TREES IN GRASSLANDS:
BIOGEOCHEMICAL CONSEQUENCES OF WOODY PLANT EXPANSION

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I. Introduction

II. Woody Plant Encroachment in Grasslands and Savannas

III. The La Copita Case Study

    A. Biogeographical and Historical Context
    B. Herbaceous Retrogression and Soil Carbon Losses
    C. Woody Plant Encroachment and Ecosystem Biogeochemistry
       1. Plant Carbon Pools
       2. NMHC Fluxes
       3. Soil C and N Pools
       4. Soil C and N Dynamics
       5. Soils as Sources and Sinks
       6. An Uncertain Future

IV. Degradation: Ecological Versus Socioeconomic

V. Implications for Ecosystem and Natural Resources Management

VI. Summary

8 March 2000

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I. Introduction

The term 'savanna' typically connotes plant communities or landscapes having a continuous grass layer with scattered woody plants. Although savannas are not the only vegetation type where contrasting plant life forms co-dominate, they are one of the most striking, geographically extensive (ca. 20% of global land surface; (Scholes and Hall, 1996) and socioeconomically important examples in tropical (Tothill and Mott, 1985; Young and Solbrig, 1993) and temperate (Burgess, 1995; McPherson, 1997; Anderson *et al.*, 1999) regions. Tropical savannas cover about 1600 M ha of the terrestrial surface (Scholes and Hall, 1996), including more than half the area of Africa and Australia, 45% of South America and 10% of India and southeastern Asia (Werner, 1991). Temperate savannas in North America occupy an estimated 50 M ha (McPherson, 1997). More importantly, savannas contain a large and rapidly growing proportion of the world's human population and a majority of its rangelands and domesticated animals. As such, they have received substantial and ever-increasing anthropogenic land use pressure.

Many savannas are dynamic ecotones between woody plant (shrub-steppe, desert scrub,woodland or forest) and grassland formations. Savannas vary substantially with respect to the stature (shrub vs. tree), canopy cover (e.g. 5% to 80%), functional form (evergreen vs. deciduous; broad-leaved vs. needle-leaved; shallow vs. deeply rooted) and spatial arrangement (random, regular or clumped) of the woody elements which comprise them. Similarly, the grass layer may consist of short vs. tall-statured species, bunch vs. rhizomatous growth forms, and C_3, C_4 or mixed C_3/C_4 photosynthetic pathway assemblages. This variation in structural/functional characteristics reflects a rich array of interactions between climate (especially the amount and seasonality of rainfall), soils (notably depth and texture), and disturbance (particularly grazing, browsing and fire) (Figure 1; Walker, 1987; Backéus, 1992).

Much of the literature on savanna ecology has been devoted to describing and classifying vegetation structure. Static classification schemes minimize the importance of temporal change and divert attention from functional processes that might explain dynamic spatio-temporal variation. Grasses and woody plants may co-exist in a dynamic equilibrium when climatic, edaphic and disturbance factors interact temporally such that neither life form can exclude the other. However, a directional change in one or more of these primary controlling factors may shift the balance in favor of one life form over the other, and move the system toward either grassland or shrubland/woodland. The probability, rate and extent of such a shift may depend on local topoedaphic factors and the life-history traits and autecology of the growthforms or species involved.

Human population growth and widespread Anglo-European settlement during the 18th and 19th centuries have influenced the balance of grass-woody plant interactions world-wide. For example, extensive clearing of trees for fuel, lumber and cropland has fragmented forests and produced anthropogenic or degraded savannas (Gadgill and Meher-Homji, 1985; Sinclair and Fryxell, 1985; Cline-Cole *et al.*, 1990; Schüle, 1990; Young and Solbrig, 1993; Mearns, 1995). Following forest clearing, pyrophytic grasses may establish and restrict woody colonization by accelerating fire cycles and maintaining low fertility soils (Hopkins, 1983; Mueller-Dombois and Goldammer, 1990; D'Antonio and Vitousek, 1992). In the Brazilian Cerrado, rates of agricultural expansion and clearing of savanna and woodland trees rivals that reported for Amazon rain forest (Klink *et al.*, 1993). In other areas, fire suppression, eradication of indigenous savanna browsers, or the introduction of grazing livestock and exotic trees and shrubs have caused a progressive increase in woody plant density, known as bush or brush encroachment (Adamoli *et al.*, 1990; Archer, 1994; Gardener *et al.*, 1990; Miller and Wigand,

1994; Noble, 1997). As a result, areas that were once forest may become savanna-like, while areas that were once grassland or open savanna may progress toward a shrubland or woodland physiognomy. The biogeochemical consequences of this latter phenomenon are the focus of this chapter.

II. Woody Plant Encroachment in Grasslands and Savannas

Woody plant encroachment has been widespread in grassland and savanna ecosystems of North and South America, Australia, Africa and southeast Asia over the past century (Table 1). This encroachment, typically by unpalatable trees and shrubs, has gone to completion on some landscapes and is in progress on others. It jeopardizes grassland biodiversity and threatens the sustainability of pastoral, subsistence, and commercial livestock grazing (Rappole *et al.*, 1986; Noble, 1997). As such, it may adversely impact   20% of the world's population (Turner *et al.*, 1990). The proximate causes for woody plant displacement of perennial grasses are the subject of debate. Land use practices such as heavy grazing and reductions in fire frequency have often been implicated. However, climate change, historic atmospheric CO_2 enrichment and exotic species introductions are potentially important contributing factors (Idso, 1995; Archer *et al.*, 1995; Polley, 1997; Polley *et al.*, 1997). Current trends in atmospheric CO_2 enrichment may exacerbate shifts from grass to woody plant domination, especially where the invasive trees/shrubs are capable of symbiotic N_2-fixation.   Expansion of woody plants into grasslands may also be favored by recent increases in atmospheric N-deposition (Köchy, 1999). In addition to influencing vegetation composition, changes in each of these factors would also have the potential to alter the storage and dynamics of C and N in savanna ecosystems. The net outcome of such interactions over the recent past is poorly understood and has not been well documented.

Although woody plant encroachment has long been a concern of land managers in grassland and savanna regions (e.g., (Fisher, 1950; Fisher, 1977), research on this problem has been primarily 'applied' and focused on the effects of woody plants on grass production and the development of chemical or mechanical methods to reduce the abundance of established trees and shrubs. Despite the long-standing recognition of woody plant encroachment as a worldwide dryland management problem, little is known of the rates and dynamics of the phenomenon, or its impact on fundamental ecological processes related to energy flow, nutrient cycling and biodiversity.   Grassland/savanna systems account for 30 to 35% of global terrestrial net primary production (Field *et al.*, 1998). Hence, when woody species increase in abundance and transform shrublands into woodlands, grasslands into savannas or savannas into shrublands and woodlands, the potential to alter C and N sequestration and cycling at regional and global scales may be significant. Consequently, this type of land cover change has potential to contribute significantly to the terrestrial global carbon sink (c.f., Ciais *et al.*, 1995). Savanna landforms may have a larger impact on the global carbon cycle than previously appreciated (Hall *et al.*, 1995; Ojima *et al.*, 1993; Scholes and Hall, 1996; Scholes and Bailey, 1996; Scholes and van der Merwe, 1996). Indeed, recent assessments suggest savanna ecosystems have among the highest potential C gain and loss rates of the world's biomes (ORNL, 1998). In addition, emissions of radiatively active trace gases, NOx and aerosols from savanna fires may contribute significantly to global emissions and influence climate and atmospheric chemistry (Crutzen and Andreae, 1990; Hao *et al.*, 1990; Crutzen and Goldammer, 1993).

Desertification has long been a topic of concern to land managers and ecologists (Moat and Hutchinson, 1995; Arnalds and Archer, 2000). More recently, changes in the storage and dynamics of C and N in the

terrestrial biosphere have been evaluated with respect to deforestation, intensive agricultural practices, succession on abandoned agricultural lands, and afforestation/reforestation (Figure 2) (Houghton *et al.*, 1987; Post, 1993). Increased abundance of woody plants in drylands has the potential to alter land surface-atmosphere interactions and atmospheric chemistry by affecting biophysical processes and C and N storage and dynamics (e.g.,(Schlesinger *et al.*, 1990; Graetz, 1991; Bonan, 1997). Even so, its significance has yet to be thoroughly evaluated or quantified. Here, we review results from a case-study of a subtropical dryland landscape which has been undergoing a transformation from grassland to savanna to woodland. Some of our recent work has explored the implications of this change in vegetation on the hydrological cycle (Brown and Archer, 1990; Midwood *et al.*, 1998; Boutton *et al.*, 1999). Here, our emphasis is on the rates of change in soil and plant carbon and nitrogen pools and fluxes.

III. The La Copita Case Study

A. Biogeographical and Historical Context

The La Copita Research Area (27° 40´ N; 98° 12´ W; elevation = 75-90 m ASL) is situated in the northeastern portion of the North American Tamaulipan Biotic Province (Blair, 1950) in the Rio Grande Plains of southern Texas. 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 about 12 million ha in Texas alone (Jones, 1975). The shrubs and small trees at the study site are characteristic of dry tropical and subtropical zones in Mexico, Central America, South America (Chaco, Caatinga, Caldenal), Africa, Australia, India and Southeast Asia. In many instances, it is believed these vegetation types have replaced grasslands over large areas since the 1800s (Table 1). Current vegetation at the La Copita site, which has been grazed by domestic livestock since the late 1800s, consists of savanna parklands in sandy loam uplands that grade into closed-canopy woodlands in clay loam lowland drainages. All wooded landscape elements (upland shrub clusters and groves; lowland playa and drainage woodlands) are typically dominated by the leguminous tree *Prosopis glandulosa* in the overstory, with an understory mixture of evergreen, winter-deciduous, and summer-deciduous shrubs. Climate of the region is subtropical (mean annual temperature = 22.4 ºC) with warm, moist winters and hot, dry summers. Mean annual rainfall is 720 mm and highly variable (C.V. = 35%).

Reports from settlers indicate much of southern Texas was grassland or open savanna in the mid-1800s (Inglis, 1964). Historical aerial photography demonstrates that woody plant cover on La Copita increased from 10% in 1941 to 40% in 1983 (Archer *et al.*, 1988). ^{13}C and radiocarbon analyses of soil organic carbon have confirmed that C_3 trees and shrubs have displaced C_4 grasses in upland and lowland portions of the landscape within the past 100 y (Boutton *et al.*, 1998). Plant growth (Archer, 1989) and transition probability models (Scanlan and Archer, 1991), substantiated by tree ring analysis (Boutton *et al.*, 1998), indicate most trees on the site have established over the past 100 y. The successional processes involved in woody plant community development and topoedaphic controls over spatial patterns of tree/shrub expansion have been elucidated (Archer, 1995b). Armed with information from these prior studies, we are now poised to ascertain the biogeochemical consequences of succession from grassland to woodland.

B. Herbaceous Retrogression and Soil Carbon Losses

Simulations with the CENTURY biogeochemistry model (Parton *et al.*, 1987; Parton *et al.*, 1988; Parton *et al.*, 1993) parameterized for assumed pre-settlement conditions ('light' grazing, fire at 10-y intervals), soil texture and climate of the La Copita, projected that soil organic carbon (SOC) would have been on the order of 2500 g m^{-2} to a depth of 0-20 cm (Hibbard, 1995). The SOC values from this assessment were then used as a baseline against which historic effects of heavy, continuous livestock grazing were evaluated. In a subsequent model run, intensification of grazing and removal of fire was initiated in 1850, a date approximating the advent of widespread, unregulated livestock grazing in southern Texas (Lehman, 1969). This simulation produced a 16-29% reduction in SOC of sandy loam upland and clay loam lowland soils, respectively (Figure 3). These results appear reasonable in that the model generated steady-state SOC levels for sandy loam uplands (2062 g m^{-2}) approximated the average pool sizes measured in present-day grassland communities on these soils (2087 g m^{-2}). Further, the grazing-induced reductions in SOC predicted by the simulation were comparable to field measurements reported for other grazed grasslands (Bauer *et al.*, 1987; Frank *et al.*, 1995); but see (Milchunas and Lauenroth, 1993). CENTURY simulations did not explicitly include potential erosion losses. The fact that simulated historic changes in SOC approximated those currently observed at the site therefore suggests such losses may have been minimal. This inference seems reasonable, since the La Copita landscapes have relatively little topographic relief (1-3% slopes) and show no obvious physical signs of erosion (e.g., pedestals, rills, gulleys). Furthermore, soil profile structure in low-lying portions of the landscape shows no pedogenic evidence of significant translocation of soils from uplands. Elevated C and N pools in soils of developing woody communities (summarized later) thus appear to be the result of *in situ* accumulations induced by trees and shrubs rather than losses from grazed grasslands.

The present-day herbaceous vegetation is dominated by a low cover of ephemeral dicots and short-statured, weakly perennial grasses. In contrast, herbaceous vegetation on relict, protected grasslands in the region is characterized by mid- to tall-statured perennial grasses whose potential productivity (500-600 g m^{-2} [SCS, 1979]), is 2-3X that which has been recorded at La Copita (<270 g m^{-2} [Vega, 1991; Hibbard, 1995]). Thus, it is reasonable to conclude that soil C and N storage has declined in herbaceous communities over the past century as a result of changes in species composition, microclimate and biomass production attributable to heavy, continuous livestock grazing on this site.

C. Woody Plant Encroachment and Ecosystem Biogeochemistry

Changes in soils and microclimate accompanying long-term heavy grazing may have shifted the balance in favor of N_2-fixing or evergreen woody plants which are better adapted than grasses to nutrient poor soils and warmer, drier microenvironments. The establishment of trees and shrubs would have been further augmented by grazing-induced reductions in herbaceous competition and fire (Archer, 1995a). In addition, the woody plants at La Copita are highly unpalatable and browsing by wildlife or cattle is minimal. However, fruits of the dominant tree invader (*Prosopis glandulosa*) are readily consumed by livestock which disperse large numbers of viable seeds into grasslands (Brown and Archer, 1987). Thus, heavy, continuous and preferential grazing of grasses by livestock has promoted woody plant encroachment via numerous direct and indirect effects (Archer, 1994). As woody communities develop in grazed grasslands, plant and soil C and N pool sizes and flux rates change as described in the following sections.

*1. **Plant Carbon Pools*** Quantitative changes in woody plant cover at La Copita are depicted in Figures 4 and 5. To ascertain the effects of these vegetation changes on plant carbon stocks, we linked CENTURY with a plant succession model developed for La Copita (Scanlan and Archer, 1991). We initiated woody plant encroachment in the late 1800s on a heavily grazed, fire-free landscape in which SOC content had been reduced by grazing (Figure 3). The landscape, consisting of a sandy loam upland and a clay loam intermittent drainage, was populated with woody plants based on rainfall-driven transition probabilities. Grassland and forest CENTURY subroutines were applied, as appropriate, to compute plant carbon and SOC (0-20 cm) stocks in wooded and herbaceous landscape elements. At each time-step, plant carbon and SOC were estimated by summing across the entire landscape (upland plus lowland vegetation patch types). Results suggest that the development of the present-day savanna parkland-woodland complex has increased plant carbon stocks 10-fold over that which would be present had the 'pristine' grassland vegetation been maintained on the site (Figure 6). Part of that increase is attributable to an increase in aboveground net primary productivity (Table 2) and part of it represents the decline in tissue turnover which occurs when herbaceous vegetation is replaced by woody vegetation. These results are conservative in that CENTURY simulations include root C mass only in the top 20 cm of soil. Biomass distributions of woody plant roots at La Copita (Watts, 1993; Boutton *et al.*, 1998; Midwood *et al.*, 1998; Boutton *et al.*, 1999; Gill and Burke, 1999) are typical of those of other dryland tree/shrub systems (Jackson *et al.*, 1996; Canadell *et al.*, 1996) where, relative to grasslands, there is substantially greater mass at deeper depths where turnover and decomposition are likely to be reduced. The fact that fluctuations in monthly woody plant root biomass in upper soil horizons exceeded monthly foliar litter inputs by one to two orders of magnitude (Table 2) suggests that belowground inputs of organic matter drive changes in soil physical and chemical properties subsequent to woody plant establishment in grasslands. These substantial fluctuations in woody plant root biomass suggest a high turnover, which is consistent with detailed observations on woody plants in other systems (Eissenstat and Yanai, 1997; Hendricks *et al.*, 1997). In addition, turnover of grass roots may be slower than has been generally assumed (Milchunas *et al.*, 1992). Thus, increases in above- and belowground net primary productivity may accompany woody plant encroachement into grasslands and foster C and N accumulation.

As an independent test of the reconstruction in Figure 6, we quantified aboveground plant carbon density in patches representing the dominant community types at La Copita. This was accomplished using allometric relationships and belt-transect surveys (Northup *et al.*, 1996). Plant carbon density was then multiplied by community area measured on aerial photographs (1950, 1976, 1990) to obtain a community-level estimate. Estimates for each community type were then summed to obtain landscape-scale estimates. For patches representing various woody and herbaceous community types, CENTURY estimates of aboveground carbon density were lower than field-based estimates (Table 3), further suggesting that model estimates were conservative. Aboveground carbon density differed substantially among the three landscapes inventoried in 1950 (Figure 7), primarily reflecting differences in woody plant cover on this date (Figure 4). By 1990, woody cover and carbon density were comparable on the three landscapes. The CENTURY-succession model estimates of aboveground carbon density for an 'average' landscape in 1950, 1976 and 1990 closely approximated those obtained from the field-historical aerial photo approach.

*2. **Non-Methane Hydrocarbon Fluxes*** On a regional basis, shifts from grass to woody plant domination have the potential to influence biophysical aspects of land-atmosphere interactions, such as albedo, evapotranspiration, boundary layer conditions, and dust loading (e.g., (Bryant *et al.*, 1990; Pilke and Avissar, 1990; Graetz, 1991). These changes in vegetation may also influence atmospheric oxidizing

capacity, aerosol burden and radiative properties by affecting emissions of non-methane hydrocarbons (NMHCs) such as terpenes, isoprene, and other aromatics (Fehsenfeld *et al.*, 1992). There are many sources of atmospheric NMHCs, but >90% of the global annual emission is from vegetation (Guenther *et al.*, 1995). NMHC emissions are therefore highly dependent on species composition as constrained by environmental conditions which influence plant physiology and production. The high temperatures and solar radiation fluxes associated with subtropical and tropical grasslands and savannas make these geographically extensive bioclimatic regions large potential sources of biogenic NMHC emissions. However, grasses are typically low emitters of NMHCs, whereas emissions from trees and shrubs in forest systems are highly variable, with some species being low emitters and other species being high emitters.

We hypothesized that foliar emissions of NMHCs in woody plants would be positively correlated with leaf longevity and inversely related to photosynthetic capacity. Plants characterized by low photosynthetic capacities and slow growth rates (e.g. evergreens) depend on extended leaf longevities to achieve a positive carbon balance. Preferential allocation to secondary compounds such as terpenes would help ensure foliage longevity by reducing levels of herbivory. Species with low photosynthetic capacities and high levels of secondary compounds should also dominate understory environments where low light levels preclude high growth rates and where plants are more accessible to browsers. In contrast, species selected for competitive ability would have high photosynthetic rates, high growth rates, and high rates of tissue turnover (e.g., deciduous shrubs). Allocation to secondary compounds that deter herbivory would be of lower priority since leaf longevity is less critical to realizing a positive return on foliar investments. Such plants would be expected to preferentially allocate resources such as nitrogen to the carboxylating enzyme and productive tissues rather than to structural tissues or secondary compounds such as terpenes, and would thus be low NMHC emitters (or isoprene emitters, since isoprene is not known to be associated with defense; Coley *et al.*, 1985).

To test these hypotheses, we screened plant species representing the major growthforms at La Copita for NMHC emissions. As expected, grasses had low NMHC emission rates and several common woody species had high emission rates (Guenther *et al.*, 1999). However, there was little evidence of emissions being consistently related to woody plant taxonomy, growthform or functional group. As a result, generalizations regarding NMHC emissions spectra for tree/shrub species assemblages in other systems do not appear feasible.

To determine if biogenic NMHC emissions have been altered as a result of the change in land cover from grass to woody plant domination at La Copita, a vegetation change model (Scanlan and Archer, 1991) was then linked with a model which predicted NMHC emissions as a function of foliar density, leaf temperature, and photosynthetic photon flux density as modulated by ambient temperature, cloud cover, precipitation, relative humidity, and wind speed (Guenther *et al.*, 1995; Guenther, 1997).

Linkage of the biogenic emissions model with the plant succession model indicated that land cover change since the early 1800s has elicited a 3-fold increase in isoprene emissions (Figure 8). This increase reflected changes in vegetation composition and increases in foliar density. Model predictions of current NMHC emissions were within 20% of those measured by a tower flux system. Detailed field measurements on two common shrub species indicated that isoprene emission increased exponentially with increases in leaf temperature from 20 to 40° C and were not suppressed by drought stress. Accordingly, the model predicted that under a projected 2X-CO_2 climate, present day biogenic NMHC emissions would double.

These estimates of changes in NMHC emissions associated with the conversion of grassland to woodland are in accordance with estimates in other ecosystems. For example, (Klinger *et al.*, 1998) documented a 4-fold increase in total terpenoid emissions per unit foliar mass along a savanna to woodland transect in Central Africa. These changes in NMHC emissions associated with vegetation change in subtropical Texas and tropical Africa also mirror those reported for temperate forest (Martin and Guenther, 1995). Together, these results indicate the magnitude of change in NMHC emissions that could occur when climate and vegetation composition are altered. The importance of these increases in NMHC emissions is magnified at La Copita, as they occur in conjunction with elevated nitric oxide (NO) emissions from shrub-modified soils (Table 2; see Soil C and N Dynamics section for elaboration).

Why are vegetation-induced increases in NMHC of concern? Biogenic hydrocarbons play an important role in generating pollutants such as O_3, CO, and organic peroxides, while influencing hydroxyl radical (OH^-) chemistry so as to reduce atmospheric oxidation capacity and increase the residence time of greenhouse gases. It has been estimated that to meet current air quality standards for tropospheric ozone, anthropogenic hydrocarbon emissions would have to be reduced by only 30% in the absence of natural isoprene emissions, but by 70% in the presence of them (Monson *et al.*, 1991). Changes in NMHC-NO emissions associated with regional conversion of grassland to shrubland may therefore constitute a 'moving baseline' from which to gauge tropospheric ozone production triggered by emissions from automobiles or industrial sources.

*3. **Soil C and N Pools*** Once established, woody plants alter soils and microclimate in their immediate vicinity to affect both pool sizes and flux rates of nutrients. The result is the formation of 'islands of fertility', a phenomenon which has been widely quantified in drylands (see (Charley and West, 1975; Schlesinger *et al.*, 1990; Scholes and Archer, 1997), special issue of Biogeochemistry 42 (1/2) 1998). Three general mechanisms have been proposed to account for this (e.g., Virginia, 1986): (1) woody plants act as nutrient pumps, drawing nutrients from deep soil horizons and laterally from areas beyond the canopy, depositing them beneath the canopy via stem flow, litter fall and canopy leaching; (2) tall, aerodynamically-rough woody plant canopies trap nutrient-laden atmospheric dust which rain washes off the leaves and into the subcanopy soil; and (3) woody plants may serve as focal points attracting roosting birds, insects and mammals seeking food, shade or cover. These animals may enrich the soil via defecation and burrowing. For these reasons, soil carbon and nitrogen pools should increase subsequent to woody plant colonization in grazed grasslands.

At La Copita, surficial (0-10 cm) soils associated with woody plants known to have encroached over the past century have a lower bulk density, contain more root biomass, have higher concentrations of SOC and total N, and have greater rates of respiration and N-mineralization than soils associated with the remaining grazed grassland communities (Table 2). As the continuity of woody plant cover increases through time, the landscape-scale soil nutrient pools and fluxes would be expected to increase and become more homogeneously distributed. Accordingly, the linked CENTURY-succession model exercise (see 'Plant Carbon Pools' section) predicted that by 1950, landscape-scale SOC had returned to levels which would have occurred had the 'pristine' grasslands been maintained on the site (Figure 9). By the early 1990s, landscape-scale SOC levels were about 10% higher than those expected for the 'pristine' grassland, and about 30% higher than those for a heavily grazed grassland not experiencing woody plant encroachment. Forward model projections suggest SOC aggradation will continue for several hundred years, reaching equilibrium levels 3X that of the present-day grazed grassland communities.

While the 'island of fertility' phenomenon has been widely recognized, little is known of the rates of

nutrient enrichment in tree-dominated patches. Total C and N in soil under *Acaciasenegal* and *Balanites aegyptiaca* tree canopies was positively correlated with tree girth (r^2=0.62 and 0.71, respectively; Bernhard-Reversat, 1982), indicating net accumulation with time of woody plant occupancy of a patch. In temperate old fields undergoing forest succession, carbon storage increased 40% in plant + soil pools over 40 years (Johnston *et al.*, 1996). At La Copita, soil C and N was quantified under *Prosopis glandulosa* trees whose age was determined by annual ring counts. Soil organic carbon storage (top 20 cm of soil) increased linearly with tree stem age at rates ranging from 11.8 to 21.5 g C m^{-2} y^{-1} in sandy loam uplands woody patch types to 47.2 g C m^{-2} y^{-1} in moister, clay loam woodland patches (Table 4). Rates of total N accumulation (top 20 cm of soil) ranged from 1.9 to 2.7 g N m^{-2} y^{-1} in sandy uplands and averaged 4.6 g N m^{-2} y^{-1} in clay loam lowlands. However, woody plant age explained only 21 to 68% of the variation in soil C and N sequestration rates. These low r^2 values may indicate that tree stem ages do not accurately reflect plant age, possibly due to past disturbance and subsequent vegetative regeneration of woody cover. Low r^2's may also indicate that factors unrelated to time of tree occupancy influence soil C and N under tree canopies. Such factors may include small-scale heterogeneity associated with large mammal or bird defecation, soil mixing by small mammals and arthropods, or patch-specific differences in the species composition, productivity, and rate of development of the understory community.

Modeling experiments allowed us to control for factors that might cause variation in field-based estimates of woody plant age-SOC relationships. Model estimates of SOC accumulation were comparable to field estimates for upland patch types and substantially lower than field estimates for lowland patch types (Table 4). Model estimates of soil N accumulation were substantially lower than field estimates, especially in lowlands. Given that woody patch age explained only 26 to 68% of the variance in soil C and N content, our field estimates of accumulation rates cannot be taken as definitive. Model results underestimated field observations, especially for N. Reliability of model estimate of soil carbon could likely be improved with a better understanding of how turnover of the substantial root mass (Table 2) might differ among patch types. Model estimates of soil N are likely constrained by lack of information on inputs associated with N_2-fixation, atmospheric N deposition, translocation between uplands and lowlands, and root turnover.

4. *Soil C and N Dynamics*
Increases in the C and N pools of soils associated with woody plant communities developing on grazed grasslands at La Copita have been accompanied by increases in soil respiration, N-mineralization and nitric oxide (NO) emissions (Table 2). The increase in NO fluxes accompanying expansion of woody plants into grasslands at La Copita is noteworthy. Nitric oxide plays several critical roles in atmospheric chemistry by contributing to acid rain and by catalyzing the formation of photochemical smog and tropospheric ozone. The latter is potentially accentuated in the La Copita setting, since NO and hydrocarbon emissions (see 'Non-Methane Hydrocarbon Fluxes' section) are concomitantly elevated subsequent to woody plant establishment.

The quality and quantity of organic matter inputs interact to drive soil metabolic activity (Zak *et al.*, 1994). Hence, annual soil respiration rates are positively correlated with net primary productivity (Raich and Schlesinger, 1992). The elevated carbon fluxes observed with the development of woody communities in semiarid La Copita grasslands may reflect increased root (Table 2) and leaf biomass inputs, and enhancement of soil moisture beneath woody plant canopies (via concentration of rainfall from stem flow; hydraulic lift, and/or reduced evaporation). Together, these biotic and abiotic factors may interact to stimulate microbial activity relative to that in grass-dominated soils. In fact, microbial biomass in woody communities is comparable to or higher than that in grassland communities at La Copita (McCulley, 1998). However, experimental irrigation which alleviated plant water stress, enhanced

photosynthesis (McMurtry, 1997), and increased soil respiration, elicited a decrease soil microbial biomass. This suggests the elevated soil respiration observed in woody plant communities at La Copita may be more a consequence of changes in root biomass (Table 2) and respiration than of changes in microbial biomass and activity.

To estimate landscape-scale changes in soil CO_2 flux, we multiplied patch/soil-specific estimates of annual soil respiration (McCulley, 1998) by patch area. We then computed changes in patch area with a succession model (Scanlan and Archer, 1991). Landscape-scale soil respiration (kg C ha^{-1} y^{-1}) is projected to have increased from 6,687 (200 YPB) to 7,377 (1990s) to 7,602 (200 years in future) (Table 5). This represents a 10.3% increase with the transition from historic grassland savanna to the present day savanna parkland/thorn woodland complex, with an additional 3% increase occurring if the present savanna parkland progresses to woodland. If mean annual temperatures increase as projected in general circulation models, further increases in soil respiration would be expected (all other factors being equal). Indeed, Q_{10} values for soil respiration in woody plant communities (1.4, 2.7 and 2.3 in cluster, grove and woodland types, respectively) exceed those of grazed grasslands (1.2) at La Copita (McCulley, 1998). This suggests that if future temperature changes occur, the importance of recent and projected future vegetation changes on soil respiration will be further magnified. For example, the magnitude of increase in soil respiration from past grassland savanna with MAT of 22.4 °C to future woodland with MAT of 28.4 °C would be 22.5% (= 6,687 to 8,197 kg C ha^{-1} y^{-1}, based on (Raich and Schlesinger, 1992) to 99.3% (= 6,687 to 13,328 kg C ha^{-1} y^{-1}, based on (McCulley, 1998) (Table 5). Potential changes in the amount, seasonality and effectiveness of rainfall would have important, but as yet unknown effects on these projections.

5. Soils as Sources and Sinks Elevated fluxes of C and N from plants and soils following grassland-to-woodland conversion at La Copita suggest a potential for augmenting greenhouse gas accumulation and altering tropospheric chemistry, particularly if woody plant encroachment has been geographically widespread (as suggested in Table 1). However, as noted in the 'Soil C and N Pools' section, organic C and N have accumulated in soils of developing woody plant communities at La Copita, despite elevated fluxes and higher turnover rates. This indicates inputs have exceeded outputs and that soils and vegetation at La Copita have been functioning as C and N sinks over the past century. A variety of factors might interact to account for the observed increases in soil C and N pools:

- The trees and shrubs which have displaced grasses may be more productive above- and belowground and hence deliver more organic matter into soils (see root biomass and ANPP in Table 2).

- Leaves of leguminous and non-leguminous woody plants at La Copita have higher [N] than grasses (2-4% vs. <1%; Archer, unpublished). However, woody plants in these landscapes are seldom browsed by livestock or wildlife, suggesting high concentrations of secondary compounds. This could result in a significant litter quality x quantity interaction, whereby

  •• a large fraction of the foliar biomass produced by trees and shrubs goes into the soil pool directly as litter rather than through the herbivory pathway. And,

  •• a larger fraction of foliar biomass inputs from woody plants may be resistant to decomposition relative to that of the grassland plants;

- Woody litter inputs and the coarser, more lignified roots of shrubs would promote C and N accumulation compared to that of grass roots and shoots.

- Shading by tree/shrub canopies reduces soil temperatures relative to those in grassland (Archer, 1995b), thus constraining potential mineralization (Q_{10} effect).

- Nitrogen accumulation is potentially a consequence of N_2-fixation by leguminous shrubs common to the site (*P. glandulosa* and several *Acacia* spp.) and/or the uptake and lateral translocation of N from grassland patches. While nodulation has been induced in controlled environments and observed under field conditions at the La Copita site (Zitzer *et al.*, 1996) and elsewhere (Virginia *et al.*, 1986; Johnson and Mayeux, 1990), methodological constraints have prevented quantification of N_2-fixation(Handley and Scrimgeour, 1997; Liao *et al.*, 1999). Root distribution studies (Watts, 1993) discount the lateral foraging hypothesis.

- La Copita is within ca. 70 km of a major oil refinery center (Corpus Christi, TX) and atmospheric N deposition has likely been significant over the past 50-75 years (e.g. (Holland *et al.*, 1999). Increased N-availability may have promoted woody plant expansion (e.g.,(Köchy, 1999) by alleviating grass-woody plant competition for soil N and by promoting growth of woody plants more so than that of grazed grasses. This, in turn, may have translated into greater organic C and N inputs into soils associated with woody plants.

6. An Uncertain Future

Prosopis glandulosa presently dominates the overstory in upland and lowland woody plant communities. Depending on patch type, it comprises 40-90% of the aboveground biomass (Archer and Boutton, unpubl.) and 30-70% of the coarse root (>1 mm diam.) biomass (Watts, 1993). As such, the dynamics of *P. glandulosa* must be a primary driver of changes in plant and soil C and N stocks at La Copita. Future increases in landscape nutrient pools and fluxes will reflect a combination of (a) continued growth of *P. glandulosa* and associated shrubs in existing woody plant communities, and (b) expansion of woody plants into the remaining grasslands.

How likely is continued expansion? That may depend on land management practices. Relaxation of grazing pressure could enable grass biomass to accumulate and fire (prescribed or natural) to occur. Together, these could retard expansion and growth of woody plants. However, the La Copita appears to have crossed a threshold, whereby soils, seed banks and vegetative regenerative characteristics are such that reductions in grazing pressure may be of little consequence (Archer, 1996). Relaxation of grazing would influence woody plant establishment in grassland primarily through its influences on the fire regime (Archer, 1995a; Brown and Archer, 1999). However, the remaining herbaceous clearings are small and discontinuously distributed. Hence, even if fine fuels were to accumulate, fires would be highly localized. Such fires might prevent future encroachment into remaining grassland clearings, but would not likely convert woody plant communities to grassland, since the trees and shrubs at La Copita quickly regenerate by sprouting after disturbance (Scanlan, 1988; Flinn *et al.*, 1992). Expenses for clearing woody vegetation via mechanical or chemical treatments are prohibitive and generally not cost-effective, especially since the treatments are relatively short-lived. Thus, the likelihood of continued woody plant dominance is high, even with aggressive land management practices which might favor grasses.

The succession model which simulates the expansion of woody plants into remaining grasslands (Scanlan and Archer, 1991) projects that with heavy grazing and no fire, woody cover will continue to

increase until the landscape goes to nearly-complete canopy closure. This assumption has been substantiated by field data which indicates extension of lateral roots beyond woody canopies is minimal (Watts, 1993). Hence, there is little opportunity for between-cluster root competition and density-dependent regulation. As a result, tree/shrub densities may continue to increase until all available herbaceous clearings have been occupied and canopy cover is nearly continuous. Accordingly, woody patches on contrasting upland soils and woody patches on uplands which border woody communities of lowlands have grown and coalesced from the 1940s through the 1990s (Archer *et al.*, 1988; Stokes, 1999). However, recent studies suggest La Copita landscapes may be reaching their carrying capacity for woody plants, owing to topoedaphic constraints (Stroh, 1995; Stokes, 1999). If this is the case, future changes in C and N pools will occur only with growth of plants in existing woody communities. Only time will tell if this is indeed the case.

As the current population of the dominant *P. glandulosa* ages, growth and biomass accumulation rates should slow, unless other woody species compensate. The understory shrubs which colonize beneath the *Prosopis* canopy subsequent to its establishment in grasslands slow *Prosopis* growth and seed production, hasten its mortality (Barnes and Archer, 1998) and prevent its re-establishment (Archer, 1995b). Thus, it appears that *P. glandulosa* will not be a component of future woodlands on this landscape. Assessments to date suggest that over the short-term, loss of *Prosopis* will not adversely affect understory shrub productivity or soil C and N pools (Hibbard, 1995; Barnes and Archer, 1996). However, none of the associated woody species appears to have the genetic potential to achieve the size of mature *Prosopis* plants, either above- or belowground. Thus, there may be less potential for carbon storage once *Prosopis* is lost from the system, unless the remaining understory species compensate by increasing their productivity. In addition, the carbon presently stored in *Prosopis* biomass would be lost via death and decomposition, albeit rather slowly. It would be interesting to explore these scenarios with a linked CENTURY-succession model. Unfortunately, we know little of the productivity of the understory shrubs. Further, the maximum age of *P. glandulosa* is unknown and we have little basis from which to prescribe mortality from the present-day population.

IV. Degradation: Ecological Versus Socioeconomic

Degradation associated with 'desertification' or 'xerification' in arid environments (West, 1986; Rapport and Whitford, 1999) or 'deforestation' in humid environments is in sharp contrast to that associated with 'thicketization' of grasslands and savannas in mesic environments (Figure 2). Desertification and deforestation typically have negative consequences both ecologically and socioeconomically. 'Thicketization' has some adverse socioeconomic implications, as it reduces the capacity of rangelands for subsistence or commercial livestock production. However, it does not necessarily represent a degraded system with respect to biodiversity, productivity, nutrient cycling and other important ecological characteristics.

Today's La Copita landscape is clearly different from that of 100-200 YBP, but is it 'degraded'? The conceptual model in Figure 10, based on the La Copita case study, proposes a degradation phase (Figure 3) followed by an aggradation phase (Figures 6 and 9, Table 2) which begins when unpalatable woody plants establish, grow, modify microclimate and enrich soil nutrients. Present-day landscapes at La Copita are a rich mosaic of productive woodlands and tree-shrub patches interspersed with remnant grass-dominated patches. Current plant and soil C and N mass is substantially greater than that which occurred under 'pristine' conditions. In addition, these landscapes are highly resilient following disturbance (Scanlan, 1988; Flinn *et al.*, 1992) and provide habitat for numerous wildlife species, both game and

non-game. So, in this case, the system which has developed following an initial degradation phase is now ecologically diverse, productive and functional. It would seem that it is 'degraded' or 'dysfunctional' (Tongway and Ludwig, 1997) only with respect to its socioeconomic value for cattle grazing. However, it has other potential socioeconomic values whose realization would necessitate a change from traditional land uses. These include alternate classes of livestock (e.g., goats), lease hunting, charcoal production and ecotourism.

Given the demonstrated potential for nutrient sequestration in the conversion from grassland or savanna to woodland (Johnston *et al.*, 1996; Scholes and van der Merwe, 1996; Scholes and Bailey, 1996; San José *et al.*, 1998), these lands may also have 'carbon credit' value to society (e.g., (Glenn *et al.*, 1992). Government or industry subsidies and payments for management practices which promote or maintain woody plant cover on rangelands would stand in sharp contrast to past rangeland management practices which have sought to eliminate or reduce woody vegetation cover using costly and often short-lived chemical or mechanical treatments which may not produce desired results (Belsky, 1996) and which may convert landscapes from sinks to sources of greenhouse gases (De Castro and Kauffman, 1998). Thus, perspective on woody plants in rangelands may shift from negative (an expensive management problem) to positive (a potential commodity).

From a biogeochemical perspective, potential benefits of C and N sequestration should be weighed against the potentially undesirable absolute increases in NO and NMHC fluxes which may accompany increases in woody plant biomass. The effects of vegetation change on the hydrological cycle must also be considered. The extent to which shifts from herbaceous to woody plant domination might reduce stem flow and groundwater/aquifer recharge remains controversial. In addition, potential increases in ecosystem transpiration associated with woody communities with high LAI and deep root systems might increase atmospheric water vapor and either offset (due to radiative properties of water) or augment (via cloud formation) benefits of C-sequestration on greenhouse gas budgets. From a biodiversity perspective, shrubland/woodland communities may be more (La Copita scenario) or less diverse (many *Juniperus* communities) than grasslands. In either case, the diversity in terms of the kinds of organisms present would be very different. The development of shrublands and woodlands would be at the expense of grassland habitats and the plants and animals characteristic of such habitats. From a socioeconomic perspective, the promotion or maintenance of woody plant biomass on grasslands and savannas would necessitate a radical change in traditional land use and range management perspectives. Revenues generated from marketing of soil and plant carbon stocks could help fund needed restoration efforts and spur economic development in many sectors, but may be socioeconomically disruptive on other fronts (Trexler and Meganck, 1993). Thus, there are many important issues to be resolved when evaluating the merits of C and N sequestration associated with vegetation change.

V. Implications For Ecosystem And Natural Resources Management

Woody plant encroachment has been and continues to be a major problem in grasslands and savannas world-wide (e.g., Grossman and Gandar, 1989). Because of its direct effects on livestock production, encroachment of woody vegetation into grasslands has been one of the most important problems facing the ranching industry in the western USA and graziers and pastoralists in arid/semiarid regions throughout the world. This structural change in vegetation also has profound effects on the functional properties of ecosystems. Since woody plant encroachment into grassland is occurring over large areas worldwide, ecosystem–level changes in nutrient pool sizes and fluxes will likely have important ramifications for regional and global biogeochemistry and climate. Thus, the replacement of grassland/savanna ecosystems

by woodlands should be viewed not only as a local problem with economic impacts on livestock husbandry, but also in the context of longer–term, regional impacts on biogeochemistry and climate that will influence future land use options in arid and semiarid ecosystems worldwide.

Since the dawn of time, humans have been cognizant of the direct (e.g., catastrophic floods, wind storms, hail, etc.) and indirect (e.g., drought effects on food availability) effects of climate on their well-being. Ecosystem science in the 1960s and 70s focused on climatic and abiotic controls over ecosystem structure and function. During this same period, it became increasingly clear that human activities were directly responsible for significant changes in atmospheric chemistry which could feed back to affect ecosystem processes (e.g., acid rain) and human health (e.g., smog). While ecologists and natural resource managers have long been concerned with impacts of humans on ecosystems, we have only recently begun to assess how alterations of ecosystem structure and function might induce changes in climate and atmospheric chemistry (Figure 11)(Graetz, 1991; Bryant *et al.*, 1990; Pielke *et al.*, 1993; Pielke *et al.*, 1998). The case study presented here explicitly documents how human activities (specifically alteration of grazing and fire regimes) have modified the structure and function of a subtropical savanna grassland system in ways that may have significant impacts on climate and atmospheric processes. Anticipating future changes will largely depend on anticipating how human populations and land use will change. Land use practices will be governed in large part by socioeconomic conditions mediated by government policy and subsidies (Figures 12 and 13). Thus, the human dimension of global change is paramount and ecologists are challenged to interface ecosystem science with social science (Turner *et al.*, 1990; Walker, 1993a,b; Walker and Steffen, 1993; Vitousek, 1994).

Changes in tree-shrub-grass ratios in drylands has policy implications for federal agencies grappling with designing and implementing carbon sequestration programs. The success of such endeavors will hinge on the ability to quantitatively monitor and inventory 'carbon credits' associated with various land management practices. In arid and semi-arid ecosystems, this means tracking changes in woody versus herbaceous cover and understanding how shifts between these growth forms influences above- and belowground C and N pools and fluxes. However, landscape-scale and regional quantification of grass-woody plant mass is challenging, because woody encroachment occurs relatively slowly (decadal time scales) in a non-linear fashion, across large and often remote areas, and in a heterogeneous manner determined by topoedaphic constraints, climate, land-use and disturbance regimes. In addition, reductions in woody biomass also occurs in drylands where trees and shrubs are cleared using fire, herbicides or mechanical means (e.g., roller chopping, chaining). As a result, landscapes within a region may be a mosaic of variable-strength C and N sources and sinks. At present, we lack comprehensive information on the rate of change, areal extent, and pattern of woody plant abundance in the world's drylands. Hence, it is difficult to objectively assess the role of savannas in regional/global C and N cycling. Recent advances in remote sensing show promise for quantifying changes in grass and woody plant biomass in drylands (Asner *et al.*, 1998b)b. These remote sensing tools, when used in conjunction with simulation modeling (Asner *et al.*, 1998a) will potentially enable functional monitoring of land use impacts on regional biogeochemistry in savanna regions.

VI. Summary

Woody plant encroachment has been widespread in grassland and savanna ecosystems over the past century. This phenomenon jeopardizes grassland biodiversity and threatens the sustainability of pastoral, subsistence, and commercial livestock grazing. As such, it may adversely impact   20% of the world's

population. Although woody plant expansion has long been a concern of land managers in grassland and savanna regions, most research on this issue has focused on woody plant effects on grass production and the development methods to limit or reduce the abundance of trees and shrubs. Little is known of the rates and dynamics of the phenomenon, or its impact on fundamental ecological processes related to energy flow and nutrient cycling. Grassland/savanna systems account for 30 to 35% of global terrestrial net primary production. Hence, when woody species increase in abundance and transform grasslands and savannas into shrublands and woodlands, the potential to alter land surface-atmosphere interactions and C and N sequestration and cycling at regional and global scales may be significant.

The La Copita case-study reveals the rate and magnitude of change in ecosystem biogeochemistry that can occur when a subtropical dryland landscape is transformed from grassland to woodland. Linked succession-biogeochemistry models, confirmed with historical aerial photography and ground measurements, indicate soil and plant C mass has increased 10% and 10-fold, respectively, with succession from pre-settlement savanna grassland to present-day savanna woodland over the past 100 years. Ecosystem C storage will continue to increase as present-day woody vegetation communities mature and expand into remaining herbaceous areas. Increases in ecosystem C mass were accompanied by increases in soil N pools. Fluctuations in monthly woody plant root biomass in upper soil horizons exceeded foliar litter inputs by one to two orders of magnitude, suggesting that belowground inputs of organic matter drive changes in soil physical and chemical properties subsequent to woody plant establishment in grasslands. Increases in C and N pools occurred in spite of increases in N mineralization, NO flux, soil respiration, and non-methane hydrocarbon emissions. These results are of potential global significance, given that large areas of Africa, South America, North America and Australia have been undergoing similar land cover changes over the past century. The demonstrated capacity for carbon sequestration in this semi-arid system suggests a need to re-evaluate traditional perspectives on woody plants in rangelands as governments and industries seek ways to mitigate greenhouse gas emissions. Regional assessments of the potential consequences for global change are presently hampered by a lack of quantitative information on the geographic balance between woody plant expansion and clearing in the world's extensive and often remote drylands. Recent developments in linked remote sensing-ecosystem modeling approaches show promise for alleviating these monitoring constraints.

ACKNOWLEDGEMENTS

CLIMATE   SOILS

subtropical location

high solar   seasonal   geomorphological   parent
radiation   rainfall   history   material

high temp-   high evap-   depth and
eratures   oration   water retention

warm dry
season

Available water   Available nutrients

Tree production   Grass production

tree biomass   grass biomass

Fire   Herbivory

                                   grazers

                                   browsers

HUMAN INFLUENCE
(from Scholes and Walker 1993)
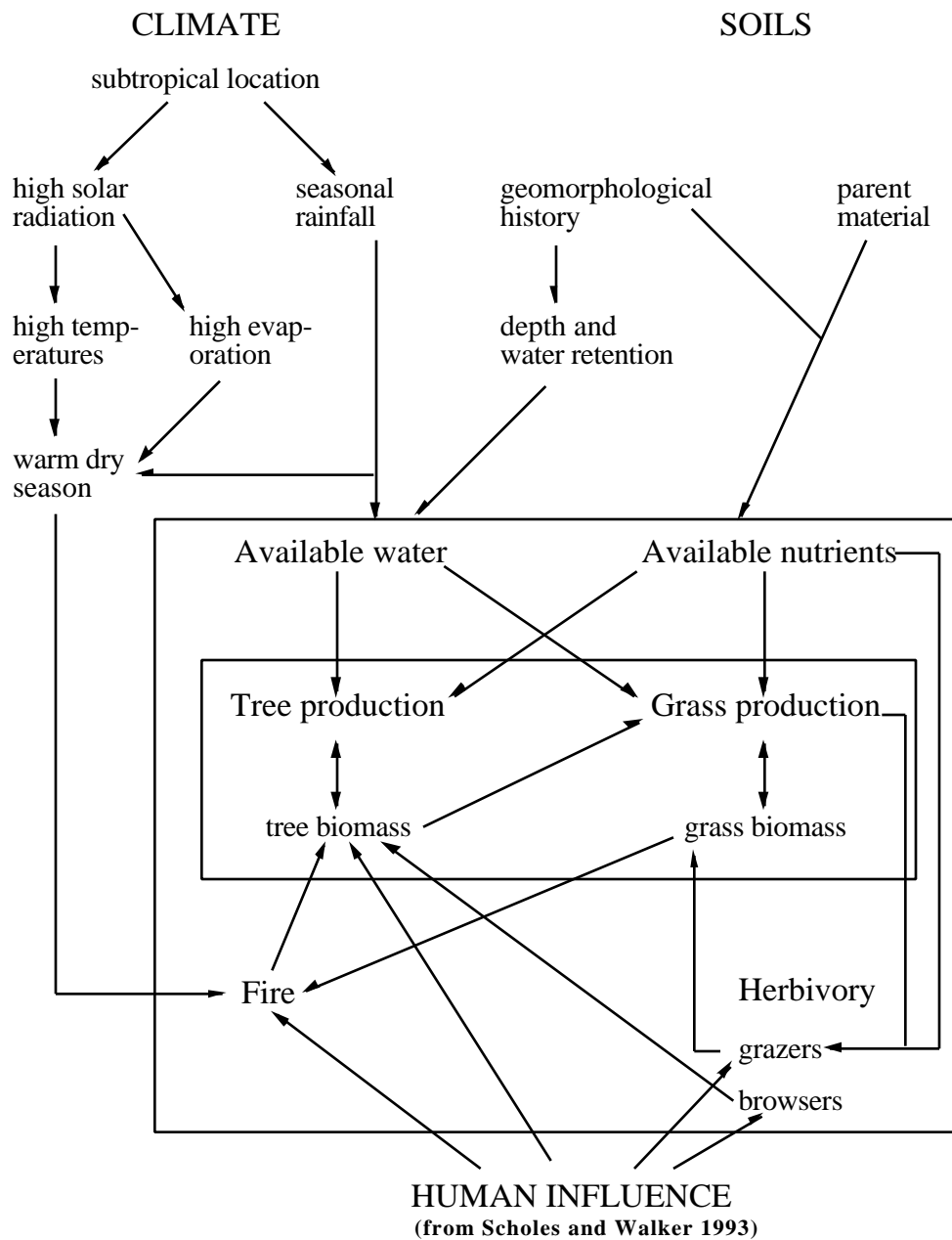
Figure 1. Numerous factors interact to affect the abundance of grasses and woody vegetation in drylands (from Scholes and Walker, 1993). The balance between trees and grasses (inner-most level) is affected by determinants of structure and function (water, nutrients, fire and herbivory). The outer-most level contains the factors which give the determinants their characteristics. Over the past century, human influences have shifted the balance to favor woody plants through selective utilization of grasses by livestock maintained at high concentrations, elimination of browsers and fire suppression (see Archer, 1994).
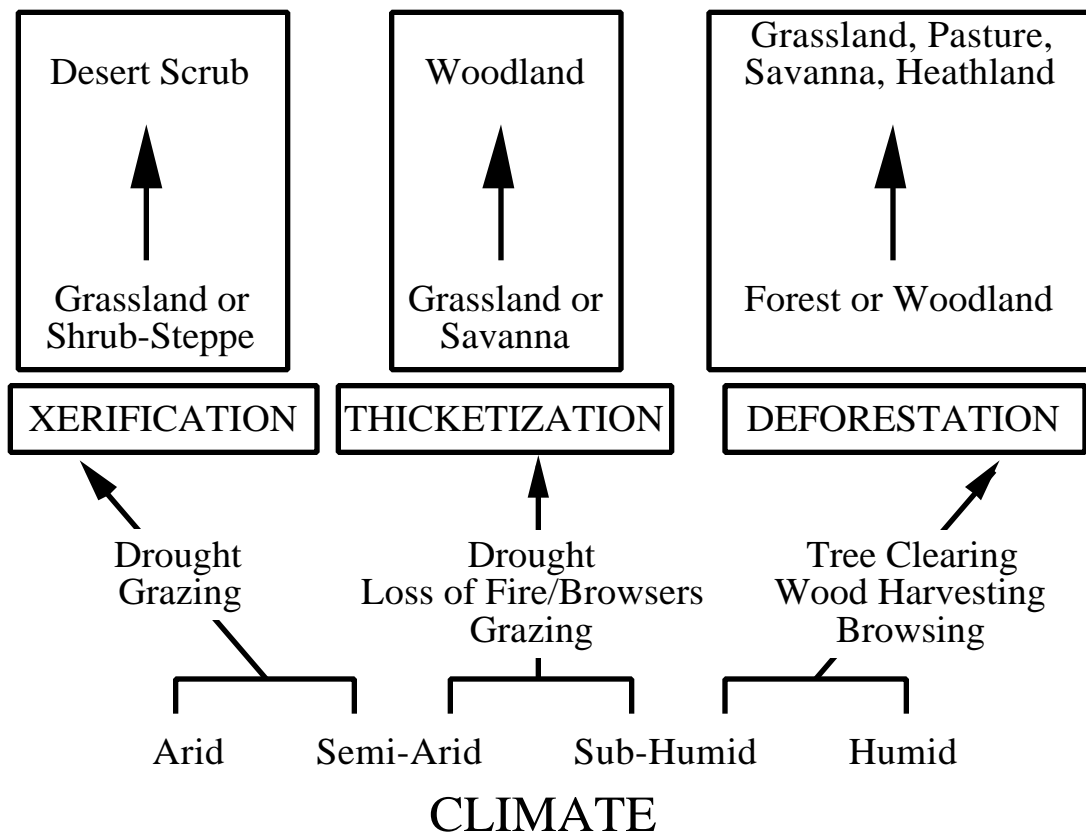
Figure 2. Xerification/desertification (West, 1986) and deforestation have received much attention. Although increases in woody plant abundance in drylands are geographically widespread and well-documented (Table 1), little is known of the ecological consequences of this vegetation change (adapted from Archer and Stokes, 2000).
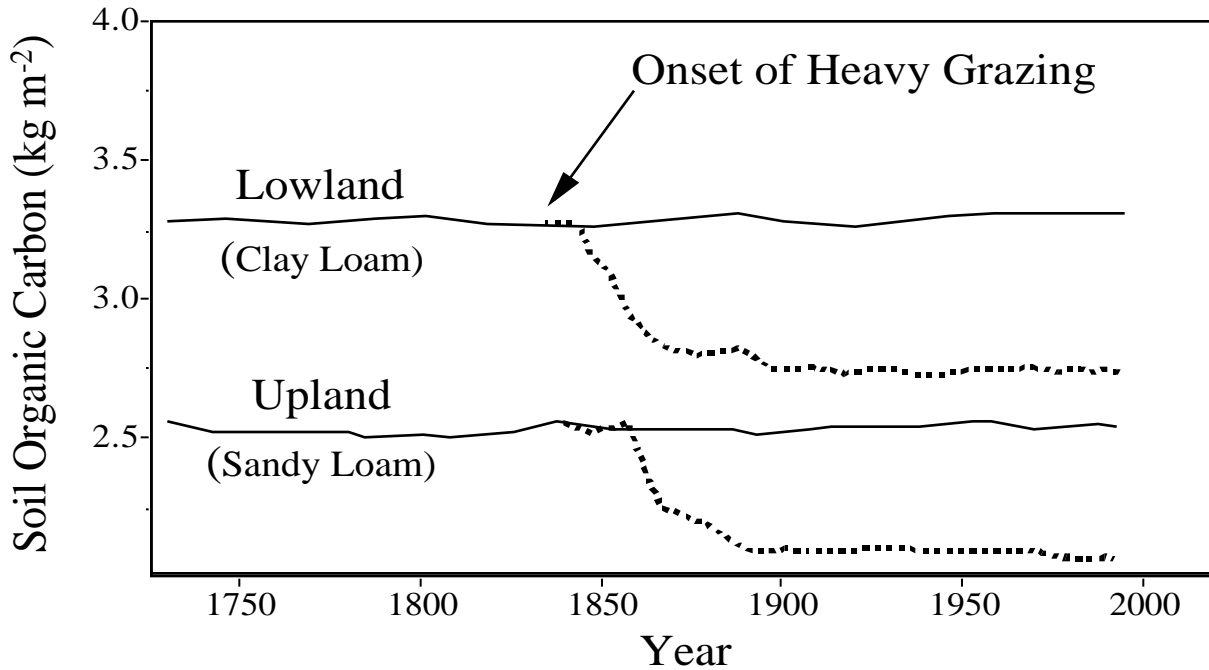
Figure 3. Simulation model reconstruction of changes in soil organic carbon (0-20 cm) on an upland, sandy loam soil and a lowland, clay loam soil at the La Copita Research Area in southern Texas, USA (from Hibbard, 1995). Solid lines depict steady state SOC values expected for the climate of the site under light grazing and fire every 10 years (pre-settlement conditions). Dashed lines depict changes in SOC predicted to occur on two major soil types after the onset of heavy, continuous livestock grazing and cessation of fire. Steady-state values for heavy, continuous grazing and cessation of fire are within 5% of field measurements on present day grasslands.
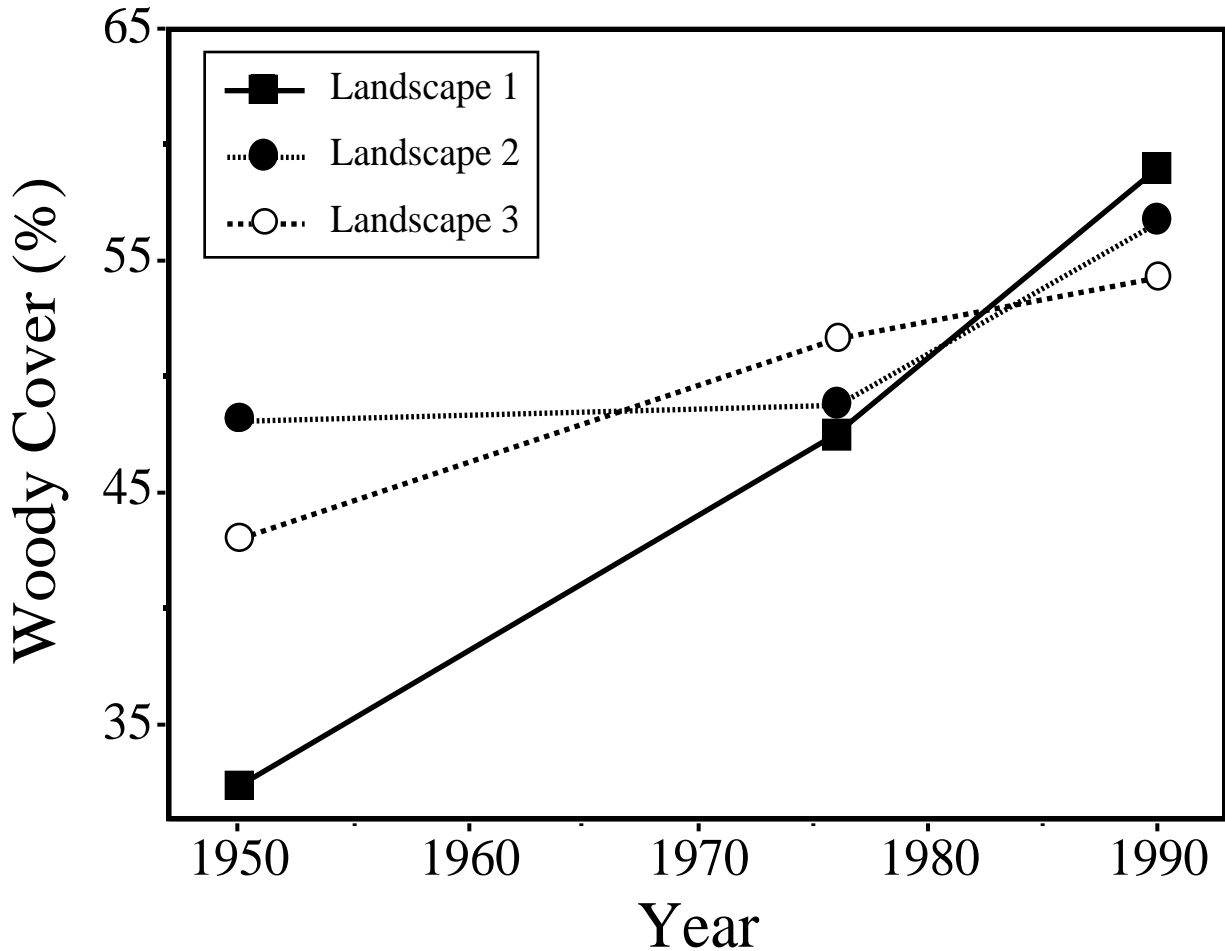
Figure 4. Changes in total woody plant cover on three replicated landscapes at the La Copita site in southern Texas, USA. See Figure 5 for spatial pattern of change in various patch types on Landscape 1 (Archer and Boutton, unpublished).
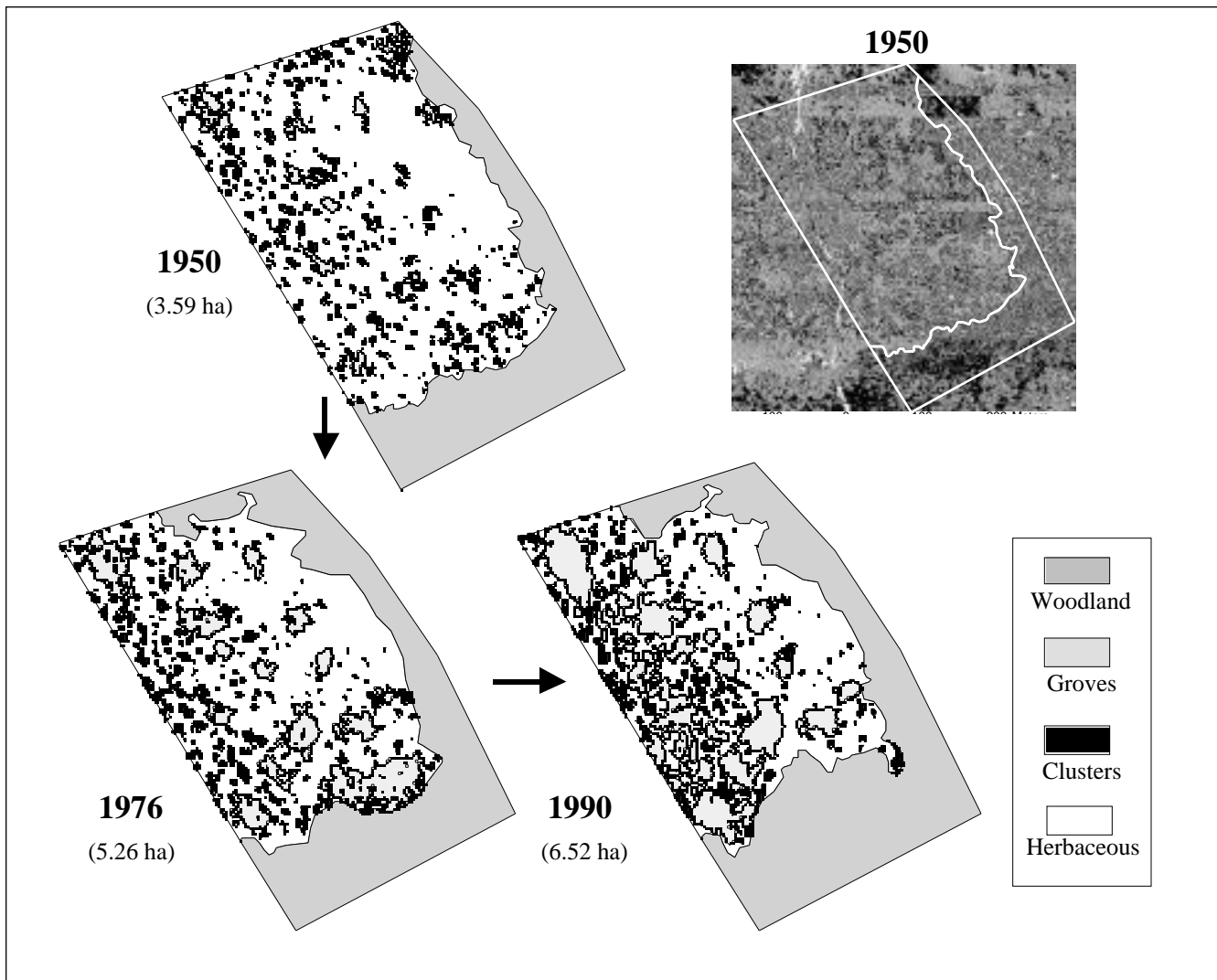
Figure 5. Landscape-scale changes in herbaceous and woody plant community cover from 1950 to 1990 in upland (herbaceous, discrete cluster and grove) and lowland (woodland) plant communities at the La Copita site in southern Texas, USA (Archer and Boutton, unpublished). Values given below dates are total hectares of woody cover (cluster + grove + woodland) for the 11.06 ha 'pixel'. See Figure 4 (Landscape 1) for changes in % woody cover.
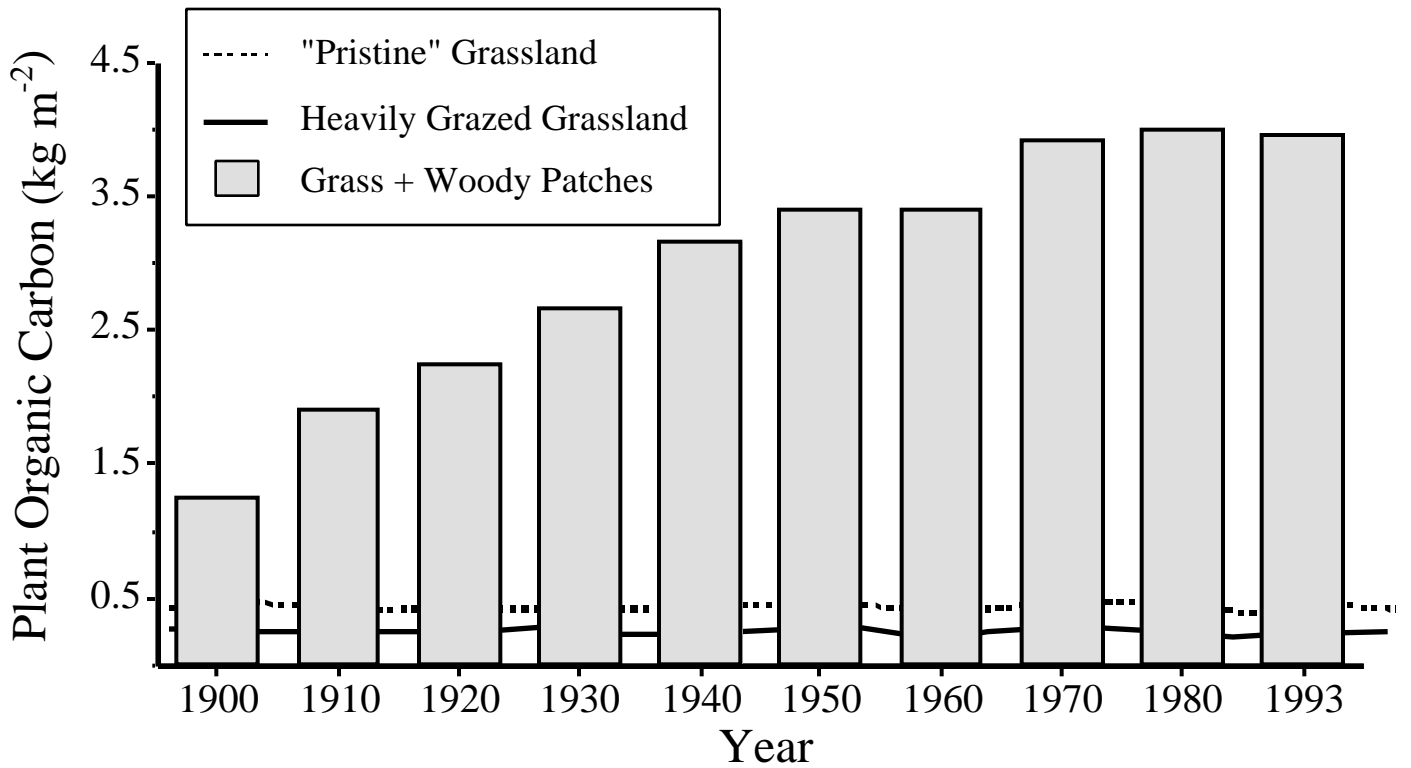
Figure 6. Modeled changes in whole-landscape (upland + lowland and all patch types therein) plant carbon density (aboveground + roots to 20 cm) accompanying succession from grassland to savanna parkland/woodland (from Hibbard, 1995). Dashed line depicts steady-state SOC expected for a lightly grazed grassland landscape (upland + lowland communities pooled) with fire at 10-y intervals and no woody plants; solid line depicts steady-state plant carbon density for heavily, continuously grazed grassland landscape with no fire and no woody plants. Changes in woody plant abundance on each soil type were directed by a succession model (Scanlan and Archer, 1991); subsequent changes in plant carbon stocks were then assessed with a biogeochemistry model (CENTURY; Parton *et al.*, 1994). See Figure 7 for validation results.
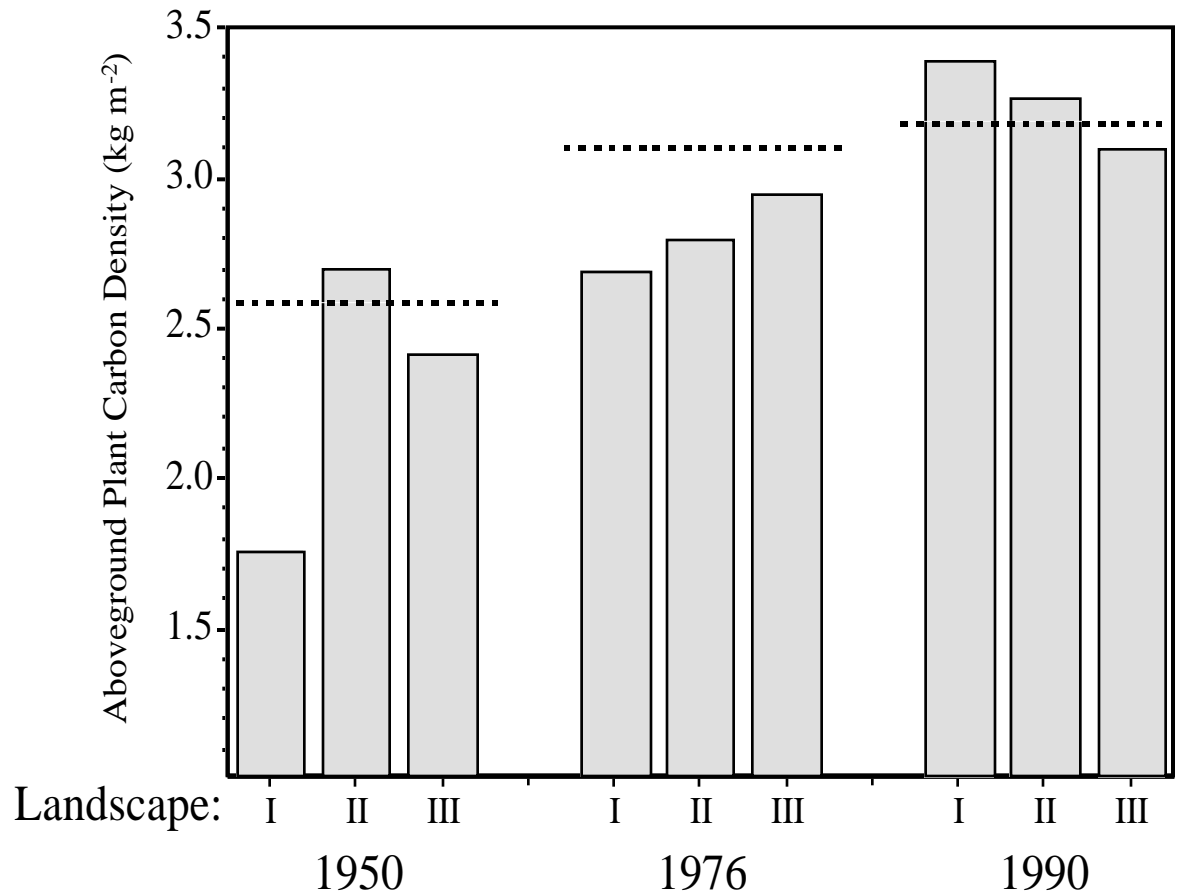
Figure 7. Changes in aboveground plant carbon density on three landscapes at the La Copita from 1950 to 1990 (Archer and Boutton, unpublished). Patch/soil-specific field estimates of plant carbon density (Northup *et al.*, 1996, McMurtry, Nelson and Archer, unpubl.) were multiplied by patch area as measured on aerial photographs to generate whole-landscape estimates. Dashed lines denote predictions from linked CENTURY-succession model (Hibbard, 1995) . See Figure 4 for changes in woody cover on the three landscapes.
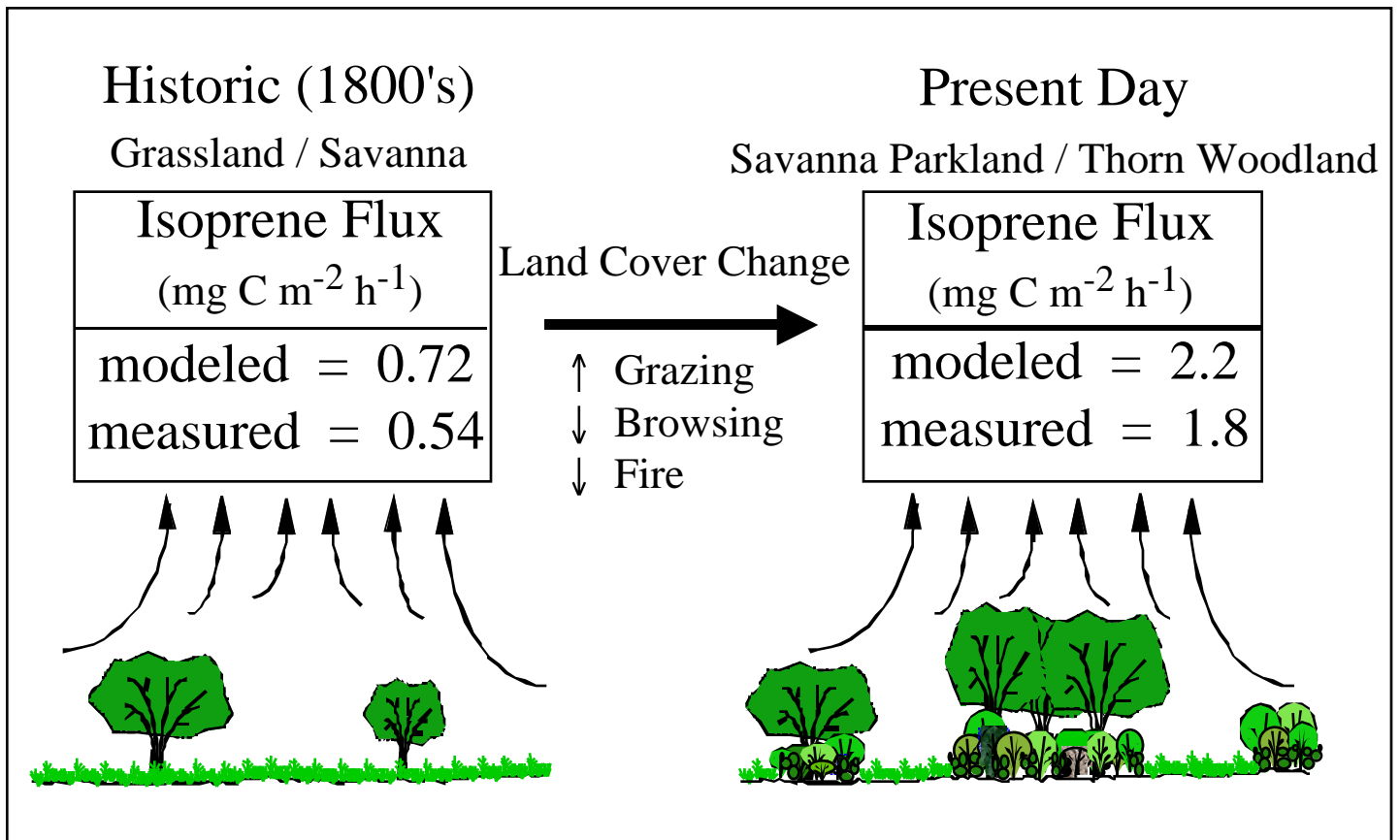
Figure 8. Changes in non-methane hydrocarbon (isoprene) emissions predicted to accompany a shift from savanna grassland to a savanna woodland at the La Copita site in southern Texas, USA (based on Guenther *et al.*, 1999). Predictions from a coupled succession-NMHC emission model are compared with values measured from flux towers. The 'measured' values shown for the historic landscape are from a tower located in a savanna grassland landscape with low woody cover.
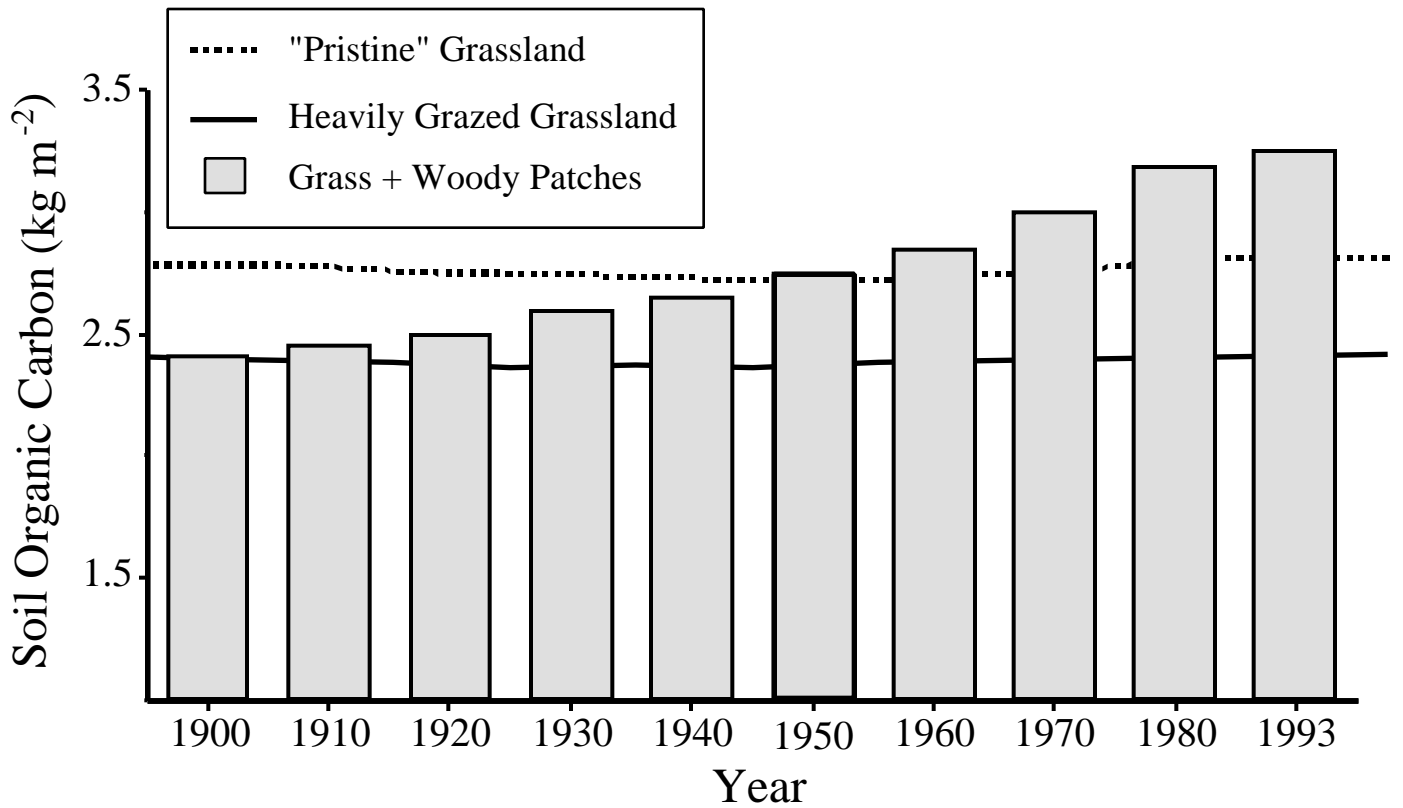
Figure 9. Changes in soil organic carbon (SOC; 0-20 cm) predicted to accompany woody plant encroachment into a grazed landscape consisting of a sandy loam uplands and clay loam intermittent drainages at the La Copita site (from Hibbard, 1995). Dashed line depicts steady-state SOC expected for a lightly grazed grassland landscape (upland + lowland communities pooled) with fire at 10-y intervals and no woody plants; solid line depicts steady-state SOC for heavily, continuously grazed grassland landscape with no fire and no woody plants (see Figure 3). Bars denote SOC summed across the entire landscape and include both grassland and woody plant communities. Note that by 1950, SOC levels had increased to a level comparable to that of the 'pristine' grassland (cross-hatched bar). Changes in woody plant abundance on each soil type were directed by a succession model (Scanlan and Archer, 1991); subsequent changes in soil carbon were then assessed with a biogeochemistry model (CENTURY; Parton *et al.*, 1994).
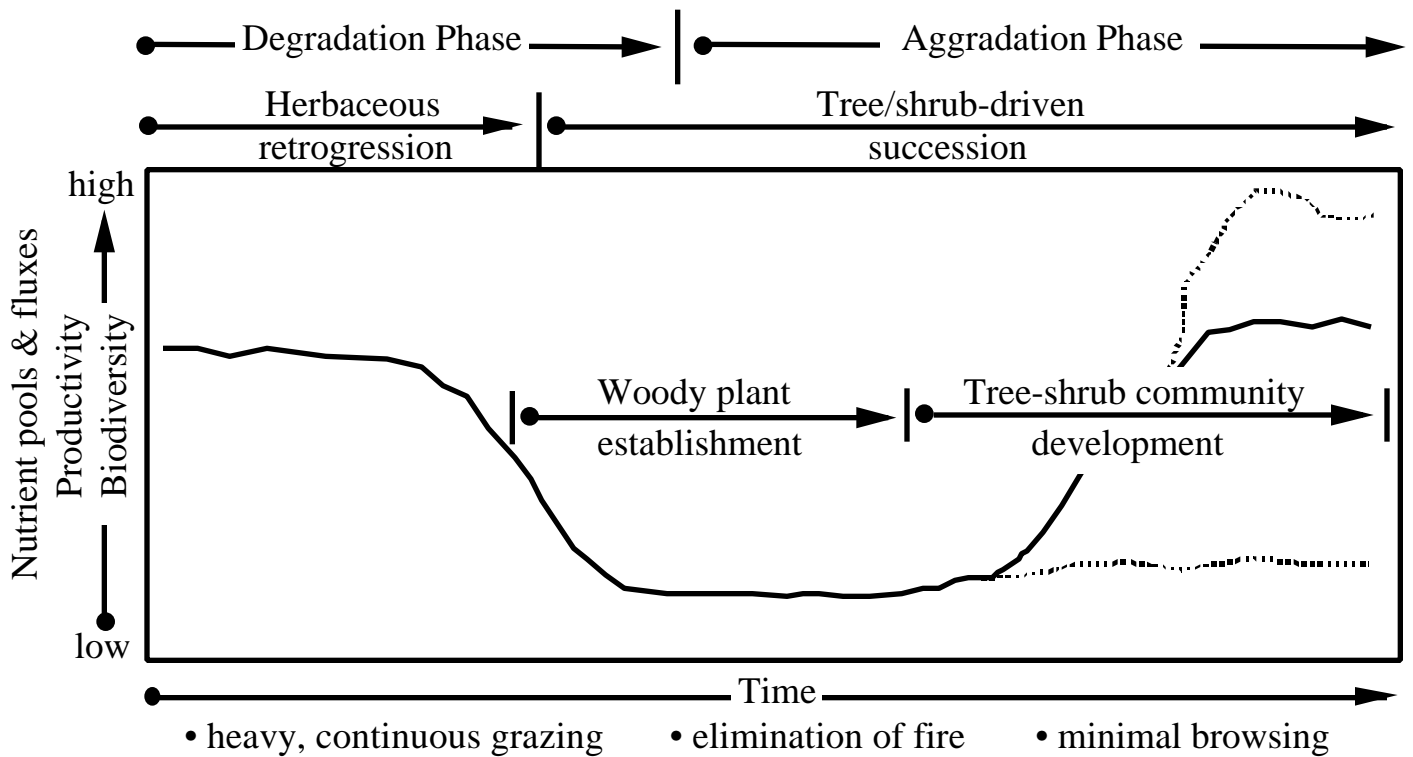
Figure 10. Conceptual model of ecosystem changes accompanying grazing-induced succession from grassland to woodland based on the La Copita case study. Dashed lines depict hypothesized upper and lower bounds of Y-values (e.g., lower bound = that which might occur in absence of woody plant encroachment [Figure 3]; upper bound = that which might occur when woody plant communities mature [e.g., forward projection of Figures 6 and 9]). Values for biodiversity will vary substantially from system to system; in some cases (e.g., *Juniperus* systems) low-diversity monocultures of woody vegetation may develop. At the La Copita, this degradation-aggradation cycle has occurred over ca. 100-150 y.

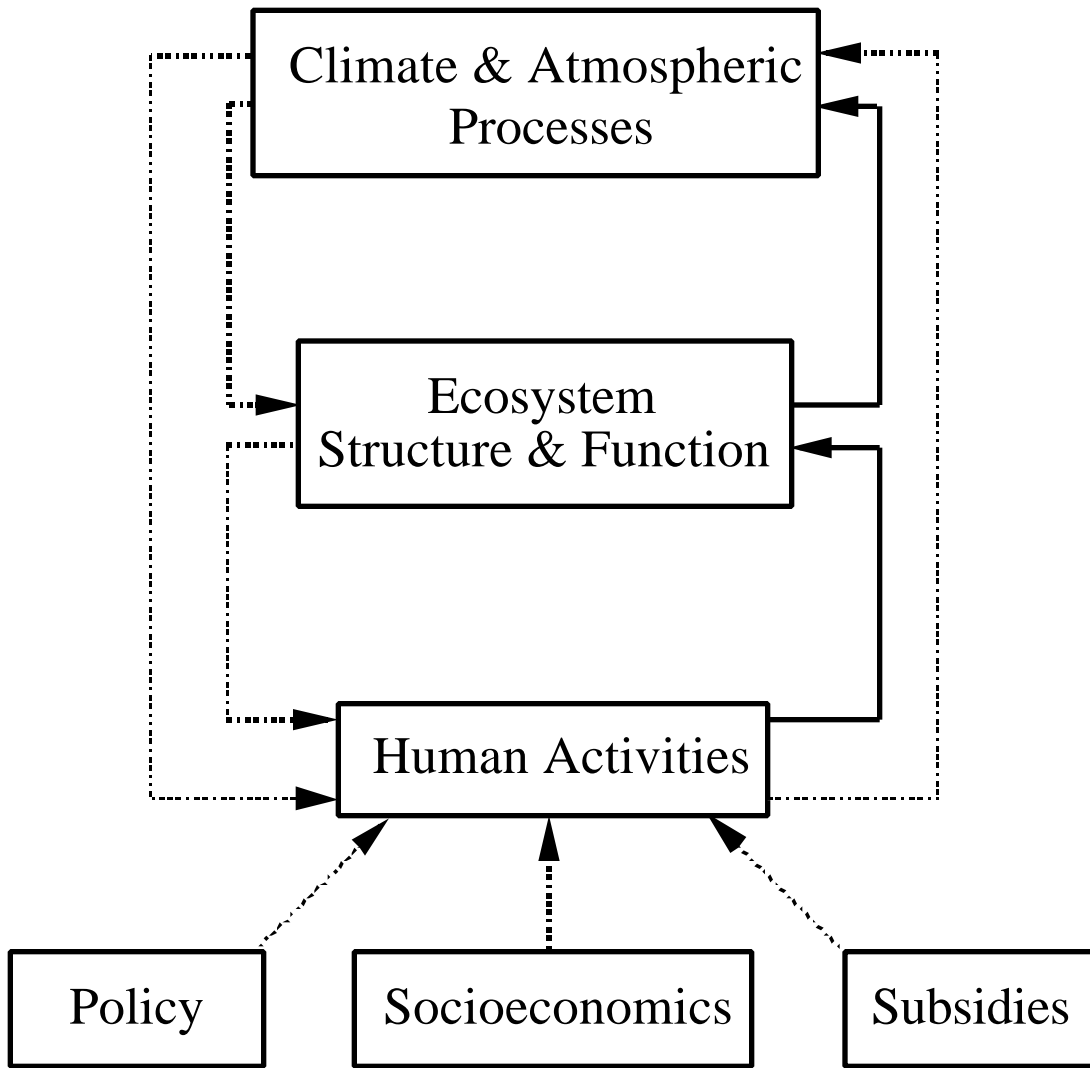**Figure 11.** Feedbacks between climate and atmospheric processes, ecosystem structure and function, and human activities. Dashed lines depict traditional research and public awareness; solid lines denote areas requiring increased research emphasis. Understanding global change will ultimately hinge on understanding how socioeconomics, policy and government subsidies influence human activities and land use (see Figures 12, 13).
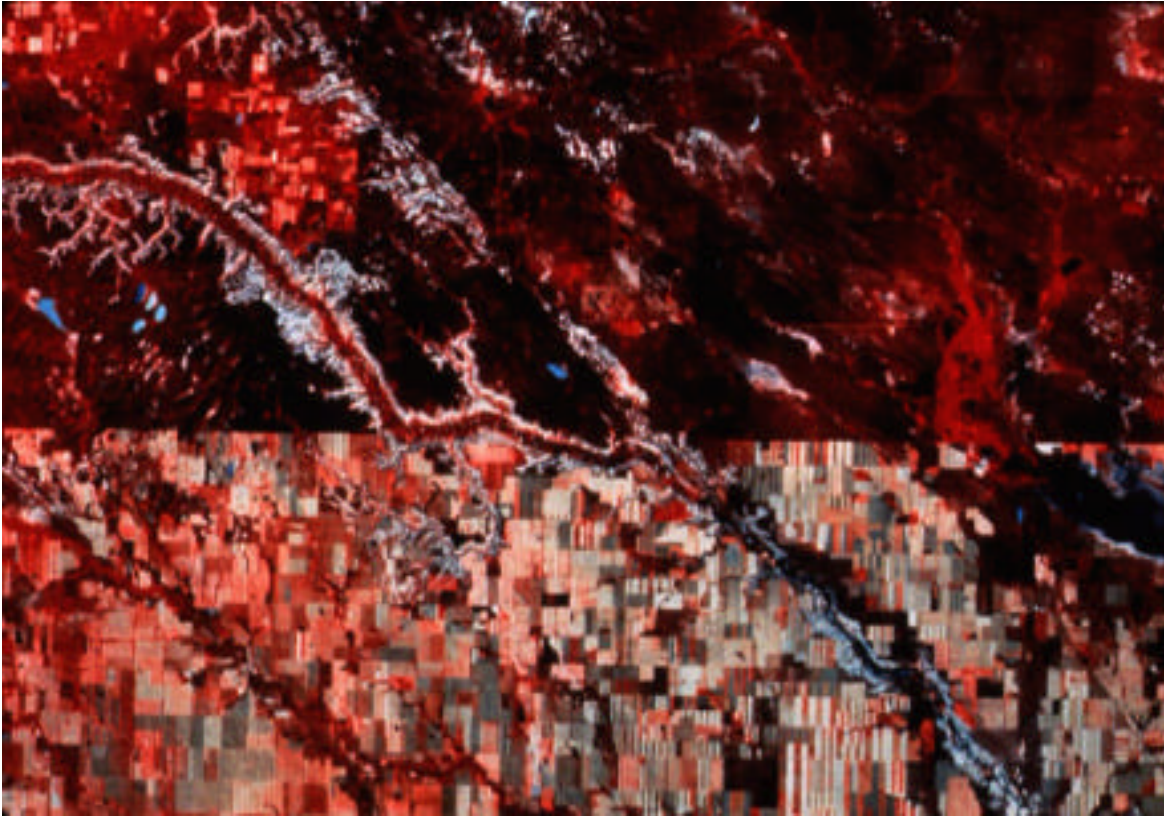
Figure 12. LANDSAT image (1978) of the Canada (Saskatchewan/Alberta) - USA (Montana) border in the vicinity of the Milk River (from Knight, 1991). Subsequent to the drought and Dust Bowl of the 1930s, farmlands in Canada were repossessed by provincial or federal governments, withdrawn from cultivation and underwent secondary succession. Intensive agriculture was maintained in the USA via elaborate farm subsidy programs. Striking contrasts in regional land cover were thus a direct result of changes in government policy.

Figure 13. Differences in biophysical properties associated with contrasting land management policies in adjacent portions of the USA and Mexico (adapted from Bryant *et al.*, 1990). Relaxation of grazing and range improvement 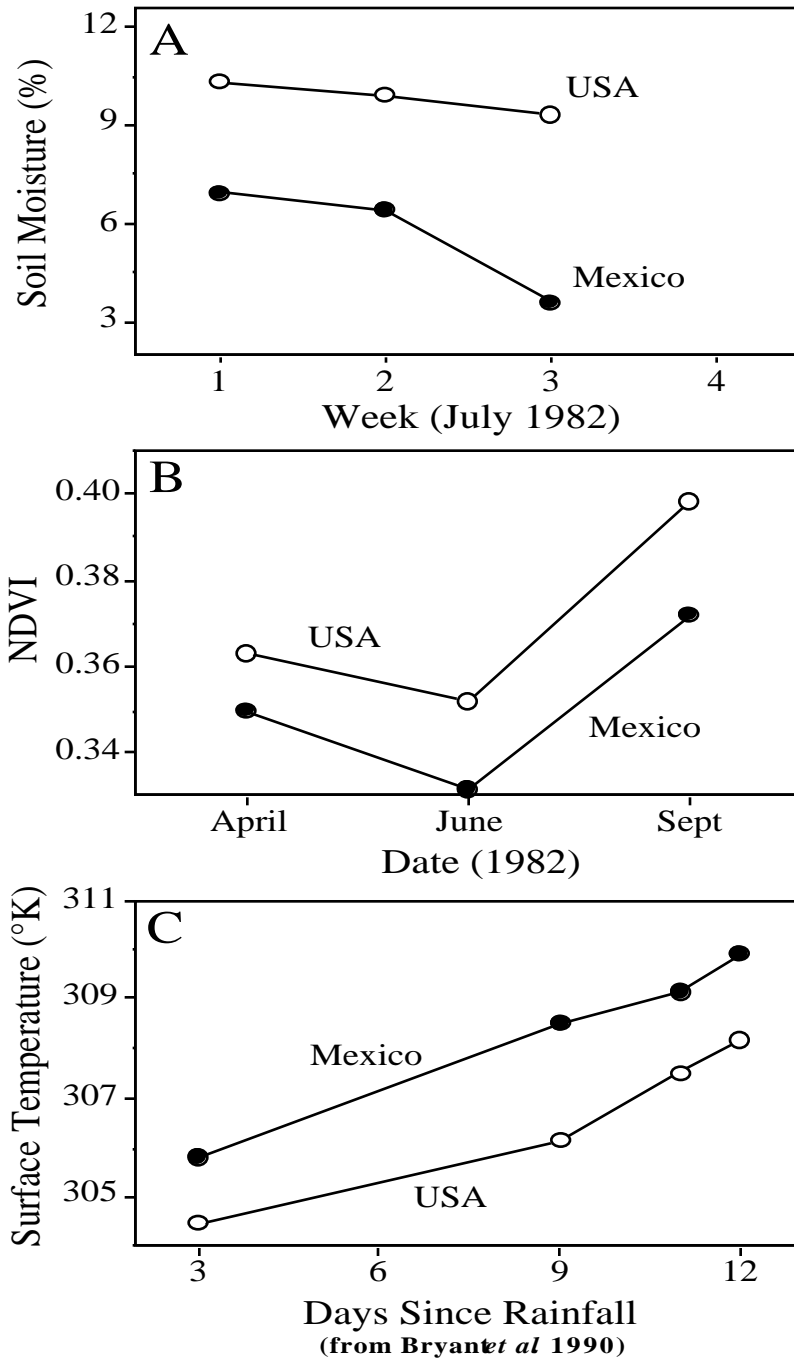programs occurred in the USA subsequent to the implementation of the Taylor Grazing Act in 1934. Changes in landscape cover resulting from a change in federal policy has had biophysical consequences.

Table 1. Survey of studies describing or quantifying woody plant encroachment into grassland, tree/shrub proliferation in savannas and tree encroachment into shrubland. Documentation includes historical observations, long-term monitoring, repeat ground or aerial photography, stable carbon isotope analysis, dendrochronology and, in some cases, simulation modeling. The focus is on arid and semi-arid 'rangelands.' Hence, studies documenting tree/shrub invasion into abandoned agricultural fields (c.f., Smith, 1975; Johnston et al., 1996; De Steven, 1991) or regeneration following forest clearing are minimally represented. Studies discussing or reviewing causes or consequences of woody encroachment into grasslands/savannas (c.f., Humphrey, 1953; Fisher, 1977; Smeins, 1983; Rappole et al., 1986; Grover and Musick, 1990; Schlesinger et al., 1990; Archer, 1994; Archer et al., 1995; Idso, 1995; Polley et al., 1997) are also excluded. Some papers in the list reference other papers which have documented woody plant increases in historical times (Backéus, 1992; Noble, 1997). An updated and more extensive version of this table, including a listing of woody genera, can be found at http://cnrit.tamu.edu/rlem/faculty/archer/.

Arizona
Arnold 1950
Bahre 1991
Bahre & Shelton 1993
Brown 1950
Brown et al. 1997
Cooper 1960
Covington & Moore 1994b
Glendening 1952
Humphrey & Mehrhoff 1958
Hastings & Turner 1965
Johnsen 1962
Kenney et al. 1986
Martin 1975
Martin & Turner 1977
McClaran & McPherson 1995
McPherson et al. 1993
Miller 1921
Reynolds & Glendening 1949
Savage & Swetnam 1990
Smith & Schmutz 1975
California
Bossard 1991
Bossard & Rejmanek 1994
Callaway & Davis 1993
McBride & Heady 1968
Hobbs & Mooney 1986
Vivrette & Muller 1977
Williams et al. 1987
Young & Evans 1981
Colorado
Baker & Weisberg 1997
Mast et al. 1997
Mast et al. 1998
Veblen & Lorenz 1991
Idaho
Anderson & Holte 1981
Burkhardt & Tisdale 1976
Zimmerman &
Neunschwander 1984
Iowa
Wang et al. 1993
Kansas

Abrams 1986
Bragg & Hulbert 1976
Briggs & Gibson 1992
Knapp & Seastedt 1986
Knight et al. 1994
Loehle et al. 1996
Owensby et al. 1973
Minnesota
Grimm 1983
Johnston et al. 1996
Montana
Arno & Gruell 1986
Arno et al. 1995
Nebraska
Johnson 1994
Steinauer & Bragg 1987
Steuter et al. 1990
New Mexico
Branscomb 1958
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Table 2. Contrasts in aboveground net primary production (ANPP), soil physical properties, organic carbon and total nitrogen pools (0-10 cm depth) and fluxes in soils associated with woody plant and grazed grassland communities in a sandy loam upland landscape at the La Copita Research Area in southern Texas, USA. Maximum and minimum monthly values for samples obtained over an annual cycle are shown for root standing crop (coarse roots = >0.1 mm diam.); a range is presented for ANPP. All other values are means $\pm$ SE.

Parameter	Community Type	
	Herbaceous	Woody Plant
ANPP ($Mg\ ha^{-1}\ y^{-1}$) [a]	1.9 - 3.4	5.1 - 6.0
Bulk Density ($g\ cm^{-3}$) [a]	1.4 $\pm$ 0.01	1.1 $\pm$ 0.04
% Clay [a]	20 $\pm$ 0.7	20 $\pm$ 1
Fine Roots ($g\ m^{-2}$) [a]	100 - 175	400 - 700
Coarse Roots ($g\ m^{-2}$) [a]	100 - 400	400 - 1,100
Organic C [a]: %	0.84 $\pm$ 0.05	2.2 $\pm$ 0.23
$g\ m^{-2}$	1165 $\pm$ 67	2352 $\pm$ 276
Potential C mineralization ($mg\ C\ kg^{-1}\ soil\ day^{-1}$) [b]	7.3 $\pm$ 5.7	15.5 $\pm$ 6.8
Soil Respiration ($mg\ CO_2\ m^{-2}\ y^{-1}$) [b]	611 $\pm$ 83	730 $\pm$ 67
Q_{10} Values for *in situ* soil respiration [b]	1.2	1.4, 2.7
Total N [a]: %	0.07 $\pm$ 0.00	0.18 $\pm$ 0.02
$g\ m^{-2}$	91 $\pm$ 6	192 $\pm$ 20
N-mineralization [a]: $g\ N\ m^{-2}\ y^{-1}$	6 $\pm$ 1	22 $\pm$ 2
$\mu g\ N\ g^{-1}\ y^{-1}$	42 $\pm$ 5	200 $\pm$ 18
NO flux ($ng\ NO\text{-}N\ cm^{-2}\ h^{-1}$) [c]		
Dry soil	0.2 $\pm$ 0.07	2.8 $\pm$ 0.25
Wet soil	1.1 $\pm$ 0.11	16.2 $\pm$ 2.03

[a]Hibbard (1995) [b]McCulley (1998) [c]Cole *et al.* (1996)

Table 3. Observed and predicted aboveground carbon density in patches representing tree/shrub and grassland communities at La Copita, Texas. Observed data (mean $\pm$ SE) are based on belt transects and plant size-biomass relationships for woody communities (Archer and Boutton, unpublished) and on clipped plots in grasslands (Archer, unpublished). Predicted values are CENTURY estimates for 100-y-old patches (Hibbard, 1995).

Topoedaphic Setting	Patch Type	Carbon Density (kg m^{-2})	
		Field Estimate	Model Estimate
Sandy Loam Upland	Cluster	2.9 $\pm$ 0.4	2.2
	Grove	6.3 $\pm$ 0.8	4.0
	Grassland[1]	0.05 $\pm$ 0.00	0.04
Clay Loam Lowland	Woodland	5.8 $\pm$ 0.8	4.5

[1]Peak aboveground biomass

Table 4. Estimated rates of organic carbon and total nitrogen accumulation in soils (0-20 cm depth) developing beneath woody plants establishing on a former grassland. Field data are from linear correlations between patch age (determined by dendrochronology) and soil C and N mass (Boutton and Archer, unpublished). Model estimates are from CENTURY simulations (Hibbard, 1995). Descriptions of contrasting woody patch types can be found in (Archer, 1995b).

Location	Soil Texture	Patch Type	---g C m^{-2} y^{-1} ---		---g N m^{-2} y^{-1} ---	
			Field	Modeled	Field	Modeled
Upland	Sandy Loam	Shrub Cluster	21.5 (r^2=0.26)	18.5	2.67 (r^2= 0.45)	1.15
		Grove	11.8 (r^2= 0.21)	10.5	1.90 (r^2= 0.51)	0.87
Lowland	Clay Loam	Woodland	47.2 (r^2= 0.57)	13.1	4.64 (r^2= 0.68)	0.58

Table 5. Projected landscape-scale changes in annual soil respiration (SR; kg C ha^{-1} y^{-1}) accompanying succession from an open savanna/grassland to woodland and potential changes in mean annual temperature. Patch- (grass and various woody communities) and soil-specific SR rates measured monthly over an annual cycle at La Copita (McCulley, 1998) were multiplied by the area of respective community types (Scanlan and Archer, 1991). Effects of mean annual temperature change (MAT, °C) on SR were estimated from (A) equations in (Raich and Schlesinger, 1992). For La Copita (MAT = 22.4 °C and MAP=720 mm) a 3 and 6 °C increase in MAT would produce a 3.9 and 7.8% increase, respectively in soil respiration; and (B) Q_{10} values of *in situ*, community-specific soil respiration from (McCulley, 1998). Estimates are probably conservative, as respiration rates used in computations were measured during a below-normal rainfall year.

Landscape-Scale Soil Respiration (kg C ha^{-1} y^{-1})

A. Based on MAT/MAP regression in Raich and Schlesinger (1992)

Mean Annual Temp	Past Grassland (200 YBP) [1]	Present Savanna Parkland/Woodland Complex	Future Thorn Woodland (200 YAP) [2]
22.4 °C	6,687	7,377	7,602
25.4 °C	6,948	7,666	7,899
28.4 °C	7,209	7,954	8,197

B. Based on Q_{10} values from McCulley (1998)

25.4 °C	8,083	9,938	10,465
28.4 °C	9,480	12,499	13,328

[1]YBP = years before present   [2]YAP = years after present

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