

## $\delta^{13}\text{C}$ values of soil organic carbon and their use in documenting vegetation change in a subtropical savanna ecosystem

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### Abstract

Plants with  $\text{C}_3$ ,  $\text{C}_4$ , and CAM photosynthesis have unique  $\delta^{13}\text{C}$  values which are not altered significantly during decomposition and soil organic matter formation. Consequently,  $\delta^{13}\text{C}$  values of soil organic carbon reflect the relative contribution of plant species with  $\text{C}_3$ ,  $\text{C}_4$ , and CAM photosynthetic pathways to community net primary productivity, and have been utilized to document vegetation change, to quantify soil organic matter turnover, and to refine our understanding of earth–atmosphere–biosphere interactions. Here, we review the basis of this methodology, and illustrate its use as a tool for studying grass–woody plant dynamics in a savanna ecosystem. In the Rio Grande Plains of southern Texas,  $\text{C}_4$  grasslands and savannas have been largely replaced by  $\text{C}_3$  subtropical thorn woodlands dominated by *Prosopis glandulosa*. We used  $\delta^{13}\text{C}$  values of soil organic matter, above- and belowground plant biomass, and litter in conjunction with radiocarbon dating and dendrochronology to test the hypotheses that: (1)  $\text{C}_3$  *Prosopis* groves in uplands and  $\text{C}_3$  *Prosopis* woodlands in low-lying drainages have been long-term components of the landscape; and (2) *Prosopis* woodlands of low-lying drainages have expanded up-slope since Anglo-European settlement. Current organic matter inputs were not in isotopic equilibrium with soil organic carbon in any of the patch types sampled. In upland

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grasslands,  $\delta^{13}\text{C}$  values of vegetation ( $-20\text{‰}$ ) were lower than those of soil organic matter ( $-17\text{‰}$ ), suggesting increased  $\text{C}_3$  forb abundance in response to long-term, heavy grazing (herbaceous retrogression). In wooded landscape elements,  $\delta^{13}\text{C}$  values of current organic matter inputs were characteristic of  $\text{C}_3$  plants ( $-28$  to  $-25\text{‰}$ ), while those of the associated soil organic matter were typically  $-20$  to  $-15\text{‰}$ . These  $\delta^{13}\text{C}$  values indicate that woodlands, groves, and shrub clusters dominated almost exclusively by  $\text{C}_3$  plants now occupy sites once dominated by  $\text{C}_4$  grasses. A particularly strong memory of the  $\text{C}_4$  grasslands that once occupied these sites was recorded in the  $\delta^{13}\text{C}$  values of organic carbon associated with fine and coarse clay fractions ( $-18$  to  $-14\text{‰}$ ), probably a consequence of the slow organic carbon turnover rates in those soil fractions. When  $\delta^{13}\text{C}$  values of soil organic carbon were evaluated in conjunction with radiocarbon measurements of that same carbon, it appeared that herbaceous retrogression and a shift from  $\text{C}_4$  grassland to  $\text{C}_3$  woodland occurred recently, probably within the last 50–100 years. Demographic characteristics of the dominant tree species corroborated the  $\delta^{13}\text{C}$  and  $^{14}\text{C}$  evidence, and indicated widespread establishment of *P. glandulosa* and associated shrubs over the past 100 years. Together, these data provide direct, spatially explicit evidence that vegetation change has occurred recently across the entire landscape at this site. Environmental conditions where  $\text{C}_3$ ,  $\text{C}_4$ , and CAM plants coexist (e.g., dry, alkaline soils) generally do not favor the preservation of pollen and phytoliths, and these same areas usually lack historical records of vegetation change. Consequently, vegetation dynamics have been difficult to quantify in grasslands, savannas, and woodlands. However, our results demonstrate clearly that  $\delta^{13}\text{C}$  values of soil organic matter afford a direct and powerful technique for reconstructing vegetation change in these areas. © 1998 Elsevier Science B.V.

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## 1. Introduction

Stable isotope ratios of elements in both organic and inorganic components of the plant–soil environment often record and integrate information relating to: (1) the identity of the processes that formed those components; (2) the rates of those processes; and (3) the environmental conditions prevailing at the time those components were formed. As a result, a wealth of pedological, biogeochemical, and ecological information can be obtained from stable isotope analyses of soils (Boutton and Yamasaki, 1996). In this paper, we focus on the carbon isotopic composition of soil organic matter and its use in reconstructing vegetation change. We briefly review the factors that influence the  $\delta^{13}\text{C}$  of soil organic matter, then present a case study to illustrate how these measurements have enabled spatially explicit reconstructions of vegetation change in a subtropical savanna ecosystem.

### 1.1. Natural abundance of stable carbon isotopes in soil organic matter: A brief review

All plants discriminate against  $^{13}\text{C}$  during photosynthesis as a result of the biochemical properties of the primary carbon fixing enzymes and limitations to  $\text{CO}_2$  diffusion into the leaf, but the extent of this discrimination is a function of

photosynthetic pathway type (Vogel, 1980; O'Leary, 1988; Farquhar et al., 1989). Plants with  $C_3$  photosynthesis have  $\delta^{13}C$  values ranging from approximately  $-32$  to  $-22\text{‰}$  (mean ca.  $-27\text{‰}$ ), while those with  $C_4$  photosynthesis have values ranging from about  $-17$  to  $-9\text{‰}$  (mean ca.  $-13\text{‰}$ ). Plants with obligate Crassulacean acid metabolism (CAM) have  $\delta^{13}C$  values similar to  $C_4$  plants; however, those with facultative CAM may range from  $-30$  to  $-10\text{‰}$ , depending on the relative amount of carbon fixed by CAM vs.  $C_3$  photosynthesis (Griffiths, 1992). These natural isotopic differences allow carbon derived from each photosynthetic pathway type to be traced through above- (Tieszen and Boutton, 1989) and belowground (Boutton et al., 1983; Martin et al., 1992; Ryan and Aravena, 1994) food webs, and ultimately into the soil organic matter compartment.

The  $\delta^{13}C$  of soil organic carbon integrates the relative contribution of plant species with  $C_3$ ,  $C_4$ , and CAM photosynthetic pathways to community net primary productivity (Troughton et al., 1974; Andreux et al., 1990; Balesdent and Mariotti, 1996; Boutton, 1996). Where vegetation has been compositionally stable, the  $\delta^{13}C$  value of soil organic carbon in the upper soil profile (ca. 0–20 cm) is similar to that of the plant community (Stout and Rafter, 1978; Stout et al., 1981; Nadelhoffer and Fry, 1988; Balesdent et al., 1993). This concordance between the isotopic composition of the soil organic matter in the upper profile and that of the plant community occurs because isotope fractionation is negligible during the early stages of organic matter decomposition in well-drained mineral soils (Melillo et al., 1989; Balesdent et al., 1993; Wedin et al., 1995; Balesdent and Mariotti, 1996; Boutton, 1996). However, older organic matter located deeper in the soil profile (below 20 cm) has  $\delta^{13}C$  values that are generally 1–3‰ greater than those for organic carbon in the upper profile (Stout et al., 1981; Nadelhoffer and Fry, 1988; Balesdent et al., 1993). These higher  $\delta^{13}C$  values deeper in the profile may reflect small but cumulative isotope effects attributable to respiration by invertebrate and microbial decomposers, differential decomposition of isotopically distinct biochemical components of litter, and/or the 1.5‰ decrease in the  $\delta^{13}C$  value of atmospheric  $CO_2$  during the past 200 years (Agren et al., 1996; Balesdent and Mariotti, 1996; Boutton, 1996).

Changes in the relative proportions of  $C_3$ ,  $C_4$ , and/or CAM plants can be recognized as a difference between the isotopic composition of the current plant community and that of the soil organic matter. This isotopic difference will be largest immediately following a vegetation change, but will decrease over time as carbon from the previous plant community decays out of the organic carbon pool and is replaced by new carbon derived from the current plant community. Thus, the isotopic discrepancy created by the vegetation change will persist for a length of time determined by the soil organic matter turnover rate. In fact, following a vegetation change (e.g.,  $C_3 \rightarrow C_4$ , or vice versa), the rate at which the  $\delta^{13}C$  value of the soil organic carbon changes to approach that of the new

plant community is a direct measure of the soil organic matter turnover rate in that system (Cerri et al., 1985; Balesdent et al., 1987; Balesdent and Mariotti, 1996; Bernoux et al., 1996).

A site-specific, spatially explicit history or chronology of relative productivity of the different photosynthetic pathway types can be developed by measuring the  $\delta^{13}\text{C}$  of soil organic matter at different depths in the soil profile, and/or soil organic matter constituents that differ in turnover rate. Radiocarbon measurements indicate that the mean age of soil organic matter increases with depth in the profile, ranging from less than 200 years near the surface to 2000–4000 years at a depth of 1 m (Scharpenseel and Neue, 1984). Thus, recent changes in relative  $\text{C}_3$ – $\text{C}_4$ –CAM productivity might only be evident in the  $\delta^{13}\text{C}$  of organic carbon near the soil surface where organic matter turnover is most rapid and current organic matter inputs are concentrated. Conversely, isotopic signatures from antecedent plant communities may persist deeper in the profile, but not in the surface soil. This approach can be extended to paleoecological time scales by measuring  $\delta^{13}\text{C}$  of organic carbon preserved in paleosols, which may range in age from thousands to millions of years. The  $\delta^{13}\text{C}$  of organic carbon in paleosols can persist without diagenetic modification for more than 5,000,000 years (Cerling et al., 1989).

Another approach for developing a temporal record of relative  $\text{C}_3$ – $\text{C}_4$ –CAM productivity in plant communities involves the measurement of  $\delta^{13}\text{C}$  of soil organic carbon pools that differ in turnover rate, such as particle size fractions, aggregate size fractions, and/or density fractions. Organic matter in clay and silt size fractions generally has a slower rate of turnover than that in sand size fractions (Christensen, 1992; Desjardins et al., 1994), and organic matter turnover rates are significantly greater in macroaggregates ( $> 212 \mu\text{m}$ ) than in microaggregates ( $< 212 \mu\text{m}$ ) (Puget et al., 1995; Jastrow et al., 1996). In addition, free particulate organic matter with a density of  $< 1.6 \text{ g cm}^{-3}$  appears to have a more rapid turnover rate than organic matter present in soil fractions with higher densities (Golchin et al., 1995; Gregorich et al., 1995). Thus, if a change in relative  $\text{C}_3$ – $\text{C}_4$ –CAM productivity has occurred, the  $\delta^{13}\text{C}$  of the current organic matter inputs should be most evident in coarser particle size fractions, macroaggregates, and relatively light density fractions, while  $\delta^{13}\text{C}$  of the previous plant community should be most evident in the silt/clay fractions, microaggregates, and heavier density fractions.  $\delta^{13}\text{C}$  measurements of organic carbon in particle size, aggregate size, or density fractions from different depths throughout the profile would, therefore, provide the most detailed chronological account of relative  $\text{C}_3$ – $\text{C}_4$ –CAM productivity at a particular site. Radiocarbon measurements on these same organic carbon fractions would further clarify the temporal dynamics of relative  $\text{C}_3$ – $\text{C}_4$ –CAM productivity.

Isotopic measurements of soil organic carbon have been utilized successfully to document the effects of land use practices on vegetation change (Martin et al., 1990; Boutton et al., 1993; Frank et al., 1995), to quantify rates and patterns of

vegetation change in natural ecosystems (Dzurec et al., 1985; Schwartz et al., 1986, 1996; Tieszen and Archer, 1990; Ambrose and Sikes, 1991; McPherson et al., 1993; Mariotti and Peterschmitt, 1994; Bond et al., 1994), to refine our understanding of earth–atmosphere–biosphere interactions (Nordt et al., 1994; Boutton et al., 1994; Victoria et al., 1995; Wada and Ueda, 1996), and to quantify soil organic matter turnover rates (Balesdent and Mariotti, 1996; Bernoux et al., 1996). Here, we illustrate the use of this methodology as a tool for studying grass–woody plant dynamics in a savanna ecosystem.

### 1.2. *Vegetation dynamics in savanna ecosystems*

Changes in the relative abundances of woody plants and grasses have significant ecological and socioeconomic implications in subtropical and tropical savanna ecosystems. Dramatic changes in tree–shrub–grass composition can occur over decadal time-frames and are strongly influenced by human manipulation of fire frequency and livestock grazing. In recent history, woody plants have increased in many grasslands and savannas in Africa, Asia, Australia, South America, and North America (Archer, 1995). Although this phenomenon has been widely recognized, surprisingly little is known of the rates, dynamics, patterns, or successional processes involved. A synthesis of existing studies (Archer, 1994) suggests that woody plant increases in savanna ecosystems have been:

1. rapid, with substantial changes occurring over 50–100 year time spans;
2. non-linear and accentuated by extreme climatic events;
3. associated with heavy livestock grazing, elimination of browsers, and/or fire suppression;
4. influenced by topographic factors;
5. driven by an influx of unpalatable, stress-tolerant, and often  $N_2$ -fixing woody plants; and
6. irreversible over time frames relevant to ecosystem management.

These dramatic changes in ecosystem structure have the potential to profoundly influence hydrology, biogeochemistry, biodiversity, landscape evolution, and future land use options in the affected areas (Schlesinger et al., 1990; Walker and Steffen, 1993). Unfortunately, our knowledge of vegetation dynamics and the historic proportion and distribution of woody plants and grasses is often confined to historical photographs and anecdotal historical accounts. Such accounts of vegetation are often conflicting, biased, and potentially misleading (Archer, 1996).

The Rio Grande Plains of southern Texas, USA 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 region has been classified as *Prosopis–Acacia–Andropogon–Setaria* savanna (Kuchler, 1964). However, the present vegetation is dominated by a subtropical thorn

woodland complex consisting of dense thickets of shrubs and small trees (McMahan et al., 1984). Historical accounts suggest that the conversion from grassland and open savanna to woodland began approximately 100–150 years ago (Johnston, 1963; Inglis, 1964; Rappole et al., 1986). Historical aerial photographs document increases in woody plant cover over the past 50 years, but also illustrate that woody plants already dominated many portions of the landscape by the time of the earliest photos (1941) (Archer et al., 1988). Reconstructions based on dynamic rainfall-driven simulations of plant growth rate (Archer, 1989) and patch transition probabilities (Scanlan and Archer, 1991) suggest that woody cover in pre-settlement landscapes would have been much less than it is today. However, these simple models are based on limited data and are not spatially explicit. The lack of spatial specificity is particularly troublesome, as woody plant distributions in this system are highly regulated by

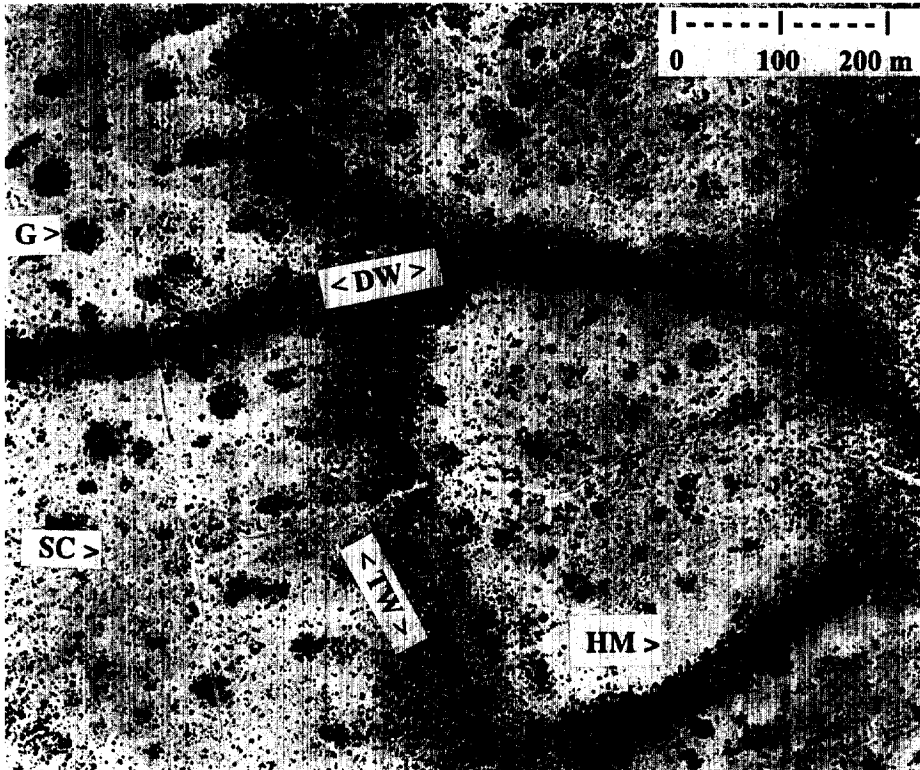


Fig. 1. Aerial view of savanna parkland landscape at La Copita Research Area in southern Texas, USA. Lighter areas are herbaceous vegetation; darker areas are woody vegetation. Sandy loam uplands are characterized by *Prosopis glandulosa* groves (*G*) and discrete shrub clusters (*SC*) embedded within a grassland or herbaceous matrix (*HM*) dominated by  $C_4$  grasses. These grade (1–3% slope) into transitional woodlands (*TW*) and clay loam drainage woodlands (*DW*) also dominated by *P. glandulosa*. We quantified *P. glandulosa* age and the  $\delta^{13}C$  of plants and soil organic carbon in these landscape elements to determine their vegetation history.

topoedaphic properties (Archer, 1995). Because photographic records and model reconstructions based on indirect assessments can generate misleading inferences (Archer, 1996), direct, reliable, and spatially explicit assessments of vegetation history are needed.

In the Rio Grande Plains, as in other subtropical and tropical savannas worldwide, the woody plant component consists exclusively of  $C_3$  species, whereas the grass component consists almost exclusively of  $C_4$  species. Therefore,  $\delta^{13}C$  values of soil organic matter can be utilized to document shifts in the relative productivities of these two structurally and functionally distinct components of the plant community. The carbon isotopic composition of soil organic matter was used to demonstrate that  $C_3$  shrub clusters in uplands developed on sites dominated previously by  $C_4$  grasses (Tieszen and Archer, 1990). However, their data did not address the vegetation history of two key topoedaphic portions of the landscape which may have an extended history of domination by  $C_3$  woody vegetation: groves of large *Prosopis* trees in uplands, and closed-canopy *Prosopis* woodlands of intermittent drainages (Fig. 1). Here we use  $\delta^{13}C$  values of soil organic matter and above- and belowground plant biomass in conjunction with radiocarbon dating and dendrochronology to test the hypotheses that: (1)  $C_3$  *Prosopis* groves in uplands and  $C_3$  *Prosopis* woodlands in low-lying drainages have been long-term components of the landscape; and (2) *Prosopis* woodlands of low-lying drainages have expanded up-slope since Anglo-European settlement.

## 2. Materials and methods

### 2.1. Study area

Research was conducted at the Texas Agricultural Experiment Station La Copita Research Area (27°40'N; 98°12'W) located 65 km west of Corpus Christi, Texas in the eastern Rio Grande Plains of the Tamaulipan Biotic Province. The climate at the site is subtropical, with a mean annual rainfall of 715 mm and mean annual temperature of 22.4°C. Topography consists of nearly level uplands which grade (1–3% slopes) into lower-lying drainages and playas; elevations range from 75 to 90 m. Recent studies of geomorphology and landscape evolution reveal that the site is situated on the middle Pleistocene Lissie Formation, and is mantled with sediments deposited from a Late Pleistocene/early Holocene eolian silt sheet located to the east (Wilding et al., 1996). Soils in the drainages formed from sediments deposited from a combination of fluvial, slopewash, and eolian processes and show development similar to the upland soils, indicating that the parent materials for the drainages and uplands were deposited coevally. Climate, soils, and vegetation of the site have been described elsewhere (Scifres and Koerth, 1987).

An aerial view of La Copita Research Area reveals a distinct patterning of vegetation strongly influenced by topoedaphic features (Fig. 1). *Prosopis glandulosa* Torr. var. *glandulosa* (mesquite) is the dominant plant in all wooded landscape elements (nomenclature follows Correll and Johnston, 1979). Sandy loam soils of the uplands (Typic and Pachic Argiustolls) are characterized by a two-phase vegetation pattern consisting of clusters of woody vegetation (discrete phase) embedded within a matrix of grasses and herbaceous dicots (continuous phase) (Whittaker et al., 1979). Formation of woody plant clusters is initiated through the colonization of grassland areas by the N<sub>2</sub>-fixing tree legume, *P. glandulosa*, which then facilitates the recruitment of other woody plant species beneath its canopy (Archer et al., 1988). Where a subsurface argillic horizon is present, clusters are spaced widely and consist of a single *P. glandulosa* tree with up to 15 understory tree/shrub species. Where the argillic horizon is absent, these clusters appear to expand laterally and fuse to form groves (Archer, 1995). Low-lying, intermittent drainages generally possess clay loam soils (Pachic Argiustolls) and are characterized by continuous-canopy woodlands dominated by *P. glandulosa*. These drainage woodlands appear to have originated via the same successional processes currently underway in the uplands, and their plant species composition is similar to that of clusters and groves in the uplands. Historical aerial photographs reveal that drainage woodlands have expanded up-slope in some areas but not in others (Fig. 1) (Archer, 1995).

## 2.2. Vegetation composition and structure

Patches representing herbaceous zones between shrub clusters (grasslands), mature discrete clusters (argillic horizon present) and groves (argillic horizon absent) of uplands, and transitional and drainage woodlands of lowlands, were sampled on two landscapes. Each landscape consisted of a hillslope gradient extending from the crown of sandy loam uplands to the bottom of clay loam intermittent drainages. Three 30 m line-intercept transects were randomly situated to traverse upland grasslands dotted with discrete shrub clusters. Transects were also randomly situated within groves, within the up-slope interior margins of drainage woodlands (hereafter termed 'transitional woodlands'), and within the topographically low portions of drainage woodlands. Canopy intercepts of woody species were recorded along each transect. Total percent cover was calculated as the total intercept of all woody species divided by transect length. Species relative cover was calculated as the absolute intercept divided by the intercepts summed across all species. *P. glandulosa* stems rooted in belts 8 m wide and centered on each transect were counted to estimate density, and their basal diameters were measured. Age-class distributions were determined by converting basal diameter to age using soil-specific basal diameter–age relationships (Flinn et al., 1994; Stoker and Archer, 1996).



Aboveground standing crop of herbaceous species was determined in June 1991 by clipping  $0.5 \times 0.5$  m plots at ground level in each of the two landscapes. Plots ( $n = 10$  plots per patch type per landscape) were placed randomly in upland grasslands, groves, and transition and drainage woodlands. In wooded patches, clipped plots were situated within 1 m of the bole of *P. glandulosa*. Grasses and forbs were separated, dried at  $50^\circ\text{C}$ , and weighed. A subset of bulk vegetation samples from ten plots within each patch type was selected randomly, ground and mixed thoroughly, and analyzed for  $\delta^{13}\text{C}$ . In addition, foliage from the dominant plant species within each major vegetation type was collected, dried at  $50^\circ\text{C}$ , pulverized, and analyzed for  $\delta^{13}\text{C}$ .

Woody plant litterfall was quantified seasonally from June 1991 to March 1992. Litter traps ( $0.5 \times 0.5 \times 0.08$  m with fine fiberglass screen bottoms) were placed within 1 m of the bole of *P. glandulosa* in six randomly selected groves, transitional and drainage woodland patches on each landscape. Litter accumulating in traps was sorted into foliar vs. non-foliar (mostly stems and twigs) constituents, dried at  $50^\circ\text{C}$ , weighed, pulverized, and stored for  $\delta^{13}\text{C}$  analysis.

### 2.3. Effect of decomposition on $\delta^{13}\text{C}$ of plant litter

The potential for change in the  $\delta^{13}\text{C}$  value of plant tissue during the early stages of decomposition was evaluated for five dominant woody plant species: *P. glandulosa*, *Zanthoxylum fagara* (L.) Sarg., *Diospyros texana* Scheele, *Celtis pallida* Torr., and *Condalia hookeri* M.C. Johnst. Foliage was collected from each species in 1987 by shaking the plants and collecting the leaves that fell onto a tarp below. Litter was air-dried for 2 weeks. Subsamples of air-dried litter were then oven-dried to obtain an air-dry/oven-dry conversion factor. Nylon mesh litter bags ( $10 \times 10$  cm; 1 mm mesh), each containing 5 g of air-dried litter (25 bags per species), were placed randomly on the soil surface beneath five upland shrub clusters (five bags of each species per cluster) in November 1987. Five litter bags of each species (one bag per species per shrub cluster) were collected at 76, 132, 193, 249, and 344 days after placement. Samples were dried at  $50^\circ\text{C}$ , sieved to remove soil contamination, weighed, pulverized, and analyzed for  $\delta^{13}\text{C}$  as described below.

### 2.4. Soil collection

In each landscape, soil cores ( $5 \text{ cm} \times 150 \text{ cm}$ ) were collected from grassland ( $n = 6$ ), discrete cluster ( $n = 6$ ), grove ( $n = 6$ ), transitional woodland ( $n = 9$ ), and drainage woodland ( $n = 9$ ) patches in May 1991. For each patch type within each landscape, one core was subjected to soil characterization, one was utilized for radiocarbon dating of soil organic carbon, and one was used for isolation of particle size separates for  $\delta^{13}\text{C}$ ; all other cores were utilized for  $\delta^{13}\text{C}$  analyses of roots and whole-soil organic carbon. In wooded landscape elements, cores

were taken within 1 m of the bole of large *P. glandulosa* trees. In grasslands, cores were taken in areas that were at least 10 m from the nearest woody vegetation. Prior to taking each core, all litter within a  $0.5 \times 0.5$  m area centered over the core location was collected. These samples were dried at 60°C, pulverized, and saved for isotopic analysis.

### 2.5. Soil characterization

Two soil cores per patch type (one from each landscape) were examined for soil profile descriptions and then subjected to soil characterization at the Soil Characterization Laboratory, Department of Soil and Crop Sciences, Texas A&M University (Lab Nos. 4305–4352). Soil texture was determined by the pipette method (Gee and Bauder, 1986). pH was determined with a glass electrode in a 1:1 soil to water suspension (McLean, 1982). Total carbon was determined by dry combustion at 1000°C and collection of CO<sub>2</sub> on ascarite (Tiessen and Moir, 1993). CaCO<sub>3</sub> equivalent was obtained using a Chittick apparatus (Dreimanis, 1962). Organic carbon was calculated as the difference between total carbon and CaCO<sub>3</sub> carbon.

### 2.6. Preparation of roots and soils for stable carbon isotope analyses

Soil cores collected for stable carbon isotope analyses were divided into six depth increments (0–15, 15–30, 30–60, 60–90, 90–120, and 120–150 cm) and coarse roots removed manually. Soil samples were then dried at 60°C, ground to pass a 2 mm screen, and fine roots removed from the soil by flotation in saturated NaCl solutions (density = 1.2 g cm<sup>-3</sup>) (Dzurec et al., 1985; McPherson et al., 1993). Although most of the floated material consisted of live and dead roots, finely comminuted leaf litter was also present in the 0–15 cm soil samples. Microscopic examination of soils confirmed that virtually all particulate organic debris was removed by this flotation procedure. Fine and coarse roots were pooled, treated with 1 N HCl to remove carbonates, dried, weighed, pulverized, and saved for isotopic analysis. Although we refer to this fraction as ‘roots’ for the remainder of the paper, it might be equally appropriate to consider this fraction equivalent to the ‘light fraction’ of free or non-complexed soil organic matter (Christensen, 1992).

Soils free of particulate organic matter were then treated with 1 N HCl at 25°C for 3 days to remove carbonate carbon, washed to neutrality with distilled water, dried, and pulverized. Controlled studies revealed no effect of acid treatment on  $\delta^{13}\text{C}$  of soil organic matter (Midwood and Boutton, 1997). Soils treated in this manner contain largely the ‘heavy fraction’ of soil organic carbon, consisting of humified, organomineral-complexed organic matter (Christensen, 1992).

Soil particle size separates ( $> 50 \mu\text{m}$ , sand;  $50\text{--}5 \mu\text{m}$ , coarse silt;  $5\text{--}2 \mu\text{m}$ , fine silt;  $2\text{--}0.2 \mu\text{m}$ , coarse clay;  $< 0.2 \mu\text{m}$ , fine clay) were isolated from one soil core in each patch type by sieving and sedimentation (Rutledge et al., 1967), and carbonates were removed from the separates with  $1 N$  HCl as described above. Particle size separates were then dried, pulverized, and saved for isotopic analysis.

### 2.7. Stable carbon isotope analyses

Plant foliage, litter, roots, and organic matter in whole soils and particle size separates were combusted to  $\text{CO}_2$  at  $900^\circ\text{C}$  for 2 h and then  $650^\circ\text{C}$  for 2 h in the presence of CuO and Cu in sealed quartz tubes (Boutton, 1991). The  $\text{CO}_2$  was isolated and purified by cryogenic distillation, and its isotopic composition determined on a Micromass-903 (VG Isogas, Middlewich, UK) dual inlet, triple collector isotope ratio mass spectrometer. All results are reported relative to the international V-PDB standard by calibration through NBS-19 (Hut, 1987; Coplen, 1995). Overall precision (machine error plus sample preparation error) was  $< 0.2\text{‰}$ .

The proportion of carbon derived from  $\text{C}_4$  sources in mixtures of herbaceous biomass, litter, roots, and soil organic matter was estimated by the mass balance equation:

$$\delta^{13}\text{C} = (\delta^{13}\text{C}_{\text{C}_4})(x) + (\delta^{13}\text{C}_{\text{C}_3})(1 - x) \quad (1)$$

where  $\delta^{13}\text{C}$  is the  $\delta^{13}\text{C}$  value of the whole sample (herbaceous biomass, litter, roots, or soil organic matter),  $\delta^{13}\text{C}_{\text{C}_4}$  is the average  $\delta^{13}\text{C}$  value of the  $\text{C}_4$  components of the sample,  $x$  is the proportion of carbon from  $\text{C}_4$  plant sources,  $\delta^{13}\text{C}_{\text{C}_3}$  is the average  $\delta^{13}\text{C}$  value of the  $\text{C}_3$  components, and  $1 - x$  is the proportion of carbon derived from  $\text{C}_3$  plant sources.

### 2.8. Radiocarbon content and mean residence time of soil organic matter

Two soil cores per patch type (one from each landscape) were analyzed for natural  $^{14}\text{C}$  content at the University of Arizona Laboratory of Isotope Geochemistry (Lab. Nos. 6826–6857). Soils from the 0–15, 15–30, 30–60, and 90–120 cm depth intervals were analyzed. Prior to  $^{14}\text{C}$  analyses, roots and particulate organic debris were removed by sieving and flotation, and carbonates were removed by treatment with HCl. Thus,  $^{14}\text{C}$  measurements were made on the same soil organic carbon fraction (humified, organomineral-complexed organic matter) as the  $\delta^{13}\text{C}$  measurements. Procedures, instrumentation, and instrument performance for  $^{14}\text{C}$  counting are described in Kalin and Long (1989).

The mean residence time (MRT) of soil organic matter was estimated using a simple proportional replacement soil carbon model described in Harkness et al. (1991). This model relates the incorporation of the  $^{14}\text{C}$  bomb spike derived from

nuclear testing in the atmosphere during the late 1950s to early 1960s to the turnover rates of soil organic matter. For soils collected in 1991, the model describes a curve which predicts a  $^{14}\text{C}$  content of 114% modern carbon (% modern) for soils with a MRT of 1 year, increasing to and peaking at 127% modern for soils with a MRT of 15 years, then dropping slowly to 109% modern for soils with a MRT of 100 years, and 96.5% modern for soils with a MRT of 500 years. Similar models have been developed by Hsieh (1993) and Bird et al. (1996).

### 3. Results

#### 3.1. Soil characterization

Soils in upland grasslands and clusters were deep, well-drained Typic Argiustolls with fine sandy loam and sandy clay loam mollic surface horizons, and sandy clay loam and clay loam argillic subsurface horizons (Fig. 2). Soils in the upland groves were Pachic Haplustolls with over-thickened mollic surface horizons, and were more coarsely textured throughout the profile than any other landscape position. Grove soils lacked the distinctive, fine-textured argillic subsurface horizon that characterized other landscape positions.

Soils in the upland/lowland transition zones were Typic and Pachic Argiustolls. These soils were generally similar to those of upland grasslands and clusters, but were richer in clay throughout the profile (Fig. 2), typical of sideslope positions. Soils in the drainage woodlands were Pachic Argiustolls with over-thickened sandy clay loam surface horizons, characteristic of landscape positions that receive excess water and sediment. Clay content was similar to or greater than that of the transition zones throughout the profile.

Organic carbon concentrations were lowest in upland grasslands, ranging from 0.77% at 0–15 cm to 0.34% at 120–150 cm (Fig. 2). Organic carbon concentrations were consistently higher in wooded landscape elements, especially between 0 and 60 cm in the profile. Among wooded patch types, drainages had the highest organic carbon concentrations, ranging from 1.60% at 0–15 cm to 0.32% at 120–150 cm.

#### 3.2. $\delta^{13}\text{C}$ values of live foliage

All major woody plants and forbs (except *Froelichia gracilis*) had  $\delta^{13}\text{C}$  values characteristic of  $\text{C}_3$  plants (Table 1).  $\delta^{13}\text{C}$  values of woody plants averaged  $-26.9 \pm 0.6\text{‰}$ , while those of the forbs averaged  $-29.4 \pm 0.4\text{‰}$ . All grasses measured were  $\text{C}_4$  species, with a mean  $\delta^{13}\text{C}$  value of  $-14.0 \pm 0.3\text{‰}$ .  $\delta^{13}\text{C}$  values of the CAM cacti, *Opuntia leptocaulis* and *O. lindheimeri*, averaged  $-15.6 \pm 0.2\text{‰}$ , similar to those of the  $\text{C}_4$  species.

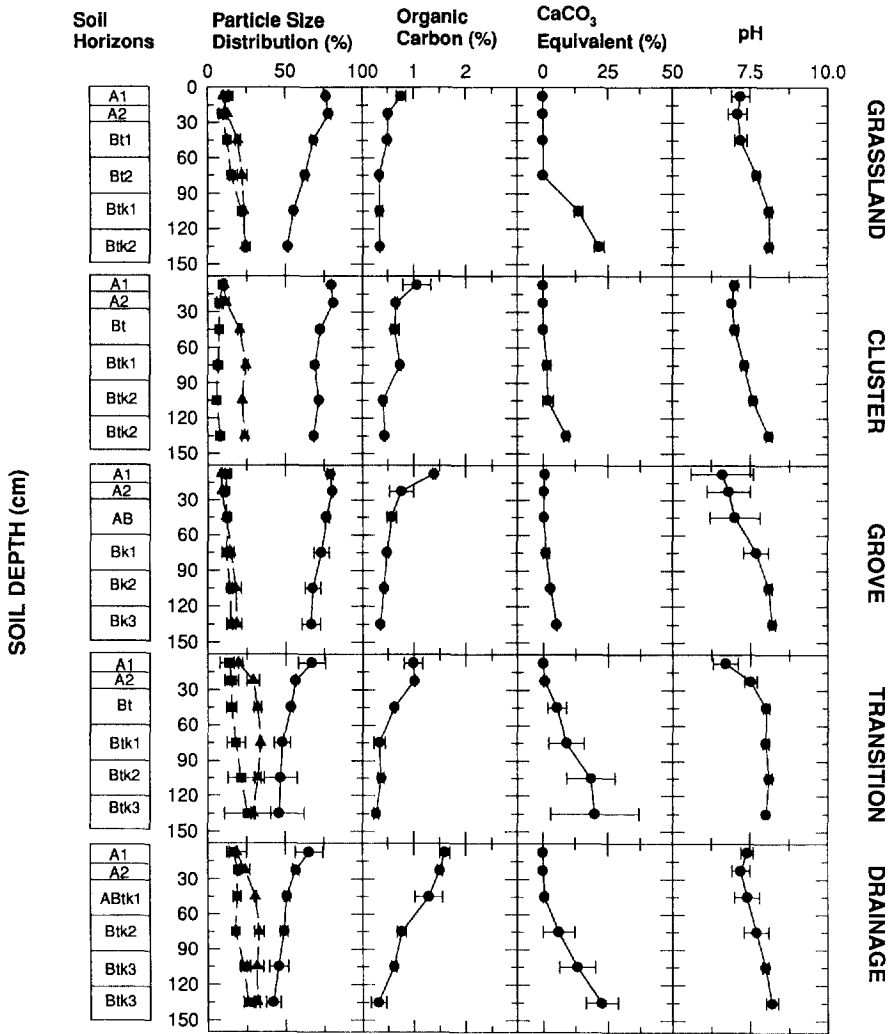


Fig. 2. Physical and chemical characteristics of soils from different landscape elements (Fig. 1) at La Copita Research Area in southern Texas. 'Cluster' refers to discrete shrub clusters; 'transition' and 'drainage' refer to closed-canopy woodlands. Each point is the mean  $\pm$  standard error of 2 replicates. Symbols used for particle sizes: ● = sand, ■ = silt, and ▲ = clay.

### 3.3. Vegetation characterization

*P. glandulosa* dominated the overstory of discrete clusters and groves in the uplands and the overstory of transitional and drainage woodlands (Table 2). Because *P. glandulosa* is typically the first woody plant to colonize grasslands, stem ages and age-class distributions of this species are indicative of differences in the timing and rate of woody patch development across the landscape.

Table 1

$\delta^{13}\text{C}$  values (‰) of leaf tissue from plant species at La Copita Research Area in southern Texas, USA

	$\delta^{13}\text{C}$ (‰)	
	Mean	S.E.
<b>C<sub>3</sub> woody plants:</b>		
<i>Celtis pallida</i> Torr.	-26.8	0.3
<i>Condalia hookeri</i> M.C. Johnst.	-27.3	0.4
<i>Diospyros texana</i> Scheele	-25.6	0.3
<i>Mahonia trifoliolata</i> (Moric.) Fedde	-27.2	0.7
<i>Prosopis glandulosa</i> Torr. var. <i>glandulosa</i>	-25.1	0.5
<i>Zanthoxylum fagara</i> (L.) Sarg.	-29.1	0.3
Mean for C <sub>3</sub> woody plants	-26.9	0.6
<b>C<sub>3</sub> forbs:</b>		
<i>Amblyolepis setigera</i> DC.	-28.7	-
<i>Ambrosia confertiflora</i> DC.	-31.0	-
<i>Aphanostephus riddellii</i> T. & G.	-31.6	-
<i>Commelina</i> sp.	-27.7	-
<i>Gaillardia pulchella</i> Foug.	-29.0	-
<i>Helenium microcephalum</i> DC.	-29.6	-
<i>Lepidium</i> sp.	-26.2	-
<i>Melampodium cinereum</i> DC.	-30.5	-
<i>Oxalis</i> sp.	-30.8	-
<i>Parthenium confertum</i> Gray	-29.7	-
<i>Parthenium hysterophorus</i> L.	-27.6	-
<i>Plantago</i> sp.	-28.7	-
<i>Verbesina encelioides</i> (Cav.) Benth. & Hook. ex Gray	-32.0	-
<i>Wedelia hispida</i> H.B.K.	-28.8	-
Mean for C <sub>3</sub> forbs	-29.4	0.4
<b>C<sub>4</sub> forbs:</b>		
<i>Froelichia gracilis</i> (Hook.) Moq.	-16.5	-
<b>C<sub>4</sub> grasses:</b>		
<i>Bouteloua hirsuta</i> Lag.	-14.1	0.1
<i>Bouteloua trifida</i> Thurb.	-15.0	0.0
<i>Chloris cucullata</i> Bisch.	-13.8	0.3
<i>Chloris pluriflora</i> (Fourn.) Clayton	-14.5	0.1
<i>Panicum hallii</i> var. <i>filipes</i> (Scribn.) Waller	-14.4	0.1
<i>Paspalum pubiflorum</i> Rupr. & Fourn.	-13.1	0.1
<i>Setaria texana</i> Emery	-12.4	0.1
<i>Tridens albescens</i> (Vasey) Woot. & Standl.	-15.0	0.2
Mean for C <sub>4</sub> grasses	-14.0	0.3
<b>CAM plants:</b>		
<i>Opuntia leptocaulis</i> DC.	-15.8	3.1
<i>Opuntia lindheimeri</i> Engelm.	-15.4	0.7
Mean for CAM plants	-15.6	0.2

Table 2

Species composition, mean relative cover (%), and species richness of common woody plants in shrub clusters in the herbaceous matrix and in groves, transitional woodlands, and drainage woodlands

	Mean relative cover (%)			
	discrete clusters	groves	woodlands	
			transitional	drainage
Overstory:				
<i>Prosopis glandulosa</i>	12.8 <sup>b</sup>	31.5 <sup>b</sup>	21.5 <sup>b</sup>	22.4 <sup>b</sup>
Shrub understory:				
<i>Aloysia gratissima</i>	0.0	0.9 <sup>b</sup>	1.1 <sup>b</sup>	12.7 <sup>b</sup>
<i>Berberis trifoliolata</i>	11.3	0.4	5.1	1.4 <sup>b</sup>
<i>Celtis pallida</i>	0.0	14.4 <sup>b</sup>	8.3 <sup>b</sup>	19.2 <sup>b</sup>
<i>Colubrina texana</i>	13.3	8.5 <sup>b</sup>	2.7	0.9
<i>Condalia hookeri</i>	7.8 <sup>b</sup>	6.3 <sup>b</sup>	12.9 <sup>b</sup>	7.7 <sup>b</sup>
<i>Diospyros texana</i>	2.3	3.0 <sup>b</sup>	6.4	10.2 <sup>b</sup>
<i>Opuntia lindheimeri</i>	16.6 <sup>b</sup>	6.3 <sup>b</sup>	9.2 <sup>b</sup>	5.1 <sup>b</sup>
<i>Zanthoxylum fagara</i>	16.3 <sup>b</sup>	14.3 <sup>b</sup>	12.5 <sup>b</sup>	11.3 <sup>b</sup>
Other species	19.6	14.4	20.3	9.1
Total relative cover	100.0	100.0	100.0	100.0
Mean No. woody species <sup>a</sup>	11	15	13	15
Total No. woody species	16	18	18	17
No. of species in common <sup>a</sup>	5	12	8	13

<sup>a</sup> For the two sites sampled.

<sup>b</sup> Encountered in sampling both sites.

Median age of *P. glandulosa* stems was lowest in upland clusters (20 years) and transitional woodlands (22 years) (Fig. 3). The age-class distribution of stems in both of these landscape elements was clearly skewed toward younger plants. In contrast, median *P. glandulosa* trunk age in upland groves (45 years) and drainage woodlands (44 years) was more than twice that of plants in discrete clusters and transitional woodlands, with larger, older plants comprising a much greater proportion of the stand population. Maximum estimated age of *P. glandulosa* boles ranged from 44 years in upland clusters to 109 years in groves. Density of *P. glandulosa* in transitional woodlands (1119 plants ha<sup>-1</sup>) was 2- to 3-times greater than in upland grove and drainage woodland landscape elements, and 4.3-times greater than in upland shrub clusters where the argillic horizon was present.

Total woody plant cover (absolute) along line-intercept transects was greatest in drainage woodland patches (167 ± 26%), followed by upland grove (144 ± 39%) and transitional woodland (88 ± 9%) patches. Woody species richness ranged from 16 in upland shrub clusters to 18 in groves and transitional

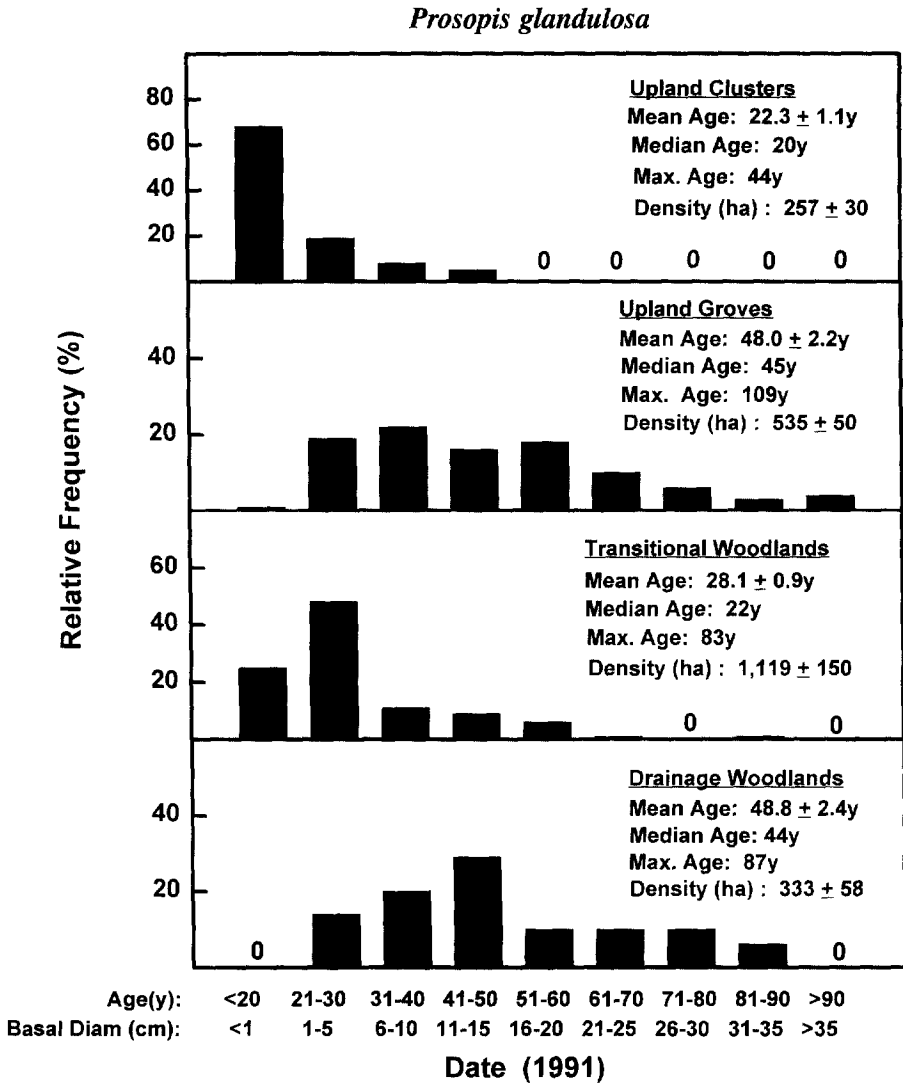


Fig. 3. Size, age, and density of *Prosopis glandulosa* stems in major landscape elements at La Copita Research Area in southern Texas.

woodlands (Table 2). Groves and drainage woodlands were most consistent in their woody composition across the two sites sampled, sharing 12 of 18 and 13 of 17 total species encountered, respectively. Discrete shrub clusters in uplands were most variable, sharing only 5 of 16 species encountered. *P. glandulosa*, *C. hookeri*, *O. lindheimeri*, and *Z. fagara* were ubiquitous, occurring in all patch types on both sites. *C. pallida*, *C. hookeri*, and *Z. fagara* dominated the understory in grove and woodland landscape elements. Among discrete clusters



Table 3

Composition and mean relative biomass (%) of grasses and forbs in the herbaceous matrix, groves, transitional woodlands and drainage woodlands

Species	Mean relative biomass (%)			
	herbaceous matrix	groves	woodlands	
			transitional	drainage
Grasses:				
<i>Bouteloua hirsuta</i>	4.7	0.0	0.4	0.0
<i>Bouteloua rigidisetata</i>	2.3	0.0	1.4	0.2
<i>Chloris cucullata</i>	11.9	2.2	4.7	0.8
<i>Chloris pluriflora</i>	0.0	4.0	2.9	1.9
<i>Panicum hallii</i>	9.8	0.0	0.2	0.0
<i>Setaria texana</i>	0.5	16.5	7.2	2.8
<i>Tridens</i> spp.	11.7	13.1	6.4	5.2
Other grasses	29.5	4.8	9.9	6.2
Total grasses (%)	70.4	40.5	33.2	17.1
Grass biomass ( $\text{g m}^{-2} \pm \text{S.E.}$ )	$86.8 \pm 7.8$	$14.7 \pm 5.2$	$10.2 \pm 4.1$	$3.2 \pm 1.8$
Forbs:				
<i>Eupatorium</i> spp.	0.1	39.8	29.9	45.9
<i>Gutierrezia sarothrae</i>	6.0	0.0	0.0	0.0
<i>Wedelia hispida</i>	21.8	10.6	31.4	29.0
Other forbs	1.7	9.1	5.4	8.0
Total forbs (%)	29.6	59.5	66.7	82.9
Forb biomass ( $\text{g m}^{-2} \pm \text{S.E.}$ )	$35.8 \pm 4.1$	$21.6 \pm 8.5$	$20.5 \pm 7.2$	$15.4 \pm 4.6$
Total biomass ( $\text{g m}^{-2} \pm \text{S.E.}$ )	$122.6 \pm 9.3$	$36.3 \pm 10.7$	$30.7 \pm 8.3$	$18.6 \pm 5.3$
Composite $\delta^{13}\text{C}$ of herb layer ( $\text{‰} \pm \text{S.E.}$ )	$-19.2 \pm 0.6$	$-23.1 \pm 2.1$	$-18.5 \pm 1.2$	$-23.8 \pm 1.5$

in uplands, *Z. fagara* and *O. lindheimeri* were the predominant understory shrub species. As noted in previous studies (Archer, 1995), the CAM species *O. lindheimeri* was distributed generally around the perimeter of shrub clusters.

The upland grasslands were dominated (70% of total biomass) by  $\text{C}_4$  grasses, primarily *Chloris cucullata*, *Tridens* spp., and *Panicum hallii* (Table 3). The isotopic signature of biomass from grasslands ( $-19.2 \pm 0.6\text{‰}$ ) was indicative of a  $\text{C}_4$ -dominated mixture of  $\text{C}_3$  forbs and  $\text{C}_4$  grasses. Grass biomass was greatly reduced in wooded patches, and the grass component of total herbaceous biomass declined from up-slope (40.5% in groves) to downslope locations (33.2% in transitional woodlands; 17.1% in drainage woodlands). With the exception of transitional woodlands, the isotopic composition of herbaceous biomass in shrub-dominated patches generally reflected this shift from grass to forb domination.  $\delta^{13}\text{C}$  values of the herbaceous layer in the transitional woodlands are probably not representative of this landscape element, as nearly all the subsamples selected at random for  $\delta^{13}\text{C}$  analysis contained higher proportions of grass biomass than suggested by the mean biomass values from

all plots. Although the relative biomass of  $C_3$  forbs increased from 29.6% to 82.3% along the catena gradient, the net result was an overall decline in forb biomass ( $35.8 \text{ g m}^{-2}$  in upland grasslands vs.  $\leq 21.6 \text{ g m}^{-2}$  in wooded patches) and total aboveground herbaceous biomass (from  $122.6 \text{ g m}^{-2}$  in upland grasslands to  $18.6 \text{ g m}^{-2}$  in drainage woodlands).

The  $\delta^{13}\text{C}$  of litter collected in traps placed in woody patch types was determined for the August 1991 collection only. Values were  $-25.6 \pm 1.0\text{‰}$  in

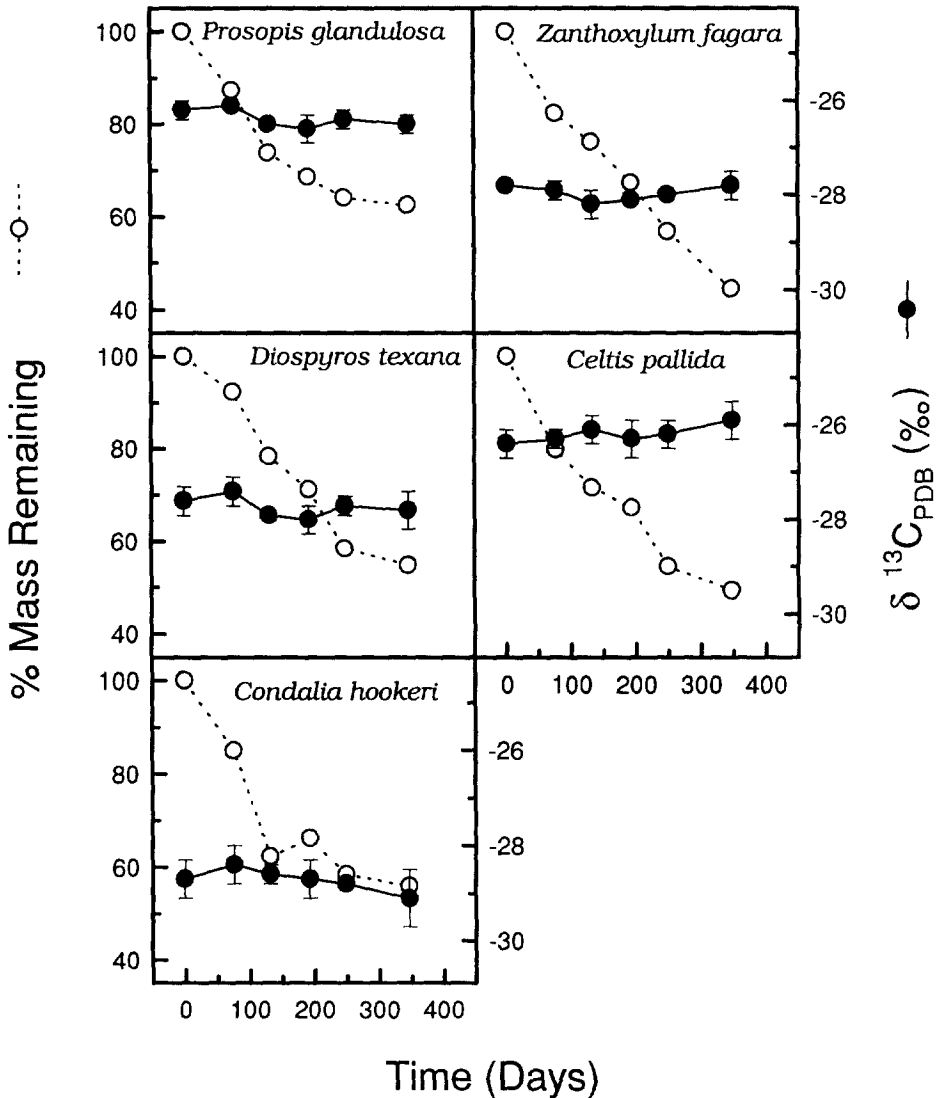


Fig. 4.  $\delta^{13}\text{C}$  (‰ vs. VPDB) values and mass loss rates during decomposition of leaves from five dominant tree/shrub species. Each point in the mean  $\pm$  standard deviation of five replicate samples. (From Boutton, 1996, with permission from Marcel Dekker, Inc.)

drainage woodlands.  $-26.7 \pm 0.7\text{‰}$  in upland groves, and  $-27.2 \pm 1.0\text{‰}$  in transitional woodlands.  $\delta^{13}\text{C}$  values of this woody plant leaf litter did not change significantly ( $\leq 0.7\text{‰}$ ) or directionally during the first year of decomposition, despite a 40–60% loss of mass (Fig. 4). Litter collected in May 1991 from the soil surface in wooded patches ranged from  $-26$  to  $-28\text{‰}$ , consistent with values for the August 1991 litter traps, and with species-specific results obtained in the decomposition study (Fig. 4).

Woody plant foliar litterfall varied seasonally, ranging from a low of 6 to 17  $\text{g m}^{-2}$  in the November–January winter period to a high of 26 to 48  $\text{g m}^{-2}$  in the hot, dry month of August (Table 4). The rank order of foliar litter input for all sample dates was groves > drainage woodlands > transitional woodlands. Similar patterns were observed for production of woody litter, which was

Table 4

Mean ( $\pm$  S.E.) monthly foliar and woody litterfall in grove and woodland landscape elements from August 1991 to March 1992

1991–1992	Litterfall ( $\text{g m}^{-2} \text{ month}^{-1}$ )		
	groves	woodlands	
		transitional	drainage
August:			
Foliar	$48 \pm 17$	$26 \pm 17$	$37 \pm 16$
Woody	$20 \pm 17$	$9 \pm 11$	$18 \pm 24$
September:			
Foliar	$29 \pm 15$	$17 \pm 14$	$22 \pm 9$
Woody	$26 \pm 37$	$2 \pm 2$	$5 \pm 5$
October:			
Foliar	$48 \pm 22$	$27 \pm 23$	$36 \pm 22$
Woody	$14 \pm 14$	$4 \pm 8$	$5 \pm 4$
Nov.–Jan.:			
Foliar	$17 \pm 11$	$6 \pm 4$	$8 \pm 4$
Woody	$9 \pm 7$	$3 \pm 3$	$14 \pm 24$
Feb.–March:			
Foliar	$34 \pm 12$	$18 \pm 11$	$25 \pm 8$
Woody	$69 \pm 164$	$4 \pm 10$	$21 \pm 52$
Projected annual litterfall ( $\text{g m}^{-2} \text{ y}^{-1}$ ) <sup>a</sup>			
Foliar	425	226	307
Woody	325	52	150
Total	750	278	457

Litter was collected monthly from traps in August–September, and at 3-month intervals from November–March. Woody components include twigs, stems and branches.

<sup>a</sup> Computed by averaging across all monthly sample dates and multiplying by 12 months.

typically lower and more variable than foliar litterfall. Projections of annual total litterfall, computed by averaging across all sample dates and multiplying by 12 months, ranged from  $278 \text{ g m}^{-2}$  in transitional woodlands to  $750 \text{ g m}^{-2}$  in groves.

Total root biomass to a depth of 150 cm was greatest in groves ( $20.2 \text{ kg m}^{-2}$ ) and lowest in the upland grasslands ( $4.4 \text{ kg m}^{-2}$ ) (Fig. 5). Root biomass was greatest in the 0–15 cm portion of the soil profile in all patch types [range = 31% (grasslands) to 47% (grove patches) of total biomass]. Decreases with depth were most apparent in groves, where 83% of the root biomass was concentrated in the upper 60 cm of the profile. Root biomass in upland grasslands had a consistently higher  $C_4$  component throughout the upper 75 cm of the soil profile ( $\delta^{13}\text{C} = -19.2$  to  $-20.8\text{‰}$ ) than did wooded patches ( $\delta^{13}\text{C} = -23.9$  to  $-24.6\text{‰}$  averaged across all woody patch types) (Fig. 6). Isotopic signatures of roots in woody patches remained fairly constant with depth ( $-24$  to  $-25\text{‰}$ ), whereas a distinct decrease in root  $\delta^{13}\text{C}$  values occurred below 90 cm in upland grasslands.

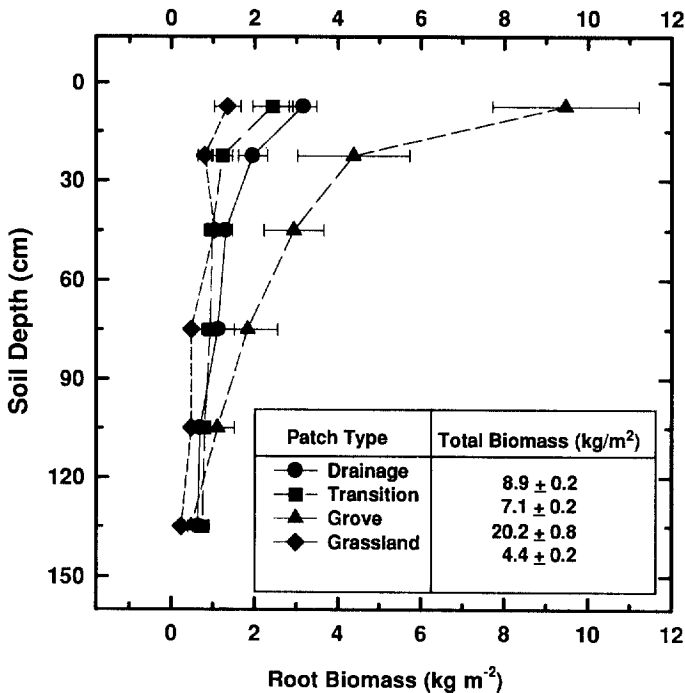


Fig. 5. Root biomass in different landscape elements at La Copita Research Area in southern Texas. Each point represents the mean  $\pm$  standard error of 6 (grasslands, groves) or 12 (transition and drainage woodlands) replicate measurements.

3.4.  $\delta^{13}\text{C}$  values of whole soils

There was no significant difference in the isotopic composition of soil organic carbon within a given patch type between the two landscapes. Therefore, data for patch types were pooled across landscapes.  $\delta^{13}\text{C}$  values of organic carbon in whole soils in the grasslands were significantly higher than those of the current organic matter inputs (roots and litter), ranging from approximately  $-18\text{‰}$  at the surface to  $-16\text{‰}$  in the middle of the profile (Fig. 6).  $\delta^{13}\text{C}$  values of whole soils in the wooded landscape elements were generally much higher ( $1\text{--}10\text{‰}$ ) than those of the associated roots and litter. With the exception of groves, whole-soil  $\delta^{13}\text{C}$  values in wooded patches were lowest near the soil surface ( $-21$  to  $-19\text{‰}$ ), and increased to maximum values ( $-17$  to  $-15\text{‰}$ ) between 15 and 45 cm. Below 45 cm,  $\delta^{13}\text{C}$  values became more negative and ap-

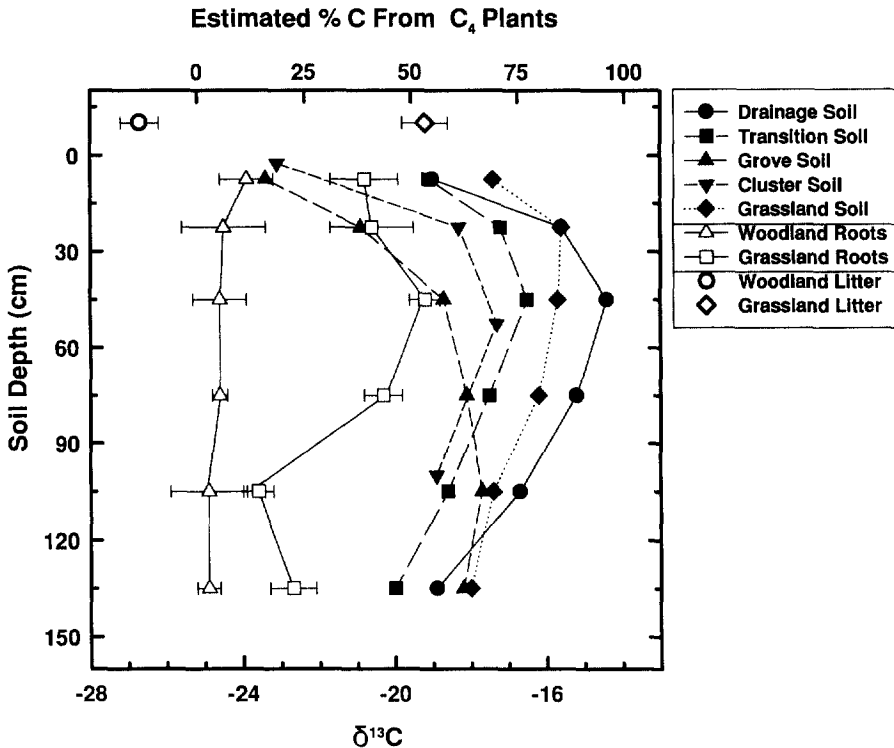


Fig. 6. Mean  $\delta^{13}\text{C}$  (‰ vs. VPDB) values of litter, roots, and soil organic carbon from landscape elements at La Copita Research Area in southern Texas. For soil organic carbon, each point is the mean of 6 (grasslands, clusters, groves) or 12 (transition zones, drainage woodlands) replicates.  $\delta^{13}\text{C}$  values for woodland roots are averages for all wooded landscape elements (clusters, groves, and transition and drainage woodlands). The approximate proportion of soil organic carbon derived from C<sub>4</sub> plant sources is indicated on the top x-axis. The upper x-axis does not apply to litter and roots. Data for clusters are from Tieszen and Archer (1990).

proached values similar to those of the surface soils. In groves, whole-soil  $\delta^{13}\text{C}$  values increased gradually from  $-24\text{‰}$  in the surface soil to  $-18\text{‰}$  below 75 cm.  $\delta^{13}\text{C}$  values of whole soils in drainage and transitional woodlands were usually within about 1–2‰ of those from the remnant grasslands throughout the soil profile. In contrast,  $\delta^{13}\text{C}$  values of soils in the upland clusters and groves were significantly lower (by 2–5‰ above 90 cm) than those in the adjacent upland grasslands.

The proportion of soil organic carbon derived from  $\text{C}_4$  plants in each landscape element was estimated from whole-soil  $\delta^{13}\text{C}$  values by mass balance (Eq. (1)). Based on  $\delta^{13}\text{C}$  values of litter and roots in wooded areas (Fig. 6), a value of  $-25\text{‰}$  was employed as an average for  $\text{C}_3$ -derived carbon.  $\delta^{13}\text{C}$  values of  $\text{C}_4$  roots and litter were not measured in this study; however, live foliage from  $\text{C}_4$  grass species had a mean  $\delta^{13}\text{C}$  value of  $-14\text{‰}$  (Table 1), which we used as the average value for  $\text{C}_4$ -derived carbon. Based on these assumptions, the proportion of soil organic carbon derived from  $\text{C}_4$  sources was greatest in drainage woodlands (55–95%), grasslands (63–86%), and transitional woodlands (45–76%), and lowest in groves (12–65%) and clusters

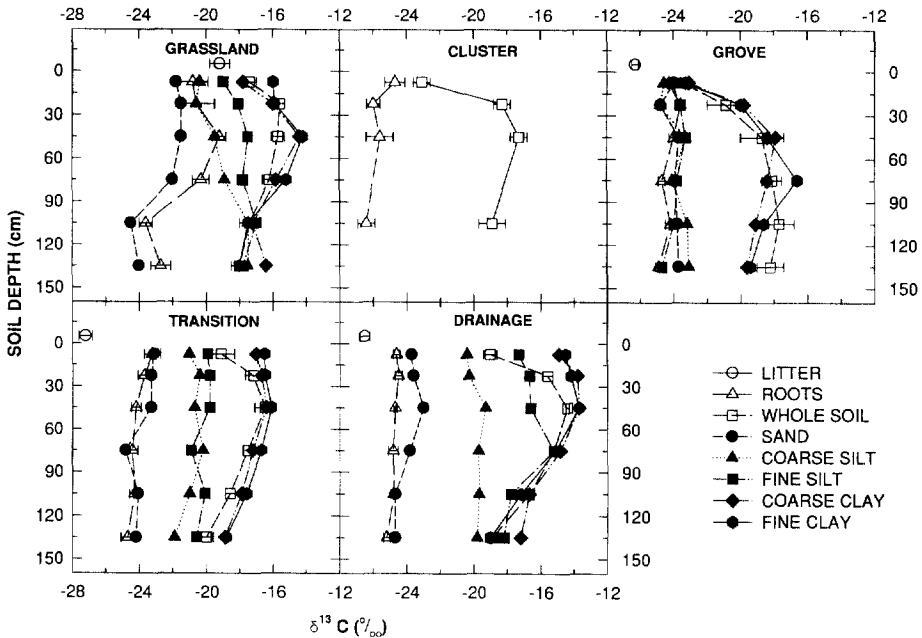


Fig. 7.  $\delta^{13}\text{C}$  (‰ vs. VPDB) values of organic carbon in particle size fractions in relation to the isotopic composition of litter, roots, and whole soils for landscape elements at La Copita Research Area in southern Texas. Particle size fractionation was conducted on one core per landscape unit. For litter, roots, and whole soils, each point is a mean  $\pm$  standard error ( $n = 6$  for grasslands, clusters, and groves;  $n = 12$  for transition and drainage woodlands). Data for clusters are from Tieszen and Archer (1990).

(18–70%) (Fig. 6). For all landscape elements, the greatest proportion of  $C_4$ -derived soil organic carbon was located between 15 and 90 cm in the soil profile.

### 3.5. $\delta^{13}C$ values of organic carbon in soil particle size fractions

$\delta^{13}C$  values of organic carbon associated with different particle size fractions isolated from the same soil sample differed by as much as 10‰ (Fig. 7). Within every landscape element, organic carbon associated with the sand fraction had the lowest  $\delta^{13}C$  values, and was generally within 1–2‰ of the values for roots and litter. In contrast, fine and coarse clay had higher  $\delta^{13}C$  values than all other particle size fractions, and were generally within 1–2‰ of the values for whole soils.  $\delta^{13}C$  values for fine and coarse silt were usually intermediate between those of the sand and clay fractions.

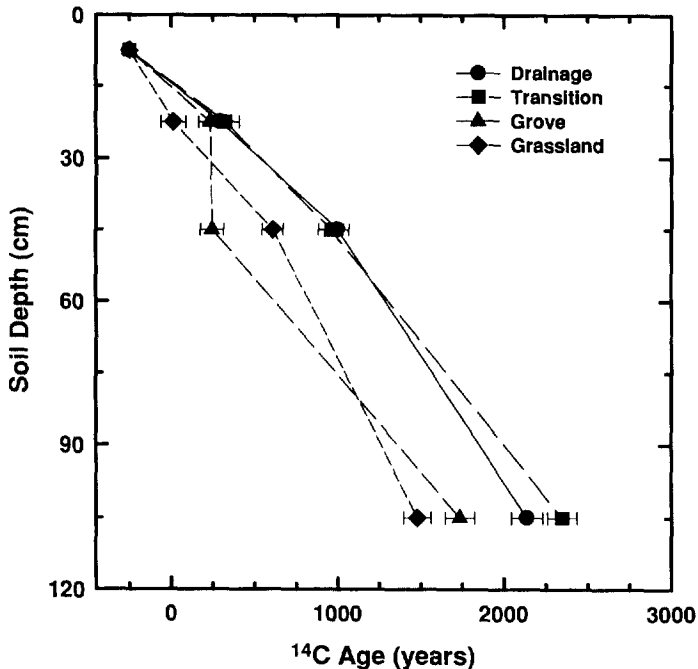


Fig. 8. Radiocarbon ages (years) of soil organic carbon as a function of soil depth in landscape elements at La Copita Research Area in southern Texas. Each point is the mean  $\pm$  standard error of 2 replicate cores. All samples in the 0–15 cm depth interval contained  $> 100\%$  modern carbon, and could not be converted to  $^{14}C$  years. Analytical error on individual radiocarbon measurements ranged from 45 to 105 years.

### 3.6. Radiocarbon age and mean residence time of soil organic carbon

The radiocarbon ( $^{14}\text{C}$ ) age of organic matter increased in a nearly linear manner with increasing depth in the soil profile within all landscape elements (Fig. 8). All soils from the 0–15 cm depth increment and three samples from the 15–30 cm depth contained  $>100\%$  modern carbon, indicating that these samples were dominated by the presence of post-1960s bomb carbon (Table 5). Conventional ages could not be assigned to these samples. Soil organic carbon below 15 cm in the profile was generally older in the lowlands than in the uplands. Soil organic matter at 90–120 cm yielded ages ranging from approximately 1500 (grasslands) to 1735 years (groves) in the uplands, and from 2140 (drainage woodlands) to 2350 years (transition woodlands) in the lowlands.

The MRT of soil organic carbon increased with depth in the profile from approximately 40–100 years in the 0–15 cm depth interval to approximately 300–500 years in the 15–30 cm interval (Table 5). Below 30 cm, the MRT of

Table 5

$^{14}\text{C}$  content and model-estimated mean residence time of soil organic matter in different landscape elements

Landscape	Soil depth (cm)	$^{14}\text{C}$ content (% modern)		Mean residence time (years)	
		core 1	core 2	core 1	core 2
Upland grassland	0–15	111.5 (0.9)	112.8 (0.7)	74 (68–81)	67 (64–71)
	15–30	102.0 (0.9)	99.8 (0.7)	232 (220–248)	312 (292–332)
	30–60	91.0 (0.8)	94.4 (0.9)	760 (690–830)	700 (645–755)
	90–120	82.8 (0.9)	83.5 (0.8)	1515 (1425–1605)	1445 (1370–1520)
Upland grove	0–15	113.0 (0.9)	119.7 (0.9) <sup>a</sup>	66 (61–72)	37 (34–40)
	15–30	97.0 (0.8)	109.8 (0.9)	472 (446–508)	89 (81–96)
	30–60	95.0 (0.9)	99.8 (0.9)	660 (580–740)	332 (312–352)
	90–120	81.0 (1.0)	79.9 (0.8)	1670 (1575–1765)	1800 (1720–1880)
Transition woodland	0–15	108.4 (1.0)	112.4 (0.9)	104 (96–118)	69 (65–74)
	15–30	100.9 (0.9)	96.0 (1.0)	288 (268–309)	540 (480–620)
	30–60	89.8 (0.8)	87.8 (0.8)	865 (790–940)	1050 (975–1125)
	90–120	70.3 (0.8)	79.3 (0.8)	2835 (2740–2930)	1860 (1780–1940)
Drainage woodland	0–15	112.5 (0.5)	119.0 (0.8) <sup>a</sup>	69 (66–72)	39 (36–42)
	15–30	97.0 (0.6)	95.8 (1.0)	472 (460–488)	560 (490–650)
	30–60	88.9 (0.9)	87.8 (0.6)	950 (875–1025)	1050 (990–1110)
	90–120	76.1 (0.8)	77.2 (1.0)	2195 (2110–2280)	2080 (1975–2185)

Numbers in parentheses following the data for  $^{14}\text{C}$  content are analytical error, while those following the mean residence times are the range of values generated by the model when analytical error is considered.

<sup>a</sup> It was not possible to uniquely determine whether these two measured  $^{14}\text{C}$  contents were on the leading or trailing edge of the curve. The other modeled solution yielded a mean residence time of 5 years. Based on the  $^{14}\text{C}$  contents of the replicate cores, it was assumed to be unlikely that the 0–15 cm depth interval would have a mean residence time of 5 years.



organic carbon continued to increase in a nearly linear manner, and could generally be estimated using conventional radiocarbon ages. For the 0–15 cm depth interval, MRTs tended to be lower in upland groves and drainage woodlands (ca. 50 years) than in upland grasslands and transitional woodlands (ca. 75 years). Below 15 cm, MRTs in upland grasslands and groves were generally lower than those from transitional and drainage woodlands (Table 5).

#### 4. Discussion

Descriptions from diaries of early explorers and settlers indicate that the vegetation of the Rio Grande Plains of southern Texas was dominated by grasslands and open savannas in the late 1800s (Inglis, 1964). However, anecdotal historical accounts are subject to many sources of error and bias (Archer, 1996). Discrepancies between present-day composition of relict stands and historical descriptions of vegetation by early travelers cast doubt on the reliability of one or both as indicators of the extent or pattern of vegetation change. In addition, rates of change required to produce shifts in vegetation composition or ranges from the time of historical observation to the present may not agree with measured or ecologically realistic rates of change (Hoffman and Cowling, 1990; Palmer et al., 1990).

Our results, based on stable carbon isotope analyses of above- and below-ground plant biomass, litter, and soils, indicate that current organic matter inputs are not in isotopic equilibrium with soil organic carbon in any of the patch types sampled.  $\delta^{13}\text{C}$  values suggest that woodlands, groves, and shrub clusters dominated almost exclusively by  $\text{C}_3$  plants now occupy sites once dominated by  $\text{C}_4$  grasses. When  $\delta^{13}\text{C}$  values of soil organic carbon are evaluated in conjunction with radiocarbon measurements of that same carbon, it appears that soil organic matter derived from  $\text{C}_3$  woody plants (evident mainly in the 0–15 cm depth increment) is dominated by post-1960s carbon, substantiating that this vegetation change occurred recently. Demographic characteristics of the dominant tree species (Fig. 3) and historical aerial photography (Archer et al., 1988) corroborate the  $\delta^{13}\text{C}$  and  $^{14}\text{C}$  evidence, and indicate widespread establishment of *P. glandulosa* and associated shrubs over the past 100 years. Together, these data provide direct, spatially explicit evidence that vegetation change has occurred within the past 50–100 years across the entire landscape in this study area.

##### 4.1. Vegetation history of upland grasslands

$\delta^{13}\text{C}$  values of whole-soil carbon in the La Copita grasslands (–18 to –16‰) were comparable to those in ungrazed, native tallgrass prairie (–17 to –14‰) dominated by  $\text{C}_4$  grasses in east-central Texas (Boutton et al., 1993), in  $\text{C}_4$  grasslands of the Brazilian Pantanal (–17.2 ± 0.6‰), and in other  $\text{C}_4$

grasslands and savannas throughout the world ( $-16.1 \pm 2.2\text{‰}$ ) (Victoria et al., 1995). Thus, the isotopic composition of grassland soils at La Copita indicates that soil organic carbon in that portion of the landscape was inherited from  $C_4$ -dominated grassland.

In the upland grasslands, which presently consist of a mixture of  $C_4$  grasses and  $C_3$  forbs, the  $\delta^{13}\text{C}$  of aboveground biomass and roots averaged  $-20\text{‰}$ , indicating that about 60% of the present productivity is from  $C_4$  grasses. However,  $\delta^{13}\text{C}$  values of soil organic carbon throughout the grassland soil profile ( $-18$  to  $-16\text{‰}$ ) were significantly higher than those of the above- and belowground biomass in the present plant community, indicating that the relative productivity of the  $C_4$  grass component must have been greater in the past. This interpretation appears reasonable, given the long history of heavy livestock grazing on the La Copita site. The adverse effects of prolonged, selective, and heavy to moderate grazing on both above- and belowground grass productivity are well-documented (Briske and Richards, 1995). It is likely, therefore, that grass biomass on the site today is much lower than it was prior to Anglo-European settlement. This inference is supported by estimates of annual production from relict grasslands in this area during years of average rainfall (SCS, 1979). Their values ( $538 \text{ g m}^{-2}$ ) are 4-times greater than those from our plots ( $< 130 \text{ g m}^{-2}$ ; Table 3) which were clipped at peak standing crop in 1991 when annual rainfall was 116% of normal. Dynamic simulations using the CENTURY model parameterized for soils and climate of the La Copita site also suggest that present-day annual herbaceous production is 48 to 76% of that prior to the introduction of domestic livestock (Hibbard, 1995).

In addition to its adverse effects on grass productivity, long-term, heavy livestock grazing typically results in an increase of the proportion of forb (=  $C_3$ ; Table 1) biomass (Archer and Smeins, 1991). Thus, both the absolute and relative amounts of  $C_4$  input to soil organic matter have likely diminished over the past century. The decrease in  $\delta^{13}\text{C}$  values of roots with increasing depth in the soil profile (from  $-20$  to  $-24\text{‰}$ ) suggests that  $C_3$  forbs in these grasslands are rooted more deeply than the  $C_4$  grasses. This is consistent with observations that: (a) grazing decreases grass root biomass and depth; (b) grazing causes the replacement of long-lived, deep-rooted grasses by short-lived, shallow-rooted grass species; and (c) grasses (fibrous roots) and forbs (tap roots) typically differ in their root architecture.

Finally, the discrepancy between the composite isotopic signature of vegetation and soils in upland grasslands may reflect lateral intrusion of  $C_3$  plant roots from discrete cluster, grove, or woodland patches. Cacti such as *O. lindheimeri* are typically associated with shrub cluster margins. These CAM plants have extensive lateral root systems, but are very shallow and would contribute  $C_4$ -like carbon to the soil (Table 1). Root biomass from shrubs in grove and cluster patches declines exponentially with distance from the canopy margins and is negligible at 2–3 m beyond the patch perimeter (Watts, 1993). Thus, is not

likely that woody plants have significantly influenced the isotopic composition of the soils in grasslands. Therefore, it appears that the vegetation history indicated by the plant–soil isotopic record in present-day grasslands has been one of decreased  $C_4$  grass production and increased  $C_3$  forb production. A likely cause for this change in herbaceous composition is heavy grazing pressure and the selective utilization of grasses by domestic livestock, which began in the 1800s in this region (Lehman, 1969).

The approximate timing of this herbaceous retrogression in the upland grasslands may be estimated from  $\delta^{13}C$  and  $^{14}C$  of soil organic carbon.  $\delta^{13}C$  values of soil organic carbon suggest that the isotopic influence of increased  $C_3$  forb abundance is primarily evident in the 0–15 cm depth increment. Measurements of  $^{14}C$  indicate that soil organic carbon within that depth interval was dominated by post-1960s bomb carbon, and the MRTs of that carbon ranged from 67 to 74 years. Thus,  $C_3$  forbs have increased in abundance in the upland grasslands primarily over the past 40–75 years. It is interesting to note that Schwartz et al. (1996) reported MRTs of 64–88 years for surface soils of tropical savannas in western Africa, similar to those reported here.

#### 4.2. *Vegetation history of woody patches*

Organic carbon concentrations in wooded landscape elements were consistently higher than those in upland grasslands. Among wooded patch types, the fine-textured soils of drainage woodlands had the highest organic carbon concentrations. This likely reflects a combination of higher rates of net primary productivity [as indicated by litterfall (Table 4) and SCS (1979) annual production data] due to a more favorable soil moisture regime, and the greater extent of organic matter protection afforded by soils rich in clay (Oades, 1988).

In all wooded landscape elements, the  $\delta^{13}C$  values of live foliage (–29 to –25‰), litter trap foliage (–27 to –26‰), ground surface litter (–28 to –26‰), and roots (–25 to –24‰) confirmed that carbon inputs are completely  $C_3$ -dominated at present. Despite this fact,  $\delta^{13}C$  values of soil organic carbon indicate clearly that a substantial proportion of organic carbon in those soils was derived from  $C_4$  plants (Figs. 6 and 7). In fact, most of the whole-soil  $\delta^{13}C$  values were between –20 and –14‰, suggesting that approximately 50–95% of soil carbon in wooded areas was  $C_4$  in origin (Fig. 6). These data provide direct chemical evidence that areas now dominated by  $C_3$  woody plants once supported plant communities dominated by  $C_4$  grasses.

$\delta^{13}C$  values of whole-soil organic carbon in wooded landscape elements indicate that most of the carbon derived from the present  $C_3$  vegetation is located in the 0–15 cm depth interval (Figs. 6 and 7). Soil organic carbon in this portion of the soil profile in wooded landscape elements is dominated by post-1960s bomb carbon, with average MRTs ranging from 37 to 104 years (Table 5). Together, the  $\delta^{13}C$  and  $^{14}C$  data suggest that grassland-to-woodland

conversion has occurred at this site within the past 50–100 years. This inference is well-supported by stem age determinations on the dominant tree species (Fig. 3), which indicate maximum tree ages ranging from 44 years (clusters) to 109 years (groves).

A particularly strong memory of the  $C_4$  grasslands that once occupied these sites was evident in the  $\delta^{13}C$  values of organic carbon associated with the fine and coarse clay fractions, which ranged from  $-18$  to  $-14\text{‰}$  across all sites and soil depths. The average  $\delta^{13}C$  value of the clay fraction in all wooded landscape elements between 15 and 90 cm in the profile was  $-16\text{‰}$ , typical of soil organic carbon in  $C_4$ -dominated grasslands throughout the world (Victoria et al., 1995). These results indicate that organic carbon associated with the fine and coarse clay fractions was derived almost exclusively from  $C_4$  plants, and that little carbon from the present  $C_3$  woodland has been incorporated into this particle size fraction. These findings are consistent with other studies demonstrating slow turnover of clay-associated organic carbon (Balesdent et al., 1988; Martin et al., 1990; Bonde et al., 1992; Christensen, 1992). Organic carbon associated with the clay fraction is comprised principally of aliphatic hydrocarbons (Oades, 1988; Baldock et al., 1992; Leinweber et al., 1993; Randall et al., 1995), which are known to be nearly inert with respect to carbon turnover (Bol et al., 1996).

In contrast to the clay fraction,  $\delta^{13}C$  values of sand-associated organic carbon in wooded landscape elements were similar to those of the current organic matter inputs (roots and litter), indicating that this fraction was comprised almost exclusively of carbon from the present  $C_3$  plant cover and that carbon turnover in this particle size fraction has been rapid. Mass spectrometric analyses of sand-associated organic carbon have revealed that this fraction is almost identical biochemically to recent plant residues (Schulten et al., 1993), and the labile nature of this carbon pool has been well-documented (Balesdent et al., 1987; Martin et al., 1990; Andreux et al., 1990; Bonde et al., 1992; Christensen, 1992).

$\delta^{13}C$  values of whole-soil organic carbon in transitional and drainage woodlands were usually within  $1\text{--}2\text{‰}$  of those in the remnant grasslands throughout the soil profile, indicating that these  $C_3$  woodlands are recent in origin, and have contributed little to the soil organic carbon pool. Whole-soil  $\delta^{13}C$  values of drainage woodland soils were actually higher than those of the upland grasslands from 15 to 120 cm in the profile. This indicates that  $C_4$  dominance and productivity at this site was once greatest in these low-lying landscape positions. This inference from the isotopic record is substantiated by estimates of net primary production in relict grasslands in this area (SCS, 1979). Annual production in drainage soils (e.g., Clareville and Racombes Series) in a normal rainfall year is ca.  $560 \text{ g m}^{-2}$ , whereas annual production from upland soils (e.g., Runge and Miguel Series) is ca.  $390$  to  $540 \text{ g m}^{-2}$ .

In contrast,  $\delta^{13}C$  values of soils in the clusters and groves were generally

2–5‰ lower than those in the adjacent upland grasslands. Lower  $\delta^{13}\text{C}$  values in the clusters and groves might indicate that woody plants have occupied these portions of the landscape for longer periods of time. However, the age–class distributions and demographic characteristics of *P. glandulosa* (Fig. 3) suggests that this is not the case, since tree stems in upland groves and drainage woodlands were of comparable median age (45 years), which was more than twice that of tree stems in clusters and transitional woodlands (20 years).

We suggest that  $\delta^{13}\text{C}$  values of soil organic carbon were higher in drainage and transition woodlands not because they developed on the landscape more recently than clusters and groves, but because soil organic matter turnover has been slower in those lower-lying landscape elements. A potential mechanism for slower turnover in these lower-lying woodlands might be the formation of highly stable aggregates which develop in the presence of high clay and calcium concentrations. Clay (Fig. 2) and calcium concentrations (unpublished) in drainage and transition woodlands are approximately twice those in groves and clusters. These high clay and calcium concentrations in low-lying landscape positions could promote the formation of aggregates which are physically, chemically, and biologically stable, thereby protecting organic matter from mineralization (Oades, 1988). Slower organic matter turnover rates in the lowlands would favor the persistence of carbon derived from the original  $\text{C}_4$  grasslands, resulting in the relatively high  $\delta^{13}\text{C}$  values observed in those landscape positions. Indeed,  $^{14}\text{C}$  measurements of soil organic carbon (Fig. 8; Table 5) indicate that, below 15 cm in the profile, the MRT of organic carbon is greater (or the turnover rate is slower) in drainage and transition woodlands than in upland groves. However, MRTs of soil organic carbon in the 0–15 cm depth are comparable for upland groves (37–66 years) and drainage woodlands (39–69 years), suggesting that further work is needed to understand the precise nature of the isotopic differences among the wooded landscape elements.

In all landscape elements,  $\delta^{13}\text{C}$  values of whole soils and particle size fractions decrease at depths greater than 60 cm in the profile. Several explanations for this phenomenon are possible. First, the decline in  $\delta^{13}\text{C}$  values at depth may be a consequence of  $\text{C}_4$  grass replacement by more deeply rooted  $\text{C}_3$  forbs (in grasslands) and woody plants (in clusters, groves, and woodlands). Because organic carbon concentrations are relatively low below 60 cm (ca. 0.3%), the addition of new carbon by deep  $\text{C}_3$  roots may have a disproportionately large impact on the  $\delta^{13}\text{C}$  of soil organic carbon. Second, these  $\delta^{13}\text{C}$  values and their associated MRTs (1400–2800 years) may reflect the presence of mixed  $\text{C}_3$ – $\text{C}_4$  plant communities at this site in the more distant past. Third, some proportion of the organic carbon present below 60 cm may have been inherited from the depositional processes that formed this landscape (Wilding et al., 1996), and therefore may be unrelated to the recent vegetation history of this site. At present, there is insufficient evidence to evaluate the relative merit of each of these possibilities.

### 4.3. Corroboration with other studies

Early studies at the La Copita site assumed that small woody plants and woody patches represented young plants and early stages of succession, and that larger plants and patches represented older plants and more advanced stages of succession (Archer et al., 1988). Although this 'space-for-time substitution' has been used widely in plant ecology to infer plant and community development, it can generate misleading interpretations (Austin, 1977; Shugart et al., 1981). Direct assessments and measurements of vegetation change are preferable. An earlier study at the La Copita site analyzed plant and soil  $\delta^{13}\text{C}$  and demonstrated that  $\text{C}_3$  shrub clusters in uplands have developed on sites dominated previously by  $\text{C}_4$  grasses, and that soil  $\delta^{13}\text{C}$  value decreased (became more  $\text{C}_3$ -like) with increasing size of *P. glandulosa* plants and clusters (Tieszen and Archer, 1990). However, their data did not provide a time-line for the change in vegetation composition, nor did it address the vegetation history of other key landscape elements: groves and woodlands (Fig. 1).  $\delta^{13}\text{C}$  and  $^{14}\text{C}$  data from this study indicate that groves and woodlands also occupy sites dominated previously by  $\text{C}_4$  grasses (Figs. 6 and 7), and indicate that this grassland-to-woodland shift occurred within the past 50–100 years (Table 5). In addition, our data on *P. glandulosa* stem demographics suggests that invasion of grass-dominated patches has occurred over the past 100 years, with greatest woody plant recruitment in upland groves and lowland drainages (Fig. 3). Stem age cannot necessarily be equated with plant age for woody species such as *P. glandulosa* which are capable of vegetative regeneration. However,  $^{14}\text{C}$  dates of *P. glandulosa* lignotubers indicate that plant ages are in fact 'modern' (< 200 years) (Archer, 1995). In addition, we know from aerial photos that groves and clusters have increased markedly in size, and that woodland margins have migrated up-slope since 1941 (Archer et al., 1988; Stroh, 1995). Model-generated reconstructions based on dynamic simulations of *P. glandulosa* and cluster growth rates (Archer, 1989) and patch transition probabilities (Scanlan and Archer, 1991) also suggest recent development of  $\text{C}_3$  woody plant communities. Taken together, these studies support the conclusion that: (a) a shift from grass to woody plant domination has occurred across the entire landscape; and (b) this vegetation change has taken place over the past 100 years.

Historical accounts and archeological records often indicate that woody vegetation was present in grasslands, but restricted to riparian corridors. It is inferred that woody plants have subsequently spread from these historic enclaves and increased in abundance in other portions of the landscape (Archer et al., 1988; Steuter et al., 1990; Archer, 1994). Historical records from the vicinity of our study site in southern Texas also indicate that woodlands may have occurred in intermittent drainages and riparian corridors at the time of Anglo-European settlement (Inglis, 1964). However, our  $\delta^{13}\text{C}$  and  $^{14}\text{C}$  measurements on soil organic carbon indicate that vegetation of intermittent drainages at La Copita

(Fig. 1) was once grassland or open savanna dominated by  $C_4$  grasses (Figs. 6 and 7). The age-class distribution of *P. glandulosa* stems in drainage and transitional woodlands (Fig. 3) suggests:

1. that development of woodlands in this landscape location has been relatively recent (within the past 100 years);
2. that *P. glandulosa* recruitment over the past 100 years was greatest in the low-lying portions of intermittent drainages;
3. that up-slope expansion of woodland boundaries has occurred over the past 60 years; and
4. that significant self-thinning may eventually occur in transitional woodlands as *P. glandulosa* plants continue to grow and mature.

## 5. Summary

Plants with  $C_3$ ,  $C_4$ , and CAM photosynthesis have unique  $\delta^{13}C$  values which are not altered significantly during decomposition and soil organic matter formation. Consequently,  $\delta^{13}C$  values of soil organic carbon reflect the relative contribution of plant species with  $C_3$ ,  $C_4$ , and CAM photosynthetic pathways to community net primary productivity, and have been utilized to document vegetation change in natural and managed ecosystems.

We used  $\delta^{13}C$  values of soil organic matter, above- and belowground plant biomass, and litter in conjunction with radiocarbon dating and dendrochronology to test the hypothesis that, in the Rio Grande Plains of southern Texas,  $C_4$  grasslands and savannas have been largely replaced by  $C_3$  subtropical thorn woodlands dominated by *Prosopis glandulosa*, an  $N_2$ -fixing woody legume. Results indicated that current organic matter inputs (above- and belowground biomass and litter) were not in isotopic equilibrium with soil organic carbon in any of the vegetation types sampled.  $\delta^{13}C$  values of current organic matter inputs in wooded landscape elements were typical of  $C_3$  plants and ranged from  $-28$  to  $-25\text{‰}$ , while those of the associated soil organic matter were between  $-20$  and  $-15\text{‰}$ . These contrasting  $\delta^{13}C$  values indicate that woodlands, groves, and shrub clusters now dominated almost exclusively by  $C_3$  plants, occupy sites once dominated by  $C_4$  grasses. The presence of the  $C_4$  grasslands that once occupied these sites was most evident in the  $\delta^{13}C$  values of organic carbon associated with fine and coarse clay ( $-18$  to  $-14\text{‰}$ ), probably a consequence of slow organic carbon turnover rates in those soil fractions.

When  $\delta^{13}C$  values of soil organic carbon are evaluated in conjunction with radiocarbon measurements of that same carbon, it appears that this vegetation change from  $C_4$  grassland to  $C_3$  woodland occurred recently, probably within the last 50–100 years. Demographic characteristics of the dominant tree species corroborate the  $\delta^{13}C$  and  $^{14}C$  evidence, and indicate widespread establishment of *P. glandulosa* and associated shrubs over the past 100 years. Together, these

data provide direct, spatially explicit documentation of a shift from C<sub>4</sub> grass to C<sub>3</sub> woody plant domination across the entire landscape in this study area.

Environmental conditions where C<sub>3</sub>, C<sub>4</sub>, and CAM plants coexist (e.g., dry, alkaline soils) generally do not favor the preservation of pollen and phytoliths, and these same areas usually lack historical records of vegetation change. Consequently, vegetation dynamics have been difficult to quantify in grasslands, savannas, and woodlands. However, our results demonstrate clearly that  $\delta^{13}\text{C}$  values of soil organic matter afford a direct and powerful technique for reconstructing vegetation change in these areas.

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