland communities. Tree age typically explained more of the variance in TN (44, 51 and 68% for clusters, groves and woodlands) than in SOC (25, 21 and 57%), perhaps reflecting the direct effects of N_2 -fixation by *Prosopis*.

COMPARISON OF FIELD- VS. MODEL-BASED ESTIMATES OF
CARBON STORAGE

Field-aerial photo assessment of changes in aboveground plant carbon pools were consistently lower than those predicted by the linked succession-biogeochemistry models (Fig. 4). The discrepancy was greatest when there was substantial landscape-to-landscape variation in woody cover and carbon density (1950), but it narrowed appreciably as the landscapes converged to relatively similar cover and aboveground carbon density levels (1990). Some of the discrepancy likely reflects the fact that landscapes responded rather individually with regard to rates of C sequestration (Table 2), whereas the modeling approach represents an “average” landscape (i.e., 54% sandy loam uplands with groves and clusters; 46% clay loam intermittent drainages with woodlands) under an annual rainfall regime characteristic of the region since the early 1900s. The modeled long-term rate of aboveground plant C sequestration ($360 \text{ kg C ha}^{-1}\text{y}^{-1}$) falls well within the broad range of observed short-term (14 to 26 y) rates (32 to $933 \text{ kg C ha}^{-1}\text{y}^{-1}$; Table 2). The fact that these very different approaches generated similar values gives us confidence that both our field-based and modeled estimates of aboveground plant carbon sequestration accompanying the conversion of grassland to woodland are reasonable and credible for these subtropical ecosystems.

Our field-based assessments of rates of SOC change accompanying woody plant community development were quite similar to those predicted by CENTURY for the two upland communities (Table 3); however, age-based regression predictions for lowland woodlands were ca. $3.6\times$ greater. We can only speculate on the reason for this rather large discrepancy. CENTURY does not account for influxes potentially associated with run-on from upslope locations, which may be reflected in the higher field-based assessment. Discrepancies between field- and model-based estimates of TN accumulation rates were much greater than those for SOC. In addition, the sign of the differences varied among the communities with modeled rates being much higher than field-estimated rates in upland

Table 3. Comparison of rates of change in soil organic carbon (SOC) and total nitrogen (TN; $\text{g m}^{-2}\text{y}^{-1}$ to 20 cm) predicted by a dynamic ecosystem simulation model (CENTURY; Hibbard *et al.*, 2003) and by regression of SOC and TN against woody patch age (see Fig. 5 for graphic display). R^2 values for regression analyses shown in parentheses.

| Community type: | Cluster | Grove | Woodland |
|-----------------|-----------------------|-----------------------|-----------------------|
| Organic carbon | | | |
| CENTURY | 18.5 | 10.5 | 13.1 |
| Regression | 21.5 ($R^2 = 0.25$) | 11.8 ($R^2 = 0.21$) | 47.2 ($R^2 = 0.57$) |
| Total nitrogen | | | |
| CENTURY | 11.5 | 0.9 | 0.6 |
| Regression | 2.7 ($R^2 = 0.44$) | 1.9 ($R^2 = 0.51$) | 4.6 ($R^2 = 0.68$) |

clusters and much lower in groves and woodlands. One must also wonder if CENTURY-predicted rates are really an order of magnitude different between cluster communities ($11.5 \text{ g N m}^{-2} \text{ y}^{-1}$) and grove/woodland communities (0.9 and $0.6 \text{ g N m}^{-2} \text{ y}^{-1}$). CENTURY is admittedly weak with respect to its handling of N_2 -fixation by plants, partly because of the paucity of reliable field assessments of this process (Vitousek and Field, 1999). The model's handling of root turnover may also be a factor, since no site-specific data were available for parameterization or validation. Field-based rate estimates were relatively more consistent across community types, but given the rather low R^2 values, this perspective also has its limitations.

A recent study comparing sites spanning a broad climatic range suggests effects of woody plants on SOC may be a function of mean annual rainfall, whereby dry sites accumulate SOC (ca. 26% gains), high rainfall sites lose SOC (ca. 44% losses), and sites with intermediate annual rainfall exhibit no net change (Jackson *et al.*, 2002). How robust is this model? Our case study site occurs in a mean annual rainfall zone predicted to exhibit no net change or a slight (ca. 18%) reduction in SOC following replacement of grasses by woody plants. However, SOC in woody communities relative to that of remnant grasslands suggests the SOC trajectory is clearly positive in this rainfall zone, with substantial increases (as much as 2- to 4-fold) occurring over the past 100 y of woody encroachment (Fig. 5). Furthermore, we saw major differences in SOC mass and accumulation rates between the various woody communities that cannot be ascribed to variations in annual rainfall. These local differences suggest that species composition, soil properties and/or topography are significant drivers of soil nutrient status. It should be noted that Jackson *et al.*'s model is based on SOC in the upper 1–3 m of the profile, so our data to 20 cm may not afford an appropriate test. However, previous measurements of the upper 1.5 m of the soil profile at our site indicate there is 30% more SOC in groves and 100% more SOC in drainage woodlands relative to remnant grasslands (Boutton *et al.*, 1998, Boutton and Archer, unpublished). It should also be noted that the increases in SOC at our study site occurred for woody plants establishing in grasslands where SOC pools appear to have been significantly depleted by heavy grazing (Hibbard *et al.*, 2003), and it is likely that the sites sampled by Jackson *et al.* may have experienced similar grazing-induced depletions in SOC. Whether the magnitude of changes recorded at the La Copita site would occur on grasslands where SOC pools had not been depleted is not known.

CONCLUSIONS

Our data suggest that predicting and understanding changes in SOC and TN following shifts in plant community life form composition cannot be reliably achieved or improved using simple, empirical relationships such as those in Fig. 5 or in Jackson *et al.* (2002). Although a linked succession-biogeochemistry model was able to generate estimates of plant and soil C storage that were consistent with field-based estimates, this model was unable to simulate changes

in soil TN comparable to field-based assessments. Further improvements in dynamic, mechanistic simulation approaches will likely be required to account for potentially important species, edaphic, topographic and land use history effects on SOC and TN. The model assessment exercises reported here suggest dynamic simulation approaches have strong potential for assessing the biogeochemical consequences of changes in vegetation structure. When such models can be successfully linked with remote sensing, our ability to dynamically monitor large-scale, land-use induced changes in vegetation cover and C and N pools and fluxes important to tropospheric chemistry and climate should improve markedly (e.g., Wessman *et al.*, 2004). To date, studies examining woody plant encroachment from a biological diversity perspective (Fig. 2) are lagging behind those emphasizing biogeochemistry. The proliferation of woody plants should not be overlooked as a threat to the conservation of the world's grassland and savanna ecosystem types.

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Carbon and Nitrogen Accumulation in a Savanna Landscape: Field and Modeling Perspectives

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Fig. 1

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Fig. 3

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