

Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: Reconstructing the past and predicting the future¹

Steve ARCHER, Department of Rangeland Ecology & Management, Texas A&M University, College Station, Texas 77843-2126, U.S.A., e-mail: sarcher@zeus.tamu.edu

Abstract: Although trends toward increased woody plant abundance in grasslands and savannas in recent history have been reported worldwide, our understanding of the processes involved is limited. Here I review and integrate a series of studies which quantify the rates, dynamics, spatial patterns and successional processes involved in tree patch and woody plant community development at a savanna parkland site in southern Texas, U.S.A. Stable carbon isotope ratios of soil organic carbon indicate C₃ woody plants currently occupy sites once dominated by C₄ grasses. Historical aerial photographs (1941-1990), tree ring analysis and plant growth models all indicate this displacement has occurred over the past 100 to 200 years. Succession from grass- to woody plant-domination occurs when the N₂-fixing arborescent, honey mesquite (*Prosopis glandulosa* (Torr.) var. *glandulosa*), invades and establishes in herbaceous patches. Over time, this plant modifies soils and microclimate to facilitate the ingress and establishment of additional woody species. The result is a landscape comprised of shrub clusters of varying ages organized around a *Prosopis* nucleus. As new clusters form and existing clusters enlarge, coalescence occurs. This process appears to be in progress on upland portions of the landscape and has progressed to completion on lowlands. Rates of cluster development and patterns of distribution appear regulated by subsurface variations in clay content and by variations in annual rainfall. Simulation models based on reconstructions and forward projections indicate succession from grassland to woodland steady states would require 400-500 years, with the most dramatic changes occurring over a 200-year period. The shrubs initially facilitated by *Prosopis* appear to contribute to its demise and prevent its re-establishment. Structure and function of future communities may therefore depend on how remaining woody plants react to changes in microclimate and nitrogen cycling that occur after *Prosopis* is gone.

Keywords: boundaries, competition, facilitation, *Prosopis glandulosa*, soil δ¹³C, succession.

Résumé: Bien qu'on rapporte partout dans le monde une tendance vers un accroissement, au cours de l'histoire récente, de l'abondance des plantes ligneuses dans les prairies et les savannes, notre compréhension des processus en cause est plutôt limitée. Nous passons ici en revue et tentons d'intégrer une série d'études quantifiant les taux ainsi que la dynamique des patrons spatiaux et des processus successionnels en cours dans le développement de communautés d'îlots arborescents et de plantes ligneuses, dans un site de la savanne arborée du sud du Texas, aux États-Unis. Le rapport des isotopes stables de carbone dans le carbone organique des sols indique que des plantes ligneuses C₃ occupent actuellement des sites jadis dominés par des graminées C₄. Les photographies aériennes anciennes (1941-1990), l'analyse dendrochronologique ainsi que les modèles de croissance des plantes indiquent que cette substitution est survenue dans les 100 à 200 dernières années. Ce changement de dominance depuis les graminées vers les plantes ligneuses est survenue au moment où *Prosopis glandulosa* (Torr.) var. *glandulosa*, un arbre fixateur de N₂, a envahi le site et s'est établi dans les plaques herbacées. Avec le temps, cette plante contribue à modifier le sol et le microclimat, ce qui favorise l'arrivée et l'établissement d'autres espèces ligneuses. La résultante de ce processus est un paysage comprenant de petits groupes d'arbustes d'âges variables s'organisant autour d'un noyau de *Prosopis*. La coalescence survient au fur et à mesure qu'apparaissent de nouveaux regroupements et que s'agrandissent les noyaux existants. Ce processus est en progression dans les hautes terres et est en voie d'achèvement dans les basses terres. Le taux de développement des groupes et leurs patrons de répartition semblent réglés par les variations dans la teneur en argile des sols et les variations dans la précipitation annuelle. Des modèles de simulation reposant sur des reconstitutions et des projections indiquent que la succession depuis la prairie jusqu'à un état d'équilibre des forêts exigerait de 400 à 500 ans, les changements les plus draconiens survenant sur une période de 200 ans. Les arbustes dont l'établissement initial a été favorisé par *Prosopis* semblent contribuer à sa mort et ils empêchent son rétablissement sur le site. La structure et le fonctionnement des communautés subséquentes dépendraient par conséquent de la façon dont les plantes ligneuses subsistantes vont réagir aux changements dans le microclimat et le recyclage de l'azote après la disparition de *Prosopis*.

Mots-clés: frontières, compétition, facilitation, *Prosopis glandulosa*, δ¹³C édaphique, succession.

Introduction

In savannas, trees produce discontinuities in an otherwise continuous layer of graminoids. These discontinuities represent patches where both the local microclimate and the availability of resources have been altered in concentric zones surrounding the woody vegetation (Belsky & Canham, 1994). Characteristics of these patches have been widely studied, but little is known of their dynamics and

how patch properties change as woody plants establish, develop and die. Patch and community dynamics in savannas are the combined result of external forces such as climate, interacting with internal processes such as competition and chance events (Walker, 1987b). Edaphic properties, seasonality and amount of rainfall, and the frequency and magnitude of disturbances such as grazing, browsing and fire interact to influence the distribution and relative proportion of grasses and woody plants (Walter, 1979;

¹Rec. 1994-01-03; acc. 1994-11-01.

over time frames relevant to ecosystem management. Shifts from grass- to woody plant-domination inevitably alter biogeochemical cycles (Schlesinger *et al.*, 1990), biodiversity and wildlife habitat. In addition, the replacement of grasses by unpalatable woody perennials has important socioeconomic implications for sustainability of pastoral or subsistence grazing (Rappole, Russel & Fulbright, 1986; Young & Solbrig, 1993).

The Rio Grande Plains of southern Texas, U.S.A. and northern Mexico appears to be one region where shifts from grass to woody plant domination have occurred in recent history. The potential natural vegetation of this area has been classified as *Prosopis-Acacia-Andropogon-Setaria* savanna (Kuchler, 1964). However, the present-day vegetation is dominated by a subtropical thorn woodland complex consisting of dense thickets of shrubs and small trees (McMahan, Frye & Brown, 1984; McLendon, 1991). Historical accounts indicate the conversion from grassland and open savanna to woodland began in the mid- to late 1800s (Johnston, 1963; Inglis, 1964). However, historical accounts of vegetation structure are conflicting (Malin, 1953) and can be misleading (Forman & Russell, 1983). In this paper, I review a series of studies which have asked the following questions: Have thorn woodlands replaced grasslands and savannas? If so, what successional processes were involved? What were the rates and dynamics of change? Could it have occurred within the 150-year time span suggested by historical accounts? Results presented to address these questions are from a case study conducted in southern Texas in collaboration with numerous students and colleagues.

Study site

Tree-grass dynamics have been a primary research focus at the Texas A&M University La Copita Research Area, 80 km west of Corpus Christi in Jim Wells County, Texas U.S.A. (27° 40' N, 98° 12' W). Prior to its designation as a research area, the site was a working cattle ranch with a history of moderate to heavy, continuous grazing since the mid-1800s. The climate is subtropical, with warm, moist winters and hot, dry summers. Mean annual temperature is 22.4°C. Daily maxima in July and August commonly exceed 38°C. Mean annual rainfall (715 mm) is bimodally distributed with maxima in late spring (May-June) and early autumn (September). Elevation ranges from 75 to 90 m above sea level. In a floristic survey, Coffey (1986) collected a total of 334 vascular plant species at the site. Poaceae was the dominant family (73 species), followed by Compositae and Leguminosae. The La Copita is habitat for 207 non-grass herbaceous species, 39 species of trees and shrubs, and 10 suffrutescent herb species. See Norwine (1978), Scifres & Koerth (1987), and Loomis (1989) for more complete descriptions of climate, plant communities and soils of the site.

Savanna parkland and thorn woodland characterize the local physiognomy. An aerial view reveals a polygonized, reticulate landscape pattern in vegetation and soils (Figure 1). Sandy loam soils of uplands are characterized by a two-phase vegetation pattern consisting of clusters of woody vegetation (discrete phase) embedded within a

matrix of C₄ grasses and herbaceous dicots (continuous phase) (Whittaker, Gilbert & Connell, 1979). Uplands give way (1-3% slope) to linear bands of continuous-canopy woodlands in low-lying, intermittent drainages with clay loam soils. Laguna or playa depressional landforms with vertic clay loams also occur within the drainages. This patterning is apparently the result of preferential dissolution of an underlying petrocalcic formation along fractures caused by deep-seated geological stresses (Barton, 1933). Honey mesquite (*Prosopis glandulosa* [Torr.] var. *glandulosa*) dominates the overstory in discrete clusters and woodlands. Understory shrubs common to both uplands and lowlands include *Zanthoxylum fagara* (L.) and *Diospyros texana* (Scheele.), broad-leaved evergreens; deciduous *Celtis pallida* (Torr.) and *Condalia hookeri* (M.C. Johnston); *Ziziphus obtusifolia* (T. & G.), stem photosynthetic and drought deciduous; and *Berberis trifoliolata* (Moric.), a sclerophyllous evergreen (plant nomenclature follows Correll & Johnston [1979]).

Methodological overview

Research to date has focused primarily on the sandy loam uplands which comprise about 80% of the land area. Our initial investigations sought to quantify the spatial and temporal development of shrub clusters and changes in overstory-understory relationships (Archer *et al.*, 1988; Scanlan, 1988; Loomis, 1989). Spatial changes were quantified by collecting data along transects extending from herbaceous zones to the center of woody clusters. Temporal changes are inferred from comparisons of clusters with different floristic composition, plant sizes and soil properties. Long-term assessments of vegetation dynamics have been derived from ¹³C/¹²C ratios in soil organic carbon (Tieszen & Archer, 1990; Boutton *et al.*, 1993; 1994), tree ring analysis and ¹⁴C analysis of woody tissue. An historical sequence of aerial photographs was used to determine changes in cluster size, total woody canopy cover, and the movement of woodland boundaries over the past 50 years (Archer *et al.*, 1988; Archer, 1989). Field experiments on woody plant dispersal, seedling establishment and plant growth have been conducted (Brown 1987; Brown & Archer, 1987; Huebner, 1991; El Youssoufi, 1992). Results from these efforts have been used to develop simulation models to assess rates and dynamics of vegetation change (Archer, 1989; Scanlan & Archer, 1991; Hsieh, 1993). Specific details of methods of data collection and analysis can be found in the studies referenced.

Successional processes

SHRUB CLUSTER FORMATION

Quantitative field inventories indicate that woody clusters on uplands represent age-states organized around a *Prosopis glandulosa* nucleus (Archer *et al.*, 1988). Their data indicate:

- Cluster development begins when *Prosopis*, a leguminous arborescent, invades and establishes in herbaceous zones.
- As the *Prosopis* plants grow and develop, they serve as recruitment foci, facilitating the ingress and establishment of subordinate woody species from other habitats (Figure 2).

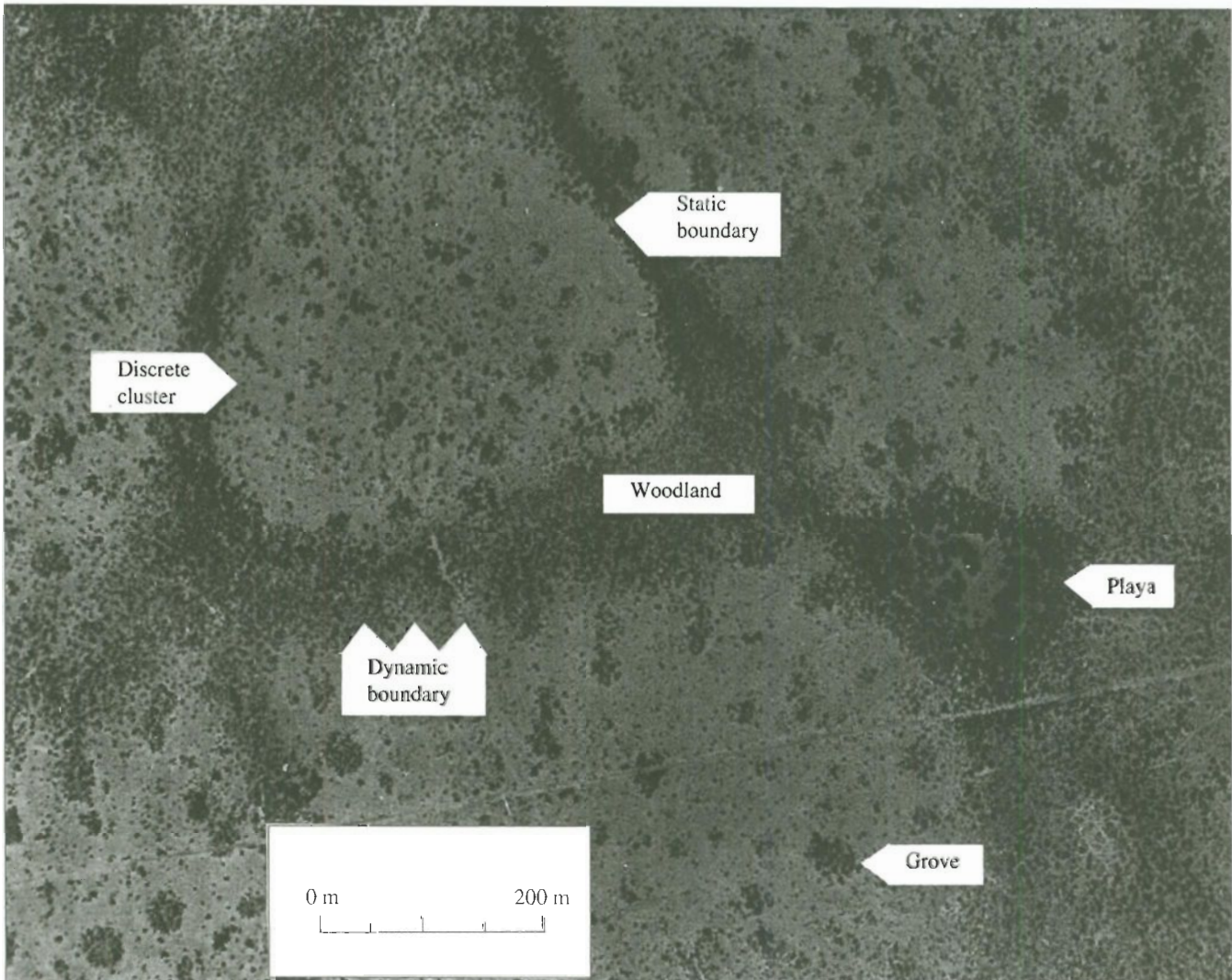


FIGURE 1. Aerial photograph of the La Copita Research Area in southern Texas, U.S.A. Convex sandy loam uplands are characterized by a two-phase pattern consisting of discrete clusters and groves of woody vegetation embedded within a grassy matrix. These grade (1–3% slope) into clay loam, intermittent drainages dominated by closed-canopy woodlands and depressional lakebeds or playas. Research to date has focused on cluster formation in uplands and on upland–lowland vegetation boundaries.

- There is typically only one *Prosopis* plant per cluster and it is the largest plant in terms of height, basal diameter and canopy area.
- Cluster size and the number of subordinate species are positively correlated with *Prosopis* size. At advanced stages of development, clusters organized around the *Prosopis* nucleus may be 5 to 7 m in diameter and contain 10–15 understory species.
- Species composition, dominance and size-class structure of mature clusters is much like that of closed-canopy woodlands in neighboring ephemeral drainages.
- 50% of the clusters on the landscape are within 5 m of another and 95% are within 15 m of another. Analysis of the size class distribution of clusters suggests most have yet to reach their growth potential. Coalescence will become increasingly probable as new clusters form and existing clusters enlarge. This phenomenon appears to be in progress on upland portions of the landscape, and appears to have reached completion to form closed-canopy woodlands on

the moister drainage sites.

There seems to be a general recruitment hierarchy in clusters. *Opuntia lindheimeri* and *Zanthoxylum fagara* are among the first to appear in association with *Prosopis*. Species such as *Ziziphus obtusifolia* and *Berberis trifoliolata* are consistently present only in large, well-developed clusters. It also appears that while woody species are added to clusters over time, few are lost. Adult understory shrubs are well-represented in the seedling/sapling size class, suggesting that they will persist into the future. Shrub species distributions appear to be random within clusters (Scanlan, 1988). One exception is the cactus, *Opuntia lindheimeri*, one of the first species to appear beneath *Prosopis*. This plant is present at all stages of cluster development, but occurs only at the cluster perimeter. Declining light levels associated with understory shrub canopy development appear to cause differential recruitment and mortality among ramets of this clonal succulent. Cladophylls to the shaded interior side of the cluster perimeter die and are not

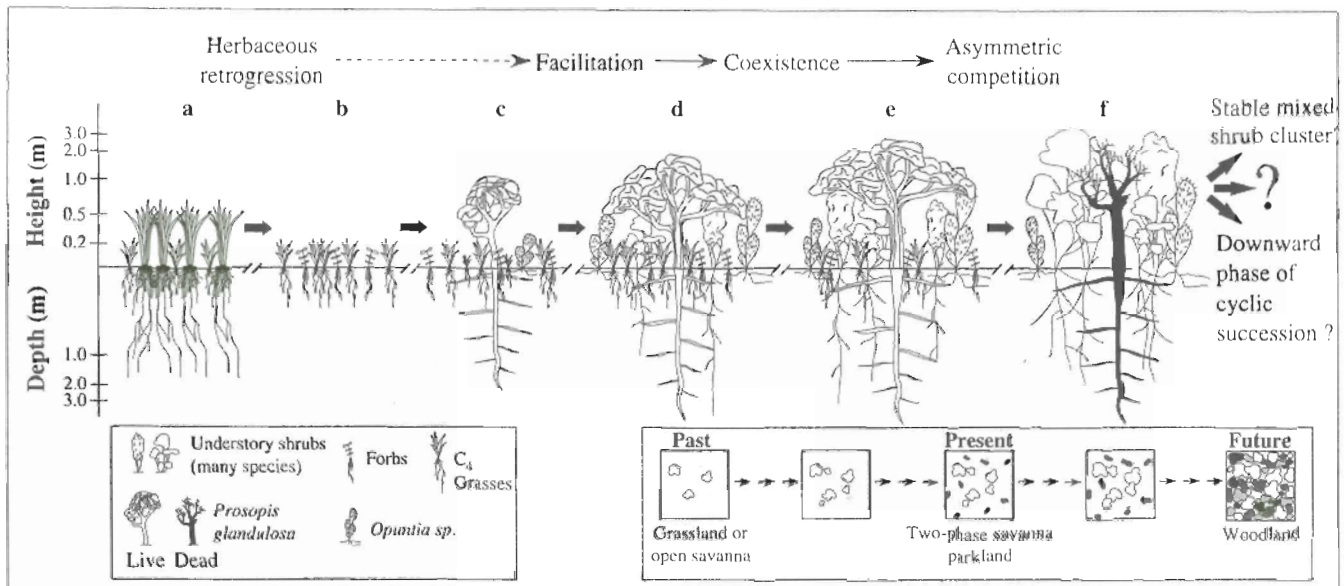


FIGURE 2. Hypothesized transition states in grassland retrogression, cluster development and landscape succession at patch (a-f) and landscape (insert) scales. See text for elaboration. Note log scale for height and depth.

replaced, while vegetative recruitment and growth continues on the outward, sunlit edge of the clone. We are not yet sure of the role this *Opuntia* plays in cluster development. It may serve as a secondary nurse plant, enhancing shrub recruitment near its spiny cladophylls by protecting seeds and seedlings from granivores and herbivores.

PROSOPIS ESTABLISHMENT

Prosopis has numerous adaptations which make it an aggressive invader of grassland not easily eliminated once established. *Prosopis* seeds are potentially long-lived in the soil (Tschirley & Martin, 1960). Germination and establishment can occur on a wide range of soil types having a variety of physical and chemical properties (Ueckert, Smith & Allen, 1979) and moisture regimes (Scifres & Brock, 1969). *Prosopis* is also capable of N_2 -fixation (see next section), a factor which may further contribute to its ability to establish in grasslands. Seedlings are capable of vegetative regeneration within a week of germination (Scifres & Hahn, 1971) and two-week old seedlings can tolerate repeated shoot removal (Weltzin, 1990). Survival of 2- and 3-year-old seedlings can exceed 80% following very hot fires (Wright, Bunting & Neuenschwander, 1976). Our experiments further suggest that livestock are much more effective agents of *Prosopis* seed dispersal than native fauna (Brown & Archer, 1987). Dispersal of *Prosopis* into grasslands would thus have increased dramatically following introduction of cattle, sheep, and horses into North America. *Prosopis* seedlings quickly develop a deep tap root which enables them to effectively access soil moisture at depths not effectively used by grasses (Brown & Archer, 1990). As a result of this resource partitioning, *Prosopis* seedling establishment in grasslands may be high, even in lightly grazed systems dominated by long-lived perennials with good ground cover and high levels of above and belowground standing crop (Brown & Archer, 1989; Goerner, 1993). These seedling establishment trials, conducted on sites where mean annual precipitation ranges from 680 to 950 mm, occurred in years of normal to slightly

below-normal monthly and annual rainfall, suggesting that *Prosopis* recruitment is not episodic with respect to climatic variables. This interpretation is also borne out in age class distribution data from the La Copita site (Archer, 1989). Results from these studies suggest recruitment of *Prosopis* from seed dispersed into grasslands may be primarily limited by abiotic factors associated with rainfall, soil texture and fire. Interference from grasses may be of secondary importance.

FACILITATION: ACTIVE OR PASSIVE?

Once established in the herbaceous zone, *Prosopis* plants initiate a chain of events that may ultimately drive succession from grassland to woodland (Figure 2). Seeds of woody plants which appear in association with *Prosopis* are typically produced in succulent, fleshy fruits. As such, they are dispersed primarily by birds. *Prosopis* may thus play a passive role in cluster development by providing a perching structure attractive to avifauna consuming seeds of woody plants in other habitats. This hypothesis was tested by constructing artificial perching structures in grasslands at a distance of up to 120 m from existing woody vegetation (Huebottler, 1991). Avian seed rain was compared among paired seed traps with and without elevated perching structures for 1.5 years. A total of 2 300 seeds from 10 woody species were recovered from traps associated with vertical structures, whereas none were recovered from traps lacking an elevated perch. The general absence of seedlings of woody species other than *Prosopis* from the herbaceous zones of this site may thus reflect dispersal rather than establishment constraints.

Potential for recruitment at perching sites may be further enhanced if birds preferentially utilize fruits whose seeds have higher viability than average (Johnson & Adkisson, 1985; Nilsson, 1985) and if seed germinability is enhanced by bird handling (Smith, 1975). The importance of perch availability has a demonstrated influence on rates of fence line, power line, old field and mine land succession (McDonnell & Stiles, 1983; McClanahan & Wolfe, 1987),

and succession in Chilean matorral (Fuentes *et al.*, 1984) and disturbed rain forest (Guevara, Purata & Van Der Maarel, 1986).

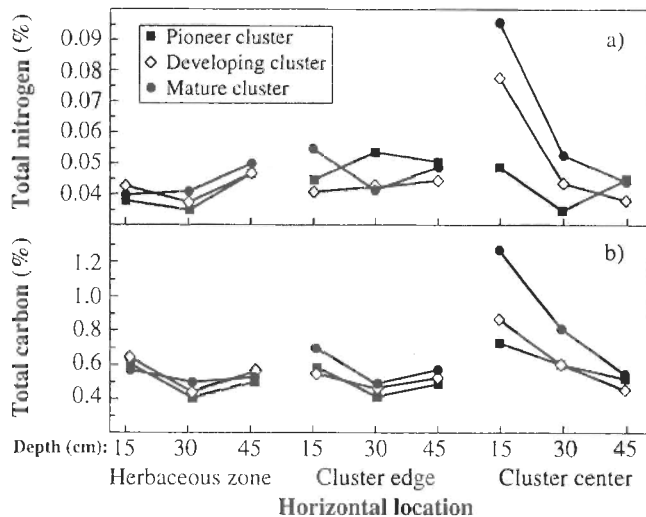


FIGURE 3. Changes in soil nitrogen (a) and soil carbon (b) along spatial gradients (herbaceous zone to cluster centers) and temporal gradients (time of occupation of site by woody vegetation) (Loomis & Archer, unpublished). Distinctions between pioneer, developing and mature clusters based on data from Archer *et al.* (1988) and reflect increases in *Prosopis* size (basal area, height and canopy diameter) and cluster size and woody species richness.

In addition to passively facilitating the ingress of woody plants, *Prosopis* may play an active role in facilitation by altering soils and microclimate in ways that increase the probability of germination and establishment of seeds of other woody species accumulating beneath its canopy. As clusters develop, surficial soil nutrient levels increase (Figure 3) and light levels and high temperature extremes decrease (Figure 4). The abiotic environment thus changes from a high light-low nutrient environment to a low light-high nutrient environment. Theoretical studies (Tilman, 1982) show that such changes in resource ratios can play a role in the species or growth form appearance sequence.

Prosopis is capable of symbiotic N_2 -fixation (Johnson & Mayeux, 1990). However, the extent to which this potential is realized under field conditions may depend upon a variety of factors. At the La Copita study site, *Prosopis* seedlings nodulate readily and reduce ethylene when inoculated with soils collected beneath and away from adult *Prosopis* plants to depths of 60 cm (Zitzer, Boutton & Archer, 1991). ^{15}N mass balance calculations further indicate that *Prosopis* obtains 30–50% of its N from fixation at this site (Boutton *et al.*, 1992). Nitrogen inputs via leaf litterfall are estimated at 8 to 11 kg N/ha. Foliar litter deposition, combined with inputs via stemflow, throughfall and root turnover (Angerer, 1991), have likely contributed to the enrichment of surficial soil N pools with time of site occupation (Figure 3). In addition, peak rates of seasonal N mineralization ($\mu\text{g N/g soil/d}$) are an order of magnitude higher in developed clusters (1.3) than in herbaceous zones (0.2); annual N_{min} in clusters is about 5X that of herbaceous zones (200 versus 42 $\mu\text{g N/g soil}$) (Hibbard *et al.*, 1993). Increases in nutrient concentrations and turnover rates following *Prosopis* establishment presumably benefit both

seedling and adult understory shrubs, many of which are shallow-rooted (Watts, 1993). Controlled environment growth of seedlings emerging on surficial soils collected from beneath clusters is superior to that of plants grown on soils collected from herbaceous zones (Scanlan, 1988; El Youssoufi, 1992), confirming the potential benefits of nutrient enrichment.

Changes in microclimate may interact with changes in soil chemistry to further enhance establishment of plants beneath *Prosopis*. Reductions in growing season peak surface soil temperatures (Figure 4a, d) coupled with the concentration of precipitation and nutrients input via stemflow (Angerer, 1991) could create microclimatic conditions more conducive to seedling establishment than those away from the *Prosopis* canopy. *Prosopis* plants on site are deeply rooted (Watts, 1993) and utilize moisture from deep in the soil (Brown & Archer, 1990; Midwood *et al.*, 1993). The possibility for 'hydraulic lift' or the transport and re-deposition of deep soil moisture to surficial layers (Caldwell, Richards & Beyschlag, 1991) thus exists. Understory shrubs, most of which are shallow-rooted (Watts, 1993), would be further benefitted if this were the case.

HERBACEOUS RETROGRESSION

Changes in herbaceous composition and production accompany shrub cluster development. Generally, as clusters develop, there is a loss of herbaceous species diversity (Figure 5a) and a replacement of C_4 grasses with C_3 forbs. The response of herbaceous species to developing woody vegetation ranges from an immediate displacement (Figure 6a,b) to initial increase in frequency of occurrence followed by subsequent elimination (Figure 6c). In contrast, some grass (*Setaria texensis*) and forb (*Eupatorium* spp.) species absent from herbaceous zones appear soon after *Prosopis* occupation and increase in frequency of occurrence as clusters develop (Figure 6d). The net result of modification of soils and micro-climate by *Prosopis* is a slight, initial stimulation of standing crop biomass in the herb layer (Figure 5b). However, as subordinate shrubs establish and grow beneath *Prosopis*, herbaceous production declines markedly. Ground cover in clusters at advanced stages of development is only about 20% (Figure 5c). The loss of herbaceous vegetation associated with cluster development is likely the combined result of decreasing light levels (Figure 4b, c, e) and an increasing density and biomass of wood plant roots in upper 40 cm of the soil horizon (Watts, 1993).

FACILITATION - COEXISTENCE - ASYMMETRIC COMPETITION

Species interactions in clusters appear to be strongly asymmetric and to change with time (Figure 2). The facilitation of other woody species by *Prosopis* has an overall and dramatic negative impact on herbaceous vegetation (Figure 5). There is typically one *Prosopis* plant in a cluster, and no seedlings or saplings (Archer *et al.*, 1988). Lack of *Prosopis* seedling recruitment in clusters appears to reflect a combination of (a) low levels of seed production; (b) high rates of seed and seedling predation; and (c) low light intensities at the soil surface (El Youssoufi, 1992). Field experiments suggest that even when limitations imposed by seed availability, predation and moisture are overcome, low light

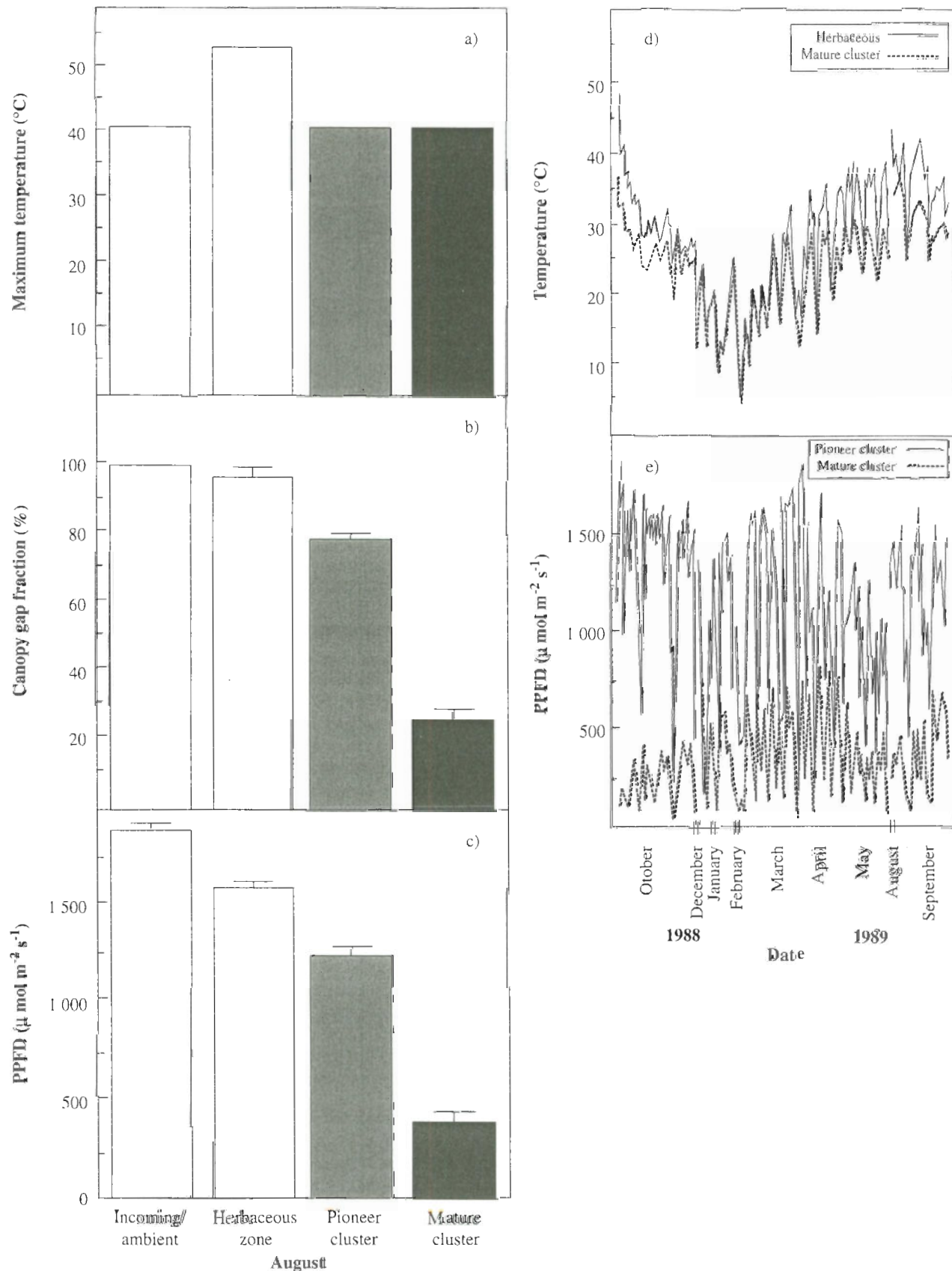


FIGURE 4. Mean maximum temperature (a), canopy gap fraction (b) and photosynthetic photon flux density (PPFD) (c) for herbaceous zones and cluster age-states on a day in August. Panels d and e illustrate differences in daily mean temperatures and PPFD at solar noon recorded continuously over a two-year period. Canopy gap fraction (b) and PPFD (c) measured at solar noon on a clear day with an integrating line quantum sensor (Decagon Devices, Inc., Pullman, Washington). Canopy gap fraction represents the proportion of the bar receiving $> 300 \mu\text{mol m}^{-2} \text{s}^{-1}$.

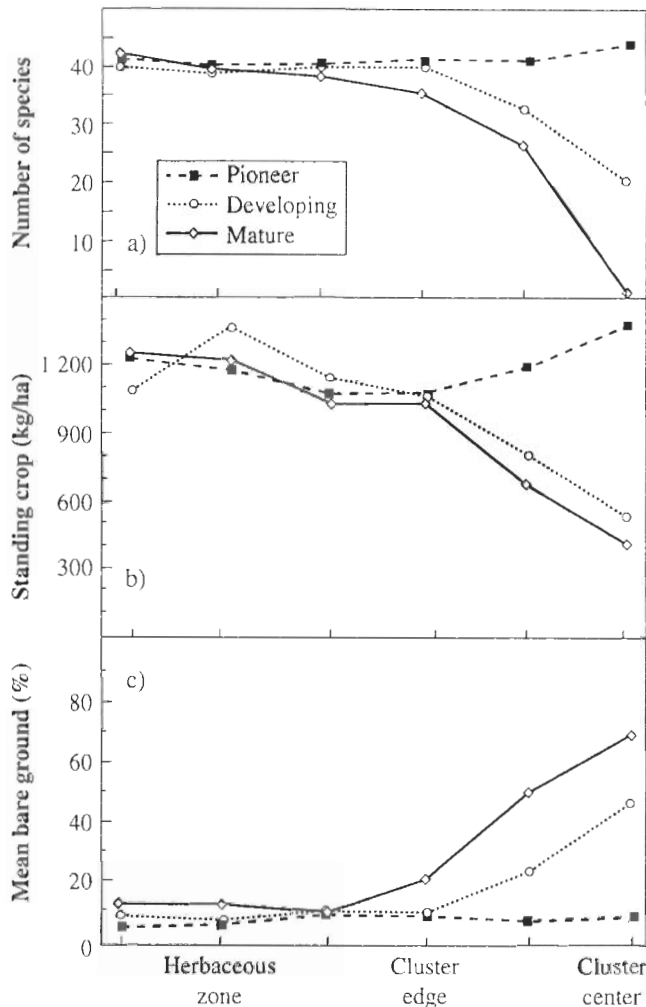


FIGURE 5. Changes in herbaceous species richness, standing crop and bare ground associated with various stages of woody cluster development (from Scanlan, 1988). See Figure 3 legend for elaboration.

levels in clusters (Figure 4b, c, e) will prevent seedling establishment. Woody plants facilitated by *Prosopis* thus prevent its regeneration subsequent to their establishment.

Prosopis and subordinate shrubs appear to partition resource use, both spatially and temporally as clusters go through a phase of species co-existence (Figure 2d, e). Root systems of understory shrubs are shallow and dense (60–100% of biomass in upper 40 cm of soil) relative to those of *Prosopis* (60–90% of root biomass below 40 cm) (Watts, 1993). Accordingly, *Prosopis* plants appear to be relatively uncoupled from surficial moisture conditions, whereas photosynthesis, water relations, and growth of *Zanthoxylum fagara*, a dominant evergreen understory shrub, is closely linked to seasonal patterns of soil moisture in the upper profiles (Figure 7) (see also Brown & Archer, 1990; Angerer, 1991; Midwood *et al.*, 1993). In addition, several of the understory shrub species are deciduous. These plants presumably carry on significant growth during warm, moist periods when leaf area of wintergreen *Prosopis* plants is minimal (ca November–March).

As understory shrubs increase in size and density, we see little evidence of facilitation by *Prosopis*. Shoot growth, photosynthesis and xylem water potential among mature

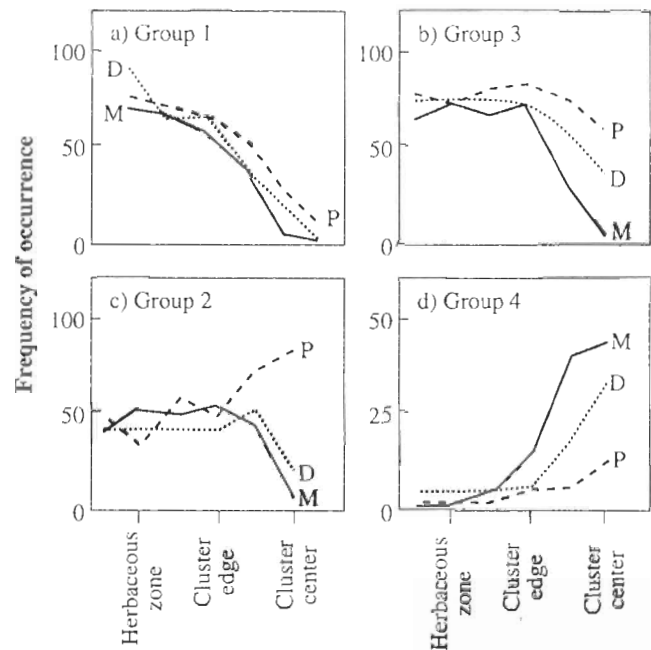


FIGURE 6. Functional classification of herbaceous species in sandy loam uplands based on their response to woody cluster development (P = pioneer cluster; D = developing; M = mature). The number of species per group ranged from one (1) (Group 1) to five (5) (Group 2) (see Scanlan, 1988 for species composition). Rare species (< 1% cover; < 2% frequency) excluded from analysis.

understory shrubs in well-developed clusters with and without a *Prosopis* overstory are seasonally comparable (Barnes & Archer, 1994). In contrast, radial trunk growth (Miller, Archer & Zitzer, 1994) and seed production (El Yousoufi, 1992) of *Prosopis* is reduced relative to that of *Prosopis* plants where the understory has been removed. Latter stages of cluster dynamics may thus be characterized by strong asymmetric competition (Figure 2e,f). Field surveys indicate *Prosopis* has died in about 25% of the clusters on the landscape (Archer *et al.*, 1988) and that the canopies of many live plants are moribund. Thus, it appears that the understory shrubs initially facilitated by *Prosopis* may contribute to its eventual demise, while at the same time preventing its regeneration. Field observations indicate that several of the understory shrubs in clusters have the genetic growth potential to "overtop" *Prosopis*. However, many of these species are near their northern distributional limit and infrequent episodes of freezing temperatures cause canopy mortality (Londard & Judd, 1985) and prevent this from happening. Farther south, this may not be the case and cluster dynamics may be quite different.

EDAPHIC INFLUENCE ON SUCCESSION

Woody plant modification of surficial soils beneath their canopy (Figure 3) is well-documented for a variety of systems (West, 1989; Belsky *et al.*, 1989; Weltzin & Coughenour 1990; Schlesinger *et al.*, 1990; Vetaas, 1992; Mordelet, Abbadie & Menaut, 1993). Reciprocal effects also occur, whereby soil texture or geomorphic properties determine the distribution, size and density of woody plants (Morison, Hoyle & Hope-Simpson, 1948; Walter, 1979; Johnson & Tothill, 1985; San Jose & Farinas, 1983; Knoop & Walker, 1985). We initially hypothesized that groves

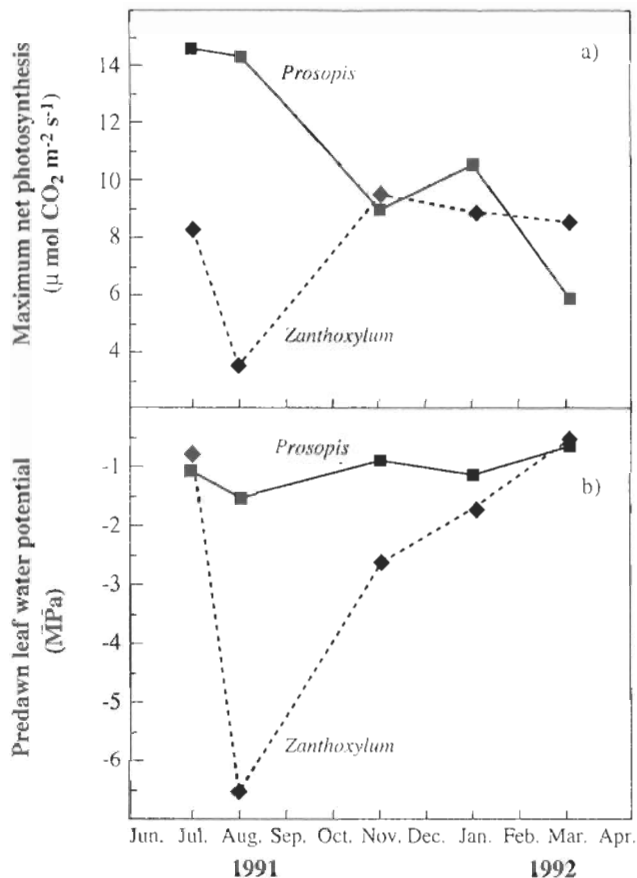


FIGURE 7. Seasonal values for maximum daily net photosynthesis (a) and predawn leaf water potential (b) in *Prosopis glandulosa* (overstory) and *Zanthoxylum fagara* (dominant understory shrub)(from Barnes & Archer, 1995).

(Figure 1) represented areas where discrete clusters had coalesced. However, subsequent horizon descriptions revealed that soils associated with groves lacked an argillic (B₁) horizon (zone of clay accumulation at about 40–100 cm depth) and were coarse-textured throughout the profile (Loomis, 1989). By contrast, the argillic horizon was well-developed and strongly expressed in upland soils supporting herbaceous vegetation and discrete clusters (Figure 8c).

The *Prosopis* plants on the non-argillic inclusions were larger than their counterparts growing on argillic soils in well-developed, but solitary clusters (Table II). This reflected the fact that *Prosopis* plants in groves were, on average, older and growing faster than *Prosopis* plants in discrete clusters. In addition, woody plants on non-argillic inclusions supported nearly 3X the above-ground biomass with only slightly (ca 30%) more below-ground biomass. The superior performance of woody plants on the non-argillic inclusions is consistent with observations in other savanna systems which indicate that their growth and development is favored on coarse-textured soils (Walter, 1979; Knoop & Walker, 1985). These coarse-textured inclusions may also capture and concentrate sub-surface water and nutrients moving along the top of the claypan horizon, further enhancing woody plant growth and production.

TABLE II. Mean (\pm S.D.) size, age and biomass of *Prosopis glandulosa* plants on upland landscapes in southern Texas

Parameter	Clusters	Discrete groves
Canopy diameter (m)	6.5 (1.1)	7.2 (2.2)
Basal diameter (cm)	15.7 (2.4)	24.1 (6.2)
Height (m)	3.7 (0.6)	5.8 (0.7)
Radial trunk growth ^a (mm/month)	0.04 (.03)	0.10 (.07)
Trunk age ^b		
Mean	49 (12)	75 (6)
Max	64	81
Biomass (kg/m ²) ^c		
Belowground biomass ^d	0.7 (0.2)	0.9 (0.2)
Aboveground biomass	2.5 (1.9)	7.4 (4.4)
Root/whole plant ratio	0.22	0.11

^a From dendrometer bands over a 2-year period.

^b From annual ring counts (Flinn *et al.*, 1994).

^c From Watts (1993).

^d To depth of 2 meters.

The presence of grove vegetation on coarse-textured soil inclusions raised the following questions: Has the presence of woody vegetation disrupted a once laterally extensive argillic horizon? Or, are the non-argillic inclusions pre-existing conditions of the landscape being differentially exploited by woody plants? Initially, we hypothesized that rodents and leaf-cutter ants (*Atta texensis*) attracted to woody clusters have disrupted and obliterated a once continuous argillic horizon via their burrowing and excavating activities. Field observations along the faces of trenches excavated through some groves did reveal extensive evidence of belowground faunal activity. For example, numerous leaf cutter ant cavities were encountered. One such cavity occurred at a depth of 2 m and was > 1 m in diameter. If the faunal mixing hypothesis is correct, we reasoned that (a) the degree of expression of the argillic horizon would diminish with cluster development and (b) total amounts of clay, when summed across all horizons, would be similar among grove and non-grove soils. These hypotheses were tested by Loomis (1989) using soil reconstruction techniques, and rejected. His work indicated a low total clay content in grove soil profiles, suggesting that non-argillic inclusions are the result of prehistoric patterns of sediment deposition and pedogenesis. The abundance of leaf-cutting ant chambers and rodent burrows observed in some groves thus appears to reflect a preference of these organisms for a sandy loam subsoil, rather than a cause of its formation. Accordingly, these faunal activities were notable in only 2 of 3 trenches excavated by Loomis (1989) and in neither of the two trenches excavated by Watts (1993).

If non-argillic inclusions are pre-existing conditions on the landscape being differentially exploited by woody vegetation, we reasoned there might be non-argillic inclusions which, by chance, have not yet been occupied by woody vegetation. We have recently prospected for such sites using ground-penetrating radar and electromagnetic induction. To date, three such sites have been located (Stroh & Archer, unpublished). Cluster density, growth and coalescence in uplands may be ultimately constrained by the size, distribution and abundance of these coarse-textured inclusions.

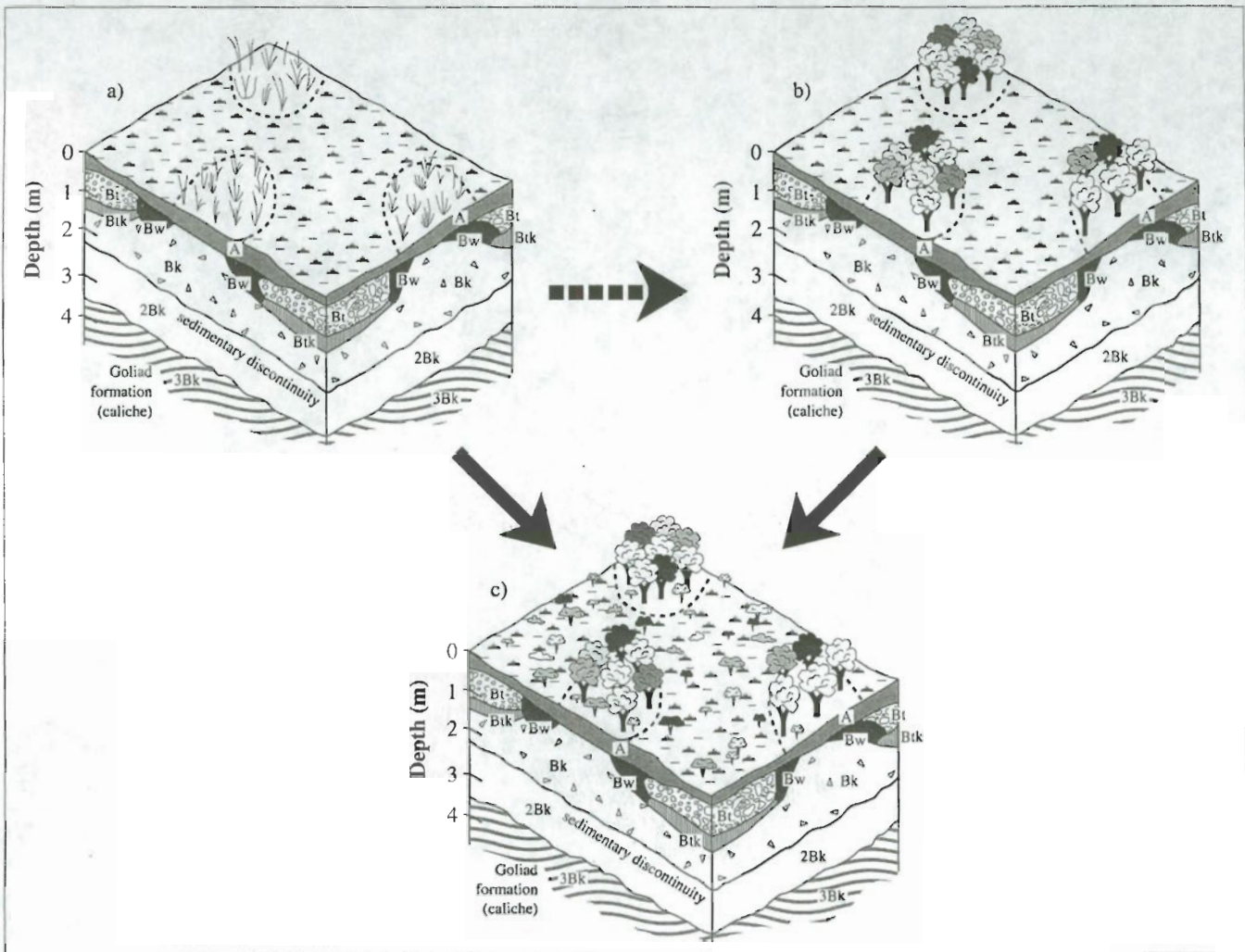


FIGURE 8. Hypothesized patterns of succession from grassland or savanna to woodland on sandy loam uplands. Each panel depicts characteristic horizonation on the site (based on data from Loomis, 1989). (a) Pre-settlement vegetation with short to mid-height grasses dominating where the laterally extensive argillic (B) horizon is present; mid-height and tall grasses dominate non-argillic (B_k) inclusions. (b) Pre-settlement vegetation similar to (a) except groves occur on non-argillic inclusions instead of grasses. (c) Present-day vegetation with groves on non-argillic inclusions and small, discrete clusters dispersed among herbaceous vegetation where argillic horizon is present. Arrows suggest pathways of directional change. Available data suggest a → c is most likely. See text for elaboration.

Reconstructing the past

DIRECT ASSESSMENTS OF VEGETATION CHANGE

The hypothesized sequence of events in succession from grassland or savanna to thorn woodland (Figure 2) are based upon 'space-for-time' studies of vegetation structure. Inferences derived from this static approach can be misleading (Glenn-Lewen & van der Maarel, 1992). However, direct assessments of vegetation change using historical aerial photographs and stable carbon isotopes confirm that woody vegetation now dominates portions of the landscape previously occupied by grasses.

$\delta^{13}\text{C}$ INDICATORS.

Ratios of $^{13}\text{C}/^{12}\text{C}$ (expressed as $\delta^{13}\text{C}$) provide diagnostic signatures which can be used to differentiate organic carbon derived from C₃ and C₄ plants. Woody plants at the La Copita site possess the C₃ photosynthetic pathway ($\delta^{13}\text{C}$ range = -27 to -32‰), whereas vegetation of grass-dominated zones between clusters are characterized by grasses with the

C₄ pathway ($\delta^{13}\text{C}$ range = -13 to -17‰) (Tieszen & Archer, 1990). If woody clusters have been long-term constituents of upland landscapes, the $\delta^{13}\text{C}$ signature of organic carbon in soils beneath them should reflect this and fall in the -27 to -32‰ range. However, if C₃ shrubs have displaced C₄ grasses, then (1) the soil $\delta^{13}\text{C}$ value would be larger (less negative) than -27 to -32‰, (2) the degree of departure from the expected ratio would decrease as time of site habitation by shrubs increases, and (3) soil $\delta^{13}\text{C}$ values would become less negative with depth along the cluster chronosequence.

An analysis of soil organic carbon $\delta^{13}\text{C}$ has confirmed these predictions (Figure 9). Results indicate organic carbon of soils beneath herbaceous zones was primarily C₄ in origin and generally reflected the composition of the current vegetation throughout the profile ($\delta^{13}\text{C}$ = -14 to -18‰). In contrast, the mean $\delta^{13}\text{C}$ value in upper horizon of soils beneath developing and mature clusters was -21 and -23‰, respectively. The decrease in $\delta^{13}\text{C}$ from -18 to -21 and -23‰ appears to reflect the additional input of C₃ carbon

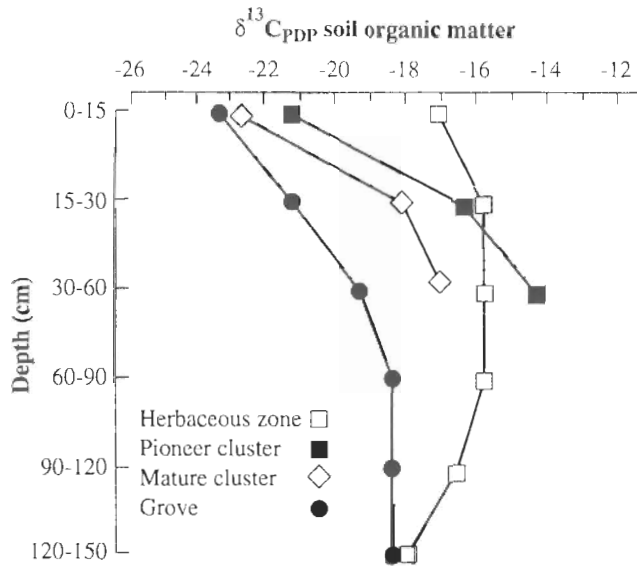


FIGURE 9. Differences in $\delta^{13}\text{C}$ of soil organic matter associated with herbaceous zones, groves and cluster age-states indicate shrub clusters (dominated by C_3 plants) occupy sites once inhabited by C_4 grasses (from Tieszen & Archer [1990] and Boutton & Archer [unpublished]). Lower values at depth for groves versus mature clusters may reflect greater C_3 biomass inputs and higher rates of organic matter turnover in groves relative to clusters.

associated with the passage of time required for *Prosopis* plants and clusters to develop. Among upland soils supporting woody vegetation, the contribution of C_3 -derived carbon decreased with depth to 60 cm, converging on the values observed for the herbaceous zones. The lowland areas dominated by closed-canopy woodlands (Figure 1) also have a much stronger C_4 isotopic signature than would be expected from the present vegetation (Boutton, Archer & Midwood, 1994). Thus, even these areas appear to have been more open and savanna-like than at present.

HISTORICAL PHOTOGRAPHY

Aerial photographs dating back to 1941 have been used to document changes in woody plant and grass distribution on the La Copita site. Total woody plant cover has increased from a mean ($n = 3$ sites) of 13% in 1941 to 36% in 1983. These changes were distinctly non-linear. Total woody cover decreased slightly during the 1941–1960 period, apparently the result of a major drought in the 1950s. During the subsequent 1960–1983 period of generally normal to above-normal annual rainfall, woody cover increased 3 to 8 fold. Increases in total woody plant cover were the combined result of cluster enlargement in uplands and upslope migration of closed-canopy woodlands. The areal extent of woodlands decreased an average of 6% during the 1941–60 period, the result of fragmentation along upland margins. By 1990, however, clusters on the two-phase portion of the landscape had expanded and coalesced along these margins, generating a 38% increase in the mean area of closed-canopy woodland relative to 1941. Some woodland margins have remained static over the past 50 years, whereas others have been quite dynamic (Figure 10). The hypothesis that static boundaries represent inherent edges associated with edaphic or geomorphic properties remains to be investigated.

RATES AND DYNAMICS OF VEGETATION CHANGE

GROWTH RATE ANALYSIS

Growth rates of individual clusters were determined from historical aerial photography. The photography encompassed a period of drought (1941–1960) and a period of normal to above-normal annual rainfall (1960–1983). We found that small clusters grew faster than large clusters and that cluster expansion in wet periods exceeded that which occurred during dry periods (Archer *et al.*, 1988). Estimates of cluster growth rates were then used to model size and age relationships for *Prosopis* plants and clusters across a range of annual rainfall scenarios. Size-class distribution of *Prosopis* plants and clusters determined in field surveys were then converted to age-class distributions using modelled size-age relationships (Archer, 1989). Results indicated that for annual rainfall regimes bracketing those likely to have occurred over the past 100 years, the age-class distribution of *Prosopis* plants and clusters on the site was that of a young population (mostly < 90 years of age) expanding geometrically. Model results indicate understory shrubs begin to appear 10–15 years after *Prosopis* colonization of the herbaceous zone. By the time *Prosopis* plants are 50–60 years of age they may have 10–15 associated woody species.

TRANSITION PROBABILITY ANALYSIS

The probability of transition between herbaceous zones, cluster age-states and woodlands was calculated on the historical aerial photography described above to generate another perspective on vegetation history. These transitions were used in conjunction with historical annual rainfall records to reconstruct and project landscape states (Scanlan & Archer, 1991). Results suggest that under a rainfall regime likely for this region, the landscape of 200 years BP would have been much more open than the one today (50% versus 15% of area occupied by herbaceous vegetation and pioneer clusters) (Table III).

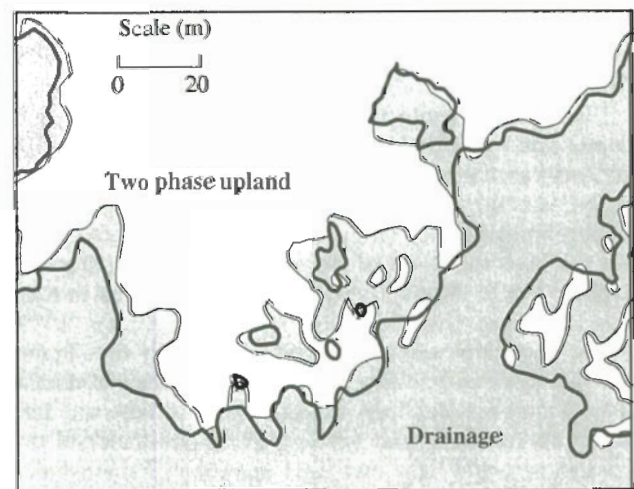


FIGURE 10. Scanned image overlays of a sandy loam upland (in white; small discrete clusters omitted for clarity) and closed-canopy woodlands of a neighboring intermittent drainage at the La Copita site. Location of woodland boundary in 1941 (solid line) and its location in 1990 (stippled area) are shown. Note that in some areas the woodland boundary has been fairly static; in other areas it has moved significantly as discrete clusters and groves in the two-phase zone coalesce into its border.

TABLE III. Changes in savanna vegetation structure predicted by a precipitation-driven transition matrix model (from Scanlan & Archer, 1991)

Vegetation state	Proportion of grid cells on landscape			
	Reverse projection	Observed		Forward projection
		1941	1983	
Woodland	32	49	59	72
Coalesced clusters	12	12	17	12
Mature clusters	06	06	05	01
Pioneer clusters	38	27	17	12
Herbaceous zones	12	06	02	03
Predicted time to steady state (years)	200	-	-	180

MODEL EVALUATION

Historical photographs and $\delta^{13}\text{C}$ values for soil organic carbon indicate that woody vegetation has replaced grassland over much of the La Copita site. Contrasting models, one based on individual plant and cluster growth (Archer, 1989) and the other based on landscape-level transition probabilities (Scanlan & Archer, 1991) both predict that these changes have occurred over the past 100 to 200 years. These model-based reconstructions are consistent with historical observations indicating that prior to the 1800s, landscapes in this region were grasslands and open savannas (Inglis, 1964). In addition, we have recently demonstrated that *Prosopis* produces true annual rings (Flinn *et al.*, 1994). In accordance with model predictions, ring counts on trunks of the largest *Prosopis* plants in discrete clusters and groves indicate ramets are typically < 100 years of age (Table II). ^{14}C dating has indicated that the belowground lignotubers giving rise to these trunks were "modern" (< 200 years old) in 4 of the 5 genets checked (Archer, unpublished). Finally, the timing and rates of woody plant encroachment reconstructed for this system are consistent with the timing and rates of woody plant encroachment documented in other arid and semi-arid grassland and savanna ecosystems around the world (Archer, 1994).

A WORKING HYPOTHESIS OF HISTORICAL LANDSCAPE DEVELOPMENT

Historical records and data collected to date at the La Copita site, with its long history of grazing, suggest the following scenario of landscape change. Prior to settlement, sandy loam uplands were dominated by tall and mid-height C_4 perennial grasses (Figure 2a). *Prosopis* density was low, perhaps the result of dispersal limitations (Brown & Archer, 1987). Alternatively, *Prosopis* densities in these grasslands may have been high (Brown & Archer, 1989), but the population was suppressed by recurring fires ignited by lightning or set by Native Americans. With the introduction of large numbers and high concentrations of domestic livestock (cattle, sheep and horses), *Prosopis* dispersal into grasslands would have increased markedly. Establishment of *Prosopis* seedlings, or the "release" of already established, but suppressed plants, would have been favored by a variety of direct and indirect effects of grazing (see review by Archer, 1994). With continued grazing, tall and mid-height perennial grasses gave way to the shallow-rooted, weakly perennial short-grasses, ephemeral forbs and annuals present today (Figure 2b).

This new herbaceous vegetation may have been even more susceptible to invasion by *Prosopis* and other unpalatable subordinate shrubs, especially if fine fuel loads and continuity were kept low by continuous grazing, thus reducing or eliminating fire. As *Prosopis* plants grew and developed, clusters began to form (Figure 2c-e) and coalesce, the process occurring most rapidly in mesic lowlands and on non-argillic inclusions in uplands. Periodic drought magnified grazing-induced stresses on the herbaceous vegetation and set the stage for pulses of woody plant recruitment during subsequent years of higher rainfall (Archer *et al.*, 1988). This process has led to the formation of groves in uplands and to the formation of much of the continuous canopy woodlands in lowlands (Figure 1). If the processes observed over the past 50 years continue (Figure 10), the two-phase pattern of discrete shrub clusters and groves embedded within a grassy matrix will give way to monophasic woodlands (Table III and Figure 2 insert). Available weather records for this region dating back to 1900 (Norwine, 1978) show cycles of drought and above-normal annual rainfall, but no clear directional climatic changes which might have produced a vegetation change.

Present day landscapes at the La Copita site contain moderate densities of discrete shrub clusters where the argillic horizon is present; groves of larger *Prosopis* trees occur where the argillic horizon is absent (Figure 8c). The postulated historic grasslands or savannas may have been edaphically controlled, with mid- and short-statured grasses dominating the upland, but interspersed with patches of taller, more productive grass species on the non-argillic inclusions (Figure 8a). Alternatively, woody plants may have dominated the coarse-textured soils of the non-argillic inclusions (Figure 8b). This latter physiognomy would be consistent with some historical reports from this region that refer to "mottes" (*i.e.* small patches of woodlands within a prairie land) (Crosswhite, 1980). In either case, woody vegetation would have been competitively excluded under the historic rainfall regimes where the argillic horizon was present. Such a system would have been prone to fire, which may have served as a secondary deterrent to woody plant community development. Three pathways of succession are thus hypothesized in Figure 8: (1) $a \rightarrow c$; (2) $b \rightarrow c$; or (3) $a \rightarrow b \rightarrow c$.

Which of these pathways is most likely? Soil organic carbon in discrete clusters and groves has a significant C_4 component, suggesting past occupation by grasses (Figure 9). Even though *Prosopis* trees growing on the non-argillic soils are much larger than the largest *Prosopis* plants growing on argillic soils in terms of height, canopy area and trunk diameter, they are only about 20 years older (Table II). The differences in size therefore partially reflect the fact that the growth rate of *Prosopis* plants on the coarse-textured inclusions is greater than that of plants on the argillic soils. Together, these data suggest that the $a \rightarrow c$ pathway in Figure 8 to be the most likely. If this were in fact the case, *Prosopis* invasion would have been initiated randomly across the upland portions of the landscape, with recruitment of plants which happened to establish on non-argillic inclusions being slightly favored over that of

plants establishing where the argillic horizon was present. Thus, there is a post-settlement element of $a \rightarrow b \rightarrow c$, but state **b** does not appear to have been part of the pre-settlement configuration.

Predicting the future

Forward simulations using transition probabilities calculated for the periods 1941-1960 and 1960-1983 predict the present landscape will develop into closed-canopy woodland within the next 180 years (Table III). This prediction is based on the following assumptions:

- The processes operating between 1941 and 1983 continue, e.g. livestock grazing and lack of fire;
- The intensity of cluster-to-cluster interactions is minimal. If this is the case, future coalescence will be likely; if not, cluster densities in uplands may stabilize prior to coalescence. Available data suggest these interactions are minimal:
 - Historical aerial photographs indicate clusters have coalesced with each other and into woodland margins (Archer *et al.*, 1988; Figure 10).
 - minimal lateral root extension beyond cluster or grove canopies (Watts, 1993) suggests inter-cluster competition should be minimal.
 - Production and ground cover in herbaceous zones associated with pioneer, developing and mature clusters is comparable (Figure 5b, c). This may not occur if roots of shrubs in clusters were exploiting soils beyond canopies.
- Edaphic constraints to cluster development are minimal. In uplands, the presence/absence of argillic horizon seems to affect primarily plant and cluster growth, not presence or absence. However, the fact that some woodland margins have been highly stable over the past 50 years while others have changed markedly (Figure 10), suggests some areas may remain open;
- Extent of canopy closure does not vary along the 1-3% slope from crown of the upland to bottom of the adjoining drainage. Changes in moisture and soil properties along this potential catena gradient have not yet been quantified. However, increases in total woody cover between 1941 and 1983 attributed to coalescence of distinctly upland clusters was comparable to that contributed by coalescence of clusters into woodland margins (Archer *et al.*, 1988);
- Clusters will persist following death of *Prosopis*. Adult woody plants appear to possess sufficient physiological plasticity to maintain growth and productivity following *Prosopis* mortality. In addition, shrubs in clusters regenerate rapidly following disturbance (Scanlan 1988). To date, we have no evidence to suggest that loss of *Prosopis* initiates a downgrade phase in a cyclic pattern of cluster initiation, growth and mortality.

Summary

The Rio Grande Plains of southern Texas and northern Mexico offer some distinct examples of processes involved in the physiognomic conversion of grasslands and savannas to woodlands. The potential natural vegetation of this region has been classified as *Prosopis-Acacia-*

Andropogon-Setaria savanna (Kuchler, 1964). However, much of the present vegetation is subtropical thorn woodland (McMahan, Frye & Brown, 1984). A component of the Tamaulipan Biotic Province, the large shrubs and small trees in this system have counterparts throughout much of the world's tropical and subtropical zones (Brown, 1982). Lowe and Brown (1982) argue that "the most complex, least known and certainly most misunderstood vegetation and flora in the North American Southwest are the tropic-subtropic deciduous forest and thorn scrub." Often transitional between savanna and moist forest, these vegetation types may result from disturbance to dry forests or woody plant encroachment into savannas. The latter has been the case throughout much of southern Texas, Mexico, Africa, South America and Australia (Table I). Although extensive in their geographic distribution and global acreage, ecological research in these systems is limited relative to that of tropical savannas and tropical forest (Murphy & Lugo, 1986).

Field surveys have identified key processes involved in succession from grassland to woodland at the La Copita site in southern Texas (Figure 2). ^{13}C values of soil organic carbon (Figure 9) corroborate inferences derived from space-for-time surveys and provide direct evidence that C_3 woody plants occupy sites once inhabited by C_4 grasses. Historical aerial photographs (1941-1990) provide a visual record of patterns of cluster initiation, growth and coalescence and woodland expansion (Figure 10). Growth rates of clusters and state-transition probabilities determined from these photographs enabled the parameterization of models of cluster development and landscape change. These contrasting models generated similar predictions of rates of community development and are in accordance with observations from early settlers which described grasslands and open savannas in the early to mid-1800s. Based on elapsed time between predicted past and future steady states, succession from open grassland to closed-canopy woodland may occur in ca 400 to 500 years (Table III). However, the most dramatic changes occurred over much shorter time periods (Scanlan & Archer, 1991).

Changes in livestock grazing and fire regimes appear to have been the driving force behind these historic changes in vegetation; however, the possibility of climatic change and the effects of increases in atmospheric CO_2 over the same period must also be considered (Archer, Schimel & Holland 1995 and references therein). The extent to which future, predicted landscape states are reached may depend upon edaphic constraints (Figure 8) and on the response of woody vegetation to the eventual loss of *Prosopis*. The shifts in life form composition described in this paper may have significant implications for understanding global processes in arid and semi-arid systems (Schlesinger *et al.*, 1990; Walker, 1994). The potential impacts of succession from grassland to woodland on carbon sequestration, nitrogen cycling, non-methane hydrocarbon emissions, and biophysical aspects of land surface-atmosphere linkages are the focus of an ongoing investigations at this site.

Acknowledgements

My thanks to the numerous colleagues, research associates

and graduate students who have participated in and contributed to this research. Their names appear throughout the citations in the text. Thanks also to D. McKown and M. Cadena, for the BBQs, their assistance with on-site logistics and for making field crews welcome on the site. Undergraduate students too numerous to mention assisted with data collection and sample processing; this story could not have been told without their outstanding help. The IUBS/MAB "Responses of Savannas to Stress and Disturbance" program provided a wonderful forum for exchange of ideas and information. Research support has come from grants in the U.S. Department of Agriculture Rangelands Research Program, the National Science Foundation-Ecosystems Program, NASA-EOS, Texas A&M University and the Texas A&M Agricultural Experiment Station. S. Jack, P. Harcombe and A. Black made constructive comments on earlier drafts. This is TAES publication TA-31456.

Literature cited

- Acocks, J. P. H., 1964. Karoo vegetation in relation to the development of deserts. Pages 100-112 in D. H. S. Davis (ed.). *Ecological Studies of Southern Africa*. Dr. Junk Publishers, The Hague.
- Adamoli, J., E. Sennhauser, J. M. Acero & A. Rescia, 1990. Stress and disturbance: Vegetation dynamics in the dry Chaco region of Argentina. *Journal of Biogeography*, 17: 491-500.
- Angerer, J. P. 1991. Leaf dynamics, stemflow and throughfall water and nutrient inputs in a subtropical savanna parkland, Texas. M. Sc. Thesis, Department of Rangeland Ecology & Management, Texas A&M University, College Station, Texas.
- Archer, S., 1989. Have southern Texas savannas been converted to woodlands in recent history? *American Naturalist*, 134: 545-561.
- Archer, S., 1990. Development and stability of grass-woody mosaics in a subtropical savanna parkland, Texas, U.S.A. *Journal of Biogeography*, 17: 453-462.
- Archer, S., 1994. Woody plant encroachment into southwestern grasslands and savannas: Rates, patterns and proximate causes. Pages 13-68 in M. Vavra, W. Laycock & R. Pieper (ed.). *Ecological Implications of Livestock Herbivory in the West Society for Range Management, Denver, Colorado*.
- Archer, S., D. S. Schimel & E. A. Holland, 1994. Mechanisms of shrubland expansion: Land use, climate or CO₂? *Climatic Change*, 29: 99-91.
- Archer, S., C. J. Scifres, C. R. Bassham & R. Maggio, 1988. Autogenic succession in a subtropical savanna: Conversion of grassland to thorn woodland. *Ecological Monographs*, 58: 111-127.
- Arno, S. F. & G. E. Gruell, 1986. Douglas fir encroachment into mountain grasslands in southwestern Montana. *Journal of Range Management*, 39: 272-276.
- Bahre, C. J. & M. L. Shelton, 1993. Historic vegetation change, mesquite increases, and climate in southeastern Arizona. *Journal of Biogeography*, 20: 489-504.
- Barnes, P. W. & S. R. Archer, 1995. Facilitation and competition between overstory and understory woody plants in a Texas subtropical savanna. *Oecologia* (submitted).
- Barton, D. C., 1933. Surface fracture system of south Texas. *Bulletin of the American Association of Petroleum Geologists*, 17: 1194-1212.
- Belsky, A. J., R. G. Amundson, R. M. Duxberry, S. J. Riha, A. R. Ali & S. M. Mwonga, S. M., 1989. The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya. *Journal of Applied Ecology*, 26: 1005-1024.
- Belsky, A. J. & C. D. Canham, 1994. Forest gaps and isolated savanna trees: An application of patch dynamics in two ecosystems. *BioScience*, 44: 77-84.
- Blackburn, W. H. & P. T. Tueller, 1970. Pinyon and juniper invasion in black sagebrush communities in east-central Nevada. *Ecology*, 51: 841-848.
- Bogusch, E. R., 1952. Brush invasion of the Rio Grande Plains of Texas. *Texas Journal of Science*, 4: 85-91.
- Booth, C. A. & P. J. Barker, 1981. Shrub invasion on sandplain country west of Wanaaring, New South Wales. *Soil Conservation Service of New South Wales*, 37: 65-70.
- Bossard, C. C. & M. Rejmanek, 1994. Herbivory, growth, seed production and resprouting of an exotic invasive shrub. *Biological Conservation*, 67: 193-200.
- Boutton, T. W., S. R. Archer & A. J. Midwood, 1994. $\delta^{13}\text{C}$ values of soil organic matter confirm increased tree/shrub abundance in a subtropical savanna ecosystem. *Bulletin Ecological Society of America*, 75: 20.
- Boutton, T. W., L. C. Nordt, S. Archer & I. Casar, 1993. Stable carbon isotope ratios of soil organic matter and their potential use as indicators of paleoclimate. *International Symposium on Applications of Isotope Techniques in Studying Past and Current Environmental Changes in the Hydrosphere and Atmosphere*. Intl. Atomic Energy Agency, Vienna.
- Boutton, T. W., S. F. Zitzer, S. Archer, & L. A. Cifuentes, 1992. Symbiotic N₂-fixation in a subtropical thorn woodland: Evidence from ¹⁵N natural abundance and nodulation potential. *Bulletin of the Ecological Society of America*, 73: 117.
- Bragg, T. B. & L. C. Hulbert, 1976. Woody plant invasion of unburned Kansas bluestem prairie. *Journal of Range Management*, 29: 19-23.
- Brown, A. L., 1950. Shrub invasions of southern Arizona desert grasslands. *Journal of Range Management*, 3: 172-177.
- Brown, D. E. (ed.), 1982. Biotic communities of the American Southwest-United States and Mexico. Special Issue of *Desert Plants*, Vol. 4. University of Arizona Press, Tucson, Arizona.
- Brown, J. R., 1987. Factors regulating the ingress and establishment of a woody plant (*Prosopis glandulosa*) in perennial grasslands. Ph. D. Dissertation, Department of Rangeland Ecology & Management, Texas A&M University, College Station, Texas.
- Brown, J. R. & S. Archer, 1987. Woody plant seed dispersal and gap formation in a North American subtropical savanna woodland: The role of domestic herbivores. *Vegetatio*, 73: 73-80.
- Brown, J. R. & S. Archer, 1989. Woody plant invasion of grasslands: Establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. *Oecologia*, 80: 19-26.
- Brown, J. R. & S. Archer, 1990. Water relations of a perennial grass and seedling versus adult woody plants in a subtropical savanna, Texas. *Oikos*, 57: 366-374.
- Buffington, L. D. & C. H. Herbel, 1965. Vegetational changes on a semidesert grassland range from 1958 to 1963. *Ecological Monographs*, 35: 139-164.
- Burrows, W. H., I. F. Beale, R. G. Silcock & A. J. Pressland, 1985. Prediction of tree and shrub population changes in a semi-arid woodland. Pages 207-211 in J. C. Tothill & J. J. Mott (ed.). *Ecology and Management of the World's Savannas*. Australian Academy of Science, Canberra.
- Caldwell, M. M., J. H. Richards, & W. Beyschlag, 1991. Hydraulic lift: Ecological implications of water efflux from roots. Pages 423-436 in D. Atkinson (ed.). *Plant Root Growth:*

- An Ecological Perspective. Blackwell Scientific Publishers, Oxford.
- Coffey, C. R., 1986. A floristic study of the La Copita Research Area in Jim Wells County, Texas. M. Sc. Thesis, Department of Rangeland Ecology & Management, Texas A&M University, College Station, Texas.
- Correll, D. S. & Johnston, M. C., 1979. Manual of the vascular plants of Texas. University of Texas at Dallas, Richardson, Texas.
- Crosswhite, F. S., 1980. Dry country plants of the south Texas Plains. *Desert Plants*, 2: 141–179.
- Cunningham, G. M. & P. J. Walker, 1973. Growth and survival of mulga *Acacia aneura* F. Muell. ex Benth.) in western New South Wales. *Tropical Grassland*, 7: 69–77.
- Ellis, D. & J. L. Schuster, 1968. Juniper age and distribution on an isolated butte in Garza County. *Southwestern Naturalist*, 13: 343–348.
- El Youssoufi, M., 1992. Factors influencing recruitment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) in a savanna woodland, Texas. Ph.D. Dissertation, Department of Rangeland Ecology & Management, Texas A&M University, College Station, Texas.
- Flinn, R. C., S. Archer, T. W. Boutton & T. Harlan, 1994. Identification of annual rings in an arid land woody plant, *Prosopis glandulosa*. *Ecology*, 75: 850–853.
- Forman, R. T. T. & E. W. B. Russell, 1983. Evaluation of historical data in ecology. *Bulletin of the Ecological Society of America*, 64: 5–7.
- Fuentes, E. R., R. O. Otaiza, M. C. Alliende, A. Hoffman & A. Poiani, 1984. Shrub clumps of the Chilean matorral vegetation: Structure and possible maintenance mechanisms. *Oecologia*, 62: 405–411.
- Glendening, G. E., 1952. Some quantitative data on the increase of mesquite and cactus on a desert grassland range in southern Arizona. *Ecology*, 33: 319–328.
- Glenn-Lewen, D. C. & E. van der Maarel, 1992. Patterns and processes of vegetation dynamics. Pages 11–59 in D. C. Glenn-Lewin, R. K. Peet & T. T. Veblin (ed.). *Plant Succession: Theory and Prediction*. Chapman & Hall, New York.
- Goerner, C. A., 1993. Aboveground interference, litter and light quality influence on *Prosopis glandulosa* var. *glandulosa* establishment in grasslands. M. Sc. Thesis, Department of Rangeland Ecology & Management, Texas A & M University, College Station, Texas.
- Guevara, S., S. E. Purata & E. van der Maarel, 1986. The role of remnant forest trees in tropical secondary succession. *Vegetatio*, 66: 77–84.
- Hardin, E. D., 1988. Succession in Buffalo Beats prairie and surrounding forest. *Bulletin of the Torrey Botanical Club*, 115: 13–24.
- Harrington, G. N., R. E. Oxley & D. J. Tongway, 1979. The effects of European settlement and domestic livestock on the biological system in poplar box (*Eucalyptus populnea*) lands. *Australian Rangeland Journal*, 1: 271–279.
- Hastings, J. R. & R. L. Turner, 1965. The changing mile: An ecological study of vegetation change with time in the lower mile of an arid and semi-arid region. University of Arizona Press, Tucson, Arizona.
- Hennessy, J. T., R. P. Gibbens, J. M. Tromble & M. Cardenas, 1983. Vegetation changes from 1935 to 1980 in mesquite dunelands and former grasslands of southern New Mexico. *Journal of Range Management*, 36: 370–374.
- Hibbard, K. A., S. Archer, D. W. Valentine & D. S. Schimel, 1993. Spatial variability in nitrogen mineralization in a *Prosopis savanna* parkland. *Bulletin of the Ecological Society of America*, 74: 275.
- Hobbs, R. J. & H. A. Mooney, 1986. Community changes following shrub invasion of grassland. *Oecologia*, 70: 508–513.
- Hsieh, Y. C., 1993. Spatial modeling of succession in a subtropical savanna. Ph.D. Dissertation, Department of Rangeland Ecology & Management, Texas A&M University, College Station, Texas.
- Huebotter, N. H., 1991. Successional processes in a Texas savanna woodland: The role of birds and rodents. M. Sc. Thesis, Department of Rangeland Ecology & Management, Texas A&M University, College Station, Texas.
- Humphrey, R. R., 1987. 90 years and 535 miles: Vegetation changes along the Mexican border. University New Mexico Press, Albuquerque, New Mexico.
- Humphrey, R. R. & L. A. Mehrhoff, 1958. Vegetation change on a southern Arizona grassland range. *Ecology*, 39: 720–726.
- Humphrey, R. R., 1958. The desert grasslands: A history of vegetational changes and an analysis of causes. *Botanical Review*, 24: 193–252.
- Huntley, B. J. & B. H. Walker (ed.), 1982. *Ecology of Tropical Savannas*. Ecological Studies 42. Springer-Verlag, New York.
- Inglis, J. M., 1964. A History of Vegetation on the Rio Grande Plains. Texas Parks and Wildlife Department Bulletin 45, Austin, Texas.
- Johnsen, T. N., 1962. One-seed juniper invasion of northern Arizona grasslands. *Ecological Monographs*, 32: 187–207.
- Johnson, W. C. & C. S. Adkisson, 1985. Dispersal of beech nuts by blue jays in fragmented landscapes. *American Midland Naturalist*, 113: 319–324.
- Johnson, H. B. & H. S. Mayeux, 1990. *Prosopis glandulosa* and the nitrogen balance of rangelands: Extent and occurrence of nodulation. *Oecologia*, 84: 176–185.
- Johnson, R. W. & J. C. Tothill, 1985. Definition and broad geographic outline of savanna lands. Pages 1–13 in J. C. Tothill & J. J. Mott (ed.). *Ecology and Management of the World's Savannas*. Australian Academy of Science.
- Johnston, M. C., 1963. Past and present grasslands of southern Texas and northeastern Mexico. *Ecology*, 44: 456–466.
- Knight, C. J. M. Briggs & M. D. Nellis, 1994. Expansion of gallery forest on Konza Prairie Research Natural Area, Kansas. *Landscape Ecology*, 9: 117–125.
- Knoop, W. T. & B. H. Walker, 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. *Journal of Ecology*, 73: 235–253.
- Kuchler, A. W., 1964. The Potential Natural Vegetation of the Conterminous United States. American Geographical Society, New York.
- Lonard, R. I. & F. W. Judd, 1985. Effects of a severe freeze on native woody plants in the Lower Rio Grande Valley, Texas. *Southwestern Naturalist*, 30: 397–403.
- Lonsdale, M. & R. Braithwaite, 1988. The shrub that conquered the bush. *New Scientist*, 15: 52–55.
- Loomis, L. E., 1989. Influence of heterogeneous subsoil development on vegetation patterns in a subtropical savanna parkland, Texas. Ph. D. Dissertation, Department of Rangeland Ecology & Management, Texas A&M University, College Station, Texas.
- Lowe, C. H. & D. E. Brown, 1982. Introduction. Pages 8–16 in D. E. Brown (ed.). *Biotic Communities of the American Southwest—United States and Mexico*. Special Issue of *Desert*

- Plants. Vol. 4. University of Arizona Press, Tucson, Arizona.
- Madany, M. H. & N. E. West, 1983. Livestock grazing-fire regime interactions within montane forests of Zion National Park, Utah. *Ecology*, 64: 661-667.
- Malin, J. C., 1953. Soil, animal, and plant relations of the grassland, historically recorded. *Scientific Monthly*, 76: 207-220.
- Martin, S. C. & R. M. Turner, 1977. Vegetation change in the Sonoran Desert region, Arizona and Sonora. *Arizona Academy of Science*, 12: 59-69.
- McBride, J. R. & H. F. Heady, 1968. Invasion of grassland by *Baccharis pilularis* DC. *Journal of Range Management*, 21: 106-108.
- McClanahan, T. R. & R. W. Wolfe, 1987. Dispersal of ornithochorous seeds from forest edges in central Florida. *Vegetatio*, 71: 107-112.
- McDonnell, M. J. & E. W. Stiles, 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia*, 56: 109-116.
- McLendon, T., 1991. Preliminary description of the vegetation of south Texas exclusive of coastal saline zones. *Texas Journal of Science*, 43: 13-32.
- McMahan, C. A., R. G. Fryc & K. L. Brown, 1984. The Vegetation Types of Texas. Texas Parks and Wildlife Department, Austin, Texas.
- McPherson, G.R. & H.A. Wright, 1990. Effects of cattle grazing and *Juniperus pinchotii* canopy cover on herb cover and production in western Texas. *The American Midland Naturalist*, 123: 144-151.
- McPherson, G. R., H. A. Wright & D. B. Wester, 1988. Patterns of shrub invasion in semiarid Texas grasslands. *The American Midland Naturalist*, 120: 391-397.
- Midwood, A. J., T. W. Boutton, S. Watts & S. Archer, 1993. Natural abundance of ^2H and ^{18}O in soil moisture, rainfall and plants in a subtropical thorn woodland ecosystem: Implications for plant water use. *International Symposium on Applications of Isotope Techniques in Studying Past and Current Environmental Changes in the Hydrosphere and Atmosphere*, International Atomic Energy Agency, Vienna.
- Miller, D., S. Archer & S. F. Zitzer, 1994. Radial growth of an invasive arborescent (*Prosopis glandulosa*) in relation to annual rainfall, soils, topography and competition. *Bulletin Ecological Society of America*, 75: 155.
- Miller, R. F. & P. E. Wigand, 1994. Holocene changes in semiarid pinyon-juniper woodlands. *BioScience* 44: 465-474.
- Mordelet, P., L. Abbadie, & J. C. Menaut, 1993. Effects of tree clumps on soil characteristics in a humid savanna of west Africa (Lamto, Côte d'Ivoire). *Plant and Soil*, 153: 103-111.
- Morison, C. G. T., A. C. Hoyle & J. F. Hope-Simpson, 1948. Tropical soil-vegetation catenas and mosaics. *Journal of Ecology*, 36: 1-84.
- Murphy, P. G. & A. E. Lugo, 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics*, 17: 67-88.
- Nelson, J. T. & P. L. Beres, 1987. Was it grassland? A look at vegetation in Brewster County, Texas, through the eyes of a photographer in 1899. *Texas Journal of Agriculture and Natural Resources*, 1: 34-37.
- Nilsson, S. G., 1985. Ecological and evolutionary interactions between reproduction of beech (*Fagus sylvatica*) and seed eating animals. *Oikos*, 44: 157-164.
- Norwine, J., 1978. Twentieth-century semiarid climates and climatic fluctuations in Texas and northeastern Mexico. *Journal of Arid Environments*, 1: 313-325.
- Petranka, J. W. & J. K. McPherson, 1979. The role of *Rhus copallina* in the dynamics of the forest-prairie ecotone in north-central Oklahoma. *Ecology*, 60: 956-965.
- Potter, L. D. & D. L. Green, 1964. Ecology of ponderosa pine in western North Dakota. *Ecology*, 45: 10-23.
- Progulske, D.R., 1974. Yellow Ore, Yellow Hair and Yellow Pine: A Photographic Study of a Century of Forest Ecology, Bulletin 616, South Dakota State University Extension Service, Brookings, South Dakota.
- Rappole, J. H., C. E. Russell & T. E. Fulbright, 1986. Anthropogenic pressures and impacts on marginal, neotropical, semiarid ecosystems: The case of south Texas. *Science of the Total Environment*, 55: 91-99.
- Robinson, T. W., 1965. Introduction, Spread and Areal Extent of Saltcedar (*Tamarix*) in the Western States. U.S. Geological Survey Professional Paper no. 491-A.
- Rosen, E., 1988. Shrub expansion in alvar grasslands in Oland. *Acta Phytogeographica Suecica*, 76: 87-100.
- San Jose, J. J. & M. R. Farinas, 1983. Changes in tree density and species composition in a protected *Trachypogon* savanna, Venezuela. *Ecology*, 64: 447-453.
- Scanlan, J. C., 1988. Spatial and temporal vegetation patterns in a subtropical *Prosopis* savanna woodland, Texas. Ph. D. Dissertation, Department of Rangeland Ecology & Management, Texas A&M University, College Station, Texas.
- Scanlan, J. C. & S. Archer, 1991. Simulated dynamics of succession in a North American subtropical *Prosopis* savanna. *Journal of Vegetation Science*, 2: 625-634.
- Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A. Virginia & W. G. Whitford, 1990. Biological feedbacks in global desertification. *Science*, 247: 1043-1048.
- Scifres, C. J. & J. H. Brock, 1969. Moisture-temperature interrelations in germination and early seedling development of mesquite. *Journal of Range Management*, 22: 334-337.
- Scifres, C. J. & R. R. Hahn, 1971. Response of honey mesquite seedlings to top removal. *Journal of Range Management*, 24: 396-298.
- Scifres, C. J. & B. H. Koerth, 1987. Climate soils and vegetation of the La Copita Research Area. Texas Agricultural Experiment Station Report MP-1626. College Station, Texas.
- Sinclair, A. R. E. & M. Norton-Griffiths (ed.), 1979. Serengeti: Dynamics of an Ecosystem. University Chicago Press, Chicago.
- Singh, J. S. & M. C. Joshi, 1979. Ecology of the semi-arid regions of India with emphasis on land-use. Pages 243-273 in B. H. Walker (ed.). *Management of Semi-Arid Ecosystems*. Elsevier, Amsterdam.
- Skarpe, C., 1990. Shrub layer dynamics under different herbivore densities in an arid savanna, Botswana. *Journal of Applied Ecology*, 27: 873-885.
- Smejns, F. E. & L. B. Merrill, 1988. Long-term change in semi-arid grassland. Pages 101-114 in B. B. Amos & F. R. Gehlbach (ed.). *Edwards Plateau Vegetation*. Baylor University Press, Waco, Texas.
- Smith, A. J., 1975. Invasion and ecesis of bird-disseminated woody plants in a temperate forest sere. *Ecology*, 56: 19-34.
- Smith, D. A. & E. M. Schmutz, 1975. Vegetative changes on protected versus grazed desert grassland ranges in Arizona. *Journal of Range Management*, 28: 453-457.
- Snook, E. C., 1985. Distribution of eastern red cedar on Oklahoma rangelands. Pages 45-52 in R. F. Wittwer & D. M. Engle (ed.). *Eastern Red Cedar in Oklahoma. Conference Proceedings, Cooperative Extension Service Division of Agriculture,*

- Oklahoma State University, Stillwater.
- Sparks, S. R., N. E. West & E. B. Allen, 1990. Changes in vegetation and land use at two townships in Skull Valley, western Utah. Pages 27–36 in E. D. McArthur, E. M. Romney, S. D. Smith & P. T. Tueller (ed.). *Cheatgrass Invasion, Shrub Die-Off and Other Aspects of Shrub Biology and Management*. U.S.D.A., Forest Service General Technical Report INT-276, Ogden, Utah.
- Steinauer, E. M. & T. B. Bragg, 1987. Ponderosa pine (*Pinus ponderosa*) invasion of Nebraska sandhills prairie. *American Midland Naturalist*, 118: 358–365.
- Tieszen, L. L. & S. Archer, 1990. Isotopic assessment of vegetation changes in grassland and woodland systems. Pages 293–321 in C. B. Osmond, L. F. Pitelka & G. M. Hidy (ed.). *Plant Biology of the Basin and Range*. Ecological Studies 80, Springer-Verlag, New York.
- Tilman, D., 1982. Resource Competition and Community Structure. *Monographs in Population Biology* 17. Princeton University Press, Princeton, New Jersey.
- Tothill, J. C. & J. J. Mott (ed.), 1985. *Ecology and Management of the World's Savannas*. Australian Academy of Science, Canberra.
- Trollope, W. S. W., 1982. Ecological effects of fire in South African savannas. Pages 292–306 in B. J. Huntley & B. H. Walker (ed.). *Ecology of Tropical Savannas*. Ecological Studies 42, Springer-Verlag, Berlin.
- Tschirley, F. H. & S. C. Martin, 1960. Germination and longevity of velvet mesquite seed in soil. *Journal of Range Management*, 13: 94–97.
- Ueckert, D. N., L.L. Smith, & B. L. Allen, 1979. Emergence and survival of honey mesquite seedlings on several soils in west Texas. *Journal of Range Management*, 32: 284–287.
- Van Vegten, J. A., 1983. Thornbush invasion in a savanna ecosystem in eastern Botswana. *Vegetatio*, 56: 3–7.
- Vetaas, O. R., 1992. Micro-site effects of trees and shrubs in dry savannas. *Journal of Vegetation Science*, 3: 337–344.
- Walker, B. H. (ed.), 1987a. *Determinants of Tropical Savannas*. IRL Press Ltd., Oxford.
- Walker, B. H., 1987b. A general model of savanna structure and function. Pages 1–12 in B.H. Walker (ed.). *Determinants of Tropical Savannas*. IRL Press Ltd., Oxford.
- Walker, B. H., 1994. Landscape to regional-scale responses of terrestrial ecosystems to global change. *Ambio*, 23: 67–73.
- Walter, H., 1979. *Vegetation of the Earth and Ecological Systems of the Geobiosphere*. Springer-Verlag, New York.
- Watts, S., 1993. Rooting patterns of co-occurring woody plants on contrasting soils in a subtropical savanna. M. Sc. Thesis, Department of Rangeland Ecology & Management, Texas A&M University, College Station, Texas.
- Weltzin, J. F., 1990. The role of prairie dogs (*Cynomys ludovicianus*) in regulating the population dynamics of the woody legume *Prosopis glandulosa*. M.Sc. Thesis, Department of Rangeland Ecology & Management, Texas A&M University, College Station, Texas.
- Weltzin, J. F. & M. B. Coughenour, 1990. Savanna tree influence on understory vegetation and soil nutrients in northwestern Kenya. *Journal of Vegetation Science*, 1: 325–334.
- Werner, P. A. (ed.), 1991. *Savanna Ecology and Management: Australian Perspectives and Intercontinental Comparisons*. Blackwell Scientific Publications, London.
- West, N. E., 1989. Spatial pattern–functional interactions in shrub-dominated plant communities. Pages 283–305 in C. M. McKell (ed.). *The Biology and Utilization of Shrubs*. Academic Press, New York.
- Whittaker, R. H., L. R. Gilbert & J. H. Connell, 1979. Analysis of a two-phase pattern in a mesquite grassland, Texas. *Journal of Ecology*, 67: 935–952.
- Williams, K., R. J. Hobbs & S. P. Hamburg, 1987. Invasion of an annual grassland in northern California by *Baccharis pulularis* ssp. *consanguinea*. *Oecologia*, 72: 461–465.
- Wondzell, S. M., 1984. Recovery of desert grassland in Big Bend National Park following 36 years of protection from grazing by domestic livestock. M. Sc. Thesis, Department of Biology, New Mexico State University, Las Cruces.
- Wright, H. A., S. C. Bunting & L. F. Neuenschwander, 1976. Effect of fire on honey mesquite. *Journal of Range Management*, 29: 567–471.
- York, J. C. & W. A. Dick-Peddie, 1969. Vegetation changes in southern New Mexico during the past one hundred years. Pages 155–166 in W. G. McGinnis & B. J. Goldman (ed.). *Arid Lands in Perspective*. University of Arizona Press, Tucson, Arizona.
- Young, J. A. & R. A. Evans, 1981. Demography and fire history of a western juniper stand. *Journal of Range Management*, 34: 501–506.
- Young, M. D. & O. T. Solbrig (ed.), 1993. *The World's Savannas: Economic Driving Forces, Ecological Constraints and Policy Options for Sustainable Land Use*. Man and the Biosphere Series Vol. 12, Parthenon Publishing Group, Carnforth.

