

Sean L. Connin · R.A. Virginia · C.P. Chamberlain

Carbon isotopes reveal soil organic matter dynamics following arid land shrub expansion

Received: 17 May 1996 / Accepted: 12 November 1996

Abstract Over the past century, overgrazing and drought in New Mexico's Jornada Basin has promoted the replacement of native black grama (*Bouteloua eriopoda* Torr.) grass communities by shrubs, primarily mesquite (*Prosopis glandulosa* Torr.). We investigated the effects of shrub expansion on the distribution, origin, turnover, and quality of light (LFC) and heavy (HFC) soil organic matter (SOM) fractions using $\delta^{13}\text{C}$ natural abundance to partition SOM into C_4 (grass) and C_3 (shrub) sources. Soil organic matter beneath grasses and mesquite was isotopically distinct from associated plant litter, providing evidence of both recent shrub expansion and Holocene plant community changes. Our $\delta^{13}\text{C}$ analyses indicated that SOM derived from mesquite was greatest beneath shrub canopies, but extended at least 3 m beyond canopy margins, similar to the distribution of fine roots. Specific ^{14}C activities of LFC indicated that root litter is an important source of SOM at depth. Comparison of turnover rates for surface LFC pools in grass (7 or 40 years) and mesquite (11 or 28 years) soils and for HFC pools by soil depth (~150–280 years), suggest that mesquite may enhance soil C storage relative to grasses. We conclude that the replacement of semiarid grasslands by woody shrubs will effect changes in root biomass, litter production, and SOM cycling that influence nutrient availability and long-term soil C sequestration at the ecosystem level.

Key words Carbon isotope · Carbon cycling · Mean residence time · Root distribution · Desertification

S.L. Connin (✉)
Department of Earth Sciences, Dartmouth College,
Hanover, NH 03755, USA
Fax: 520-670-6806; e-mail: lachlan @sun1paztcn.wr.usgs.gov

R.A. Virginia
Environmental Studies Program, Dartmouth College,
Hanover, NH 03755, USA

C.P. Chamberlain
Department of Earth Sciences, Dartmouth College,
Hanover, NH 03755, USA

Introduction

Spatial patterns of soil fertility and net primary productivity (NPP) are closely linked to soil organic matter (SOM) pools in desert ecosystems (Garcia-Moya and McKell 1970). As a result, the distribution, quality, and turnover of SOM may control structural/functional properties of dryland communities and their response to human disturbance and climate change (Schlesinger et al. 1990). In desertified arid lands worldwide, woody shrubs have proliferated at the expense of perennial grasses (Kelly and Walker 1976; Van Vegten 1983; Archer et al. 1988). Shrub expansion alters community-level SOM storage and cycling (Connin et al., in press). However, its impact on the distribution, quality, and residence time of active and stable SOM fractions are still poorly understood. These data will be necessary to predict the long-term consequences of vegetation change on carbon (C) cycling, soil fertility, and NPP in arid land ecosystems.

In New Mexico's Jornada Basin, replacement of perennial black grama (*Bouteloua eriopoda* Torr.) grasslands by woody shrubs, primarily mesquite (*Prosopis glandulosa* Torr.), has been attributed to overgrazing by livestock and recurrent periods of drought since the late 1800s (Buffington and Herbel 1965; Hennessy et al. 1983; Gibbens and Beck 1985). The associated ecosystem-scale changes have included reduced vegetative cover, increased soil erosion, and an increase in the spatial variation of soil moisture (Schlesinger et al. 1990). As a result, detrital production and biotic activity are now concentrated beneath shrub canopies, forming the "islands of fertility" that characterize many desert shrublands worldwide (Garcia-Moya and McKell 1970; Virginia and Jarrell 1983; Goldberg and Turner 1986).

Shrub expansion also changes the distribution and proportion of fine and coarse root biomass in desertified communities. These transformations, in turn, may alter the composition and turnover of constituent SOM pools. An increase in mesquite dominance has been shown to alter belowground production, from fine root biomass distributed in surface horizons to deeper coarse root bio-

mass concentrated beneath shrub canopies (Cable 1969; Heitschmidt et al. 1988; Brown and Archer 1990). While total root weight increases in soils beneath mesquite, relative to grasses (McPherson et al. 1993), the proportion of fine root biomass (<2 mm) apparently declines (Virginia et al. 1992). These changes may be linked to SOM loss in mesquite vs. mixed mesquite/grass habitats in the Jornada Basin (Virginia et al. 1992). However, we do not know if these differences in SOM content between communities reflect a transient vs. equilibrium response to shrub establishment.

Short- (i.e., historical) and long-term impacts of shrub expansion on SOM may be distinguished by differentiating between active (turnover, τ , one to tens of years) and stable (τ hundreds to thousands of years) SOM fractions, respectively (Cheng and Molina 1995; Connin et al., in press). Loss of SOM in Jornada mesquite dunes probably results from removal of active substrates linked to low-density (<2.0 g/cm³) or "light" SOM (LFC), which responds rapidly to changing litter inputs (Spycher et al. 1983) and/or mineralization rates (Janzen et al. 1992). Loss of heavier (>2.0 g/cm³), more stable substrates (HFC) may also have contributed to these changes. In either case, soil nutrient availability and long-term C storage capacity may be altered by variations in LFC and HFC pools, respectively (Spycher et al. 1983; Sollins et al. 1984). Therefore, to understand specific impacts of shrub expansion on soil fertility and C storage, we must first identify changes in the origin, distribution, and turnover of LFC and HFC.

Natural ¹³C isotope abundance techniques have been used to proportion SOM by fraction based on the photosynthetic pathway of contributing plant species (Dzurec et al. 1985). The average $\delta^{13}\text{C}$ value of C₄ plant tissue (-12‰) is distinct from C₃ plants (-26‰) (Bender 1968; Smith and Epstein 1971); these differences are maintained in plant litter (Ludlow et al. 1976). Thus, the $\delta^{13}\text{C}$ of SOM can be used to identify C₃/C₄ vegetation changes along modern ecotones (Dzurec et al. 1985; Mariotti and Peterschmidt 1994), including the displacement of C₄ grasses by C₃ shrubs (McPherson et al. 1993). Since black grama is a C₄ plant and mesquite is a C₃ plant, SOM derived from these species is isotopically distinct.

We hypothesized that the historical replacement of Jornada grasslands by mesquite has produced discernible changes in LFC and HFC pools which can be directly linked to patterns of nutrient cycling and soil C storage. We also predicted that the shift from C₄ to C₃ dominance created differences in the $\delta^{13}\text{C}$ of plants and associated SOM. The objectives of this study were: (1) to identify changes in SOM production and plant rooting patterns following mesquite establishment, (2) to determine the spatial extent and rate at which mesquite influence LFC and HFC pools, and (3) to quantify the mean residence time (MRT) of LFC and HFC fractions. To test our predictions, we used ¹³C natural abundance techniques, ¹⁴C dating, and C/N analyses to examine changes in the amount, distribution, source (C₃ or C₄), quality, and flux-

es of LFC and HFC following mesquite expansion in the Jornada Basin.

Methods

Site description

This study was conducted at the USDA Jornada Experimental Range approximately 40 km north-northeast of Las Cruces, Dona Ana County, N.M., USA. The study area encompasses approximately 18,266 ha of the Jornada Del Muerto basin in the northern Chihuahuan Desert (Hennessy et al. 1983) ranging in elevation from 1,260 m on basin plains to 2,833 m at the crest of the San Andres Mountains (Gibbens et al. 1983). Mean annual precipitation is 211 mm (Houghton 1972) with 53% falling between July and September. The mean annual temperature is 15.6° C. However, ambient conditions are variable, with temperatures occasionally falling below freezing during winter months and exceeding 40° C in the summer (Buffington and Herbel 1965).

We sampled a remnant C₄-dominated grass community and an adjacent mesquite dune complex to evaluate changes in SOM following shrub expansion. Both communities reside on fluvial basin sediments of the early-to mid-Pleistocene La Mesa Geomorphic Surface (400–1,500 ka) (Gile and Grossman 1979). The grassland site is dominated by the C₄ grasses black grama, poverty threeawn (*Aristida divaricata* Willd.), and mesa dropseed (*Sporobolus flexuosus* Thurb.). Interspersed C₃ species include mesquite and yucca (*Yucca elata* Engelm.). Soils consist of coarse loamy, mixed, thermic Typic Haplargids or loamy, mixed, thermic Typic Calciorthids (Gile and Grossman 1979).

The dune site is dominated by mesquite. Four-wing salt bush (*Atriplex canescens* (Pursh) Nutt.), a C₄ shrub, and bush muhly (*Muhlenbergia porteri* Scribn.), a C₄ grass, occur infrequently beneath shrub canopies. Intershrub surfaces may contain scattered C₃ species such as broom snakeweed (*Gutierrezia sphaerocephala* Gray), but are largely unvegetated. Aeolian processes have modified soil profiles such that surface horizons are eroded from intershrub soils and coarser particle fractions are, in part, redeposited beneath mesquite, forming coppice dunes (Hennessy et al. 1985). As a result, dunes consist of mixed Typic Torripsamments, while interdune soils are taxonomically equivalent to the Calciorthid grassland soils (Gile and Grossman 1979). Most dunes range from 0.3 to 2.5 m in height and 1.5 to 12 m in width (Gile 1966) and are less than 100 years old (Gile and Grossman 1979).

Sample collection

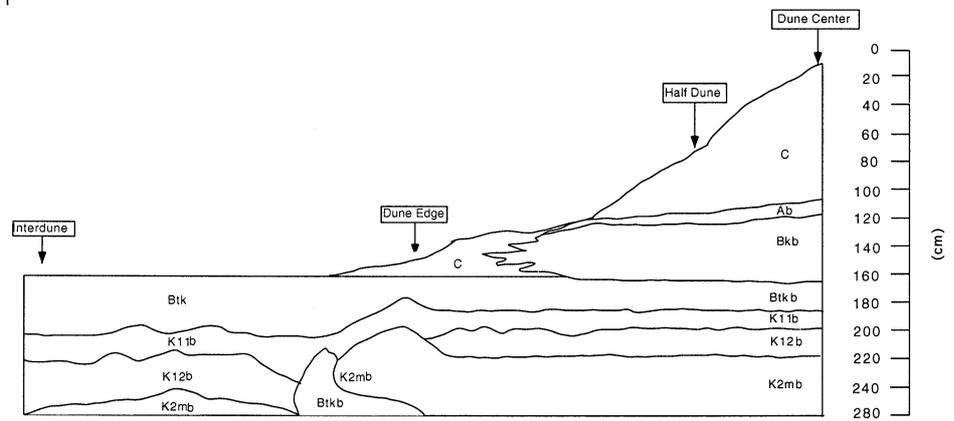
Mesquite dunes

During March 1994, we excavated trenches in two mesquite coppice dunes (D1 and D2). The selected dunes were >1 m in height above surrounding deflational surfaces, at least 10 m (at their periphery) from adjacent dunes, and showed little evidence of burrowing activity. Trenches (~1.5 m wide) were excavated with a backhoe from north to south extending 3 m beyond the edge of each dune. In the interdune soils, trenches extended to 1 m depth, providing a lower baseline for sampling within dunes. At the time of sampling, no C₄ species were evident.

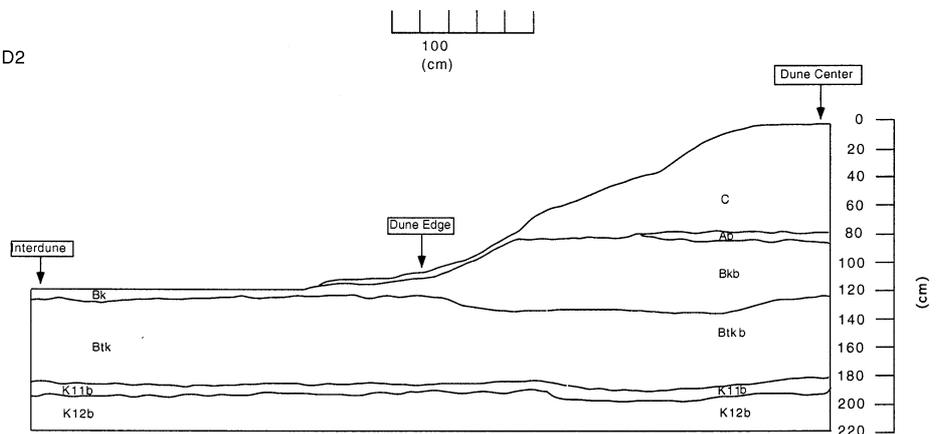
Following excavation, grids divided into 20-cm² sections were placed along the western face of each trench and root intersections in three size classes (<3 mm, 3–10 mm, >10 mm) were counted to estimate root densities. Soils were collected at 10-cm depth increments at dune center, half dune (i.e., midway between dune center and edge), dune edge, and 3 m beyond the dune periphery (Fig. 1). Soil $\delta^{13}\text{C}$ analyses were limited to a subset of the material collected. In D1, we analyzed soils at 10-cm depth intervals from all four positions along the dune complex. Having defined the major isotopic trends, we reduced our analyses in D2 to three positions, measured at 20-cm intervals.

Fig. 1 Soil profile characteristics in two mesquite dune trenches: **A** D1, **B** D2. Capital letters *A*, *B*, *C*, and *K* represent master horizons. We use the *K* horizon to designate a zone of maximum CaCO_3 accumulation (Gile et al. 1965). Intra-horizon subdivisions are represented by *number*. Lower case letters (used as suffixes) represent specific kinds of master horizons: *b* buried, *t* accumulation of silicate clay, *k* accumulation of carbonates, *m* indurated

A. D1



B. D2



Grassland

In August 1994, three trenches (6 m long \times 1.5 m wide \times 1 m deep) were excavated in the grassland site. The replicate trenches were located 100–200 m apart. Locations were selected such that distances to nearby C_3 plant species (including mesquite) exceeded 5 m. Root densities were counted by size class and soils were collected at 10-cm depth increments along three positions, one in the middle and two at either end of each trench. Four profiles (TG1, TG2, TG3, TG4) were selected for subsequent $\delta^{13}\text{C}$ analyses (Fig. 2). In TG1, $\delta^{13}\text{C}$ SOM values were determined at 10-cm increments to insure adequate sampling resolution; all other profiles were analyzed at 20-cm increments.

Replicate mesquite and grass litter samples were collected at several locations in the basin to determine the $\delta^{13}\text{C}$ values of end-member vegetation types (i.e., C_4 grass vs. C_3 mesquite) and to examine $\delta^{13}\text{C}$ variability within individual species (e.g., Ehleringer and Cooper 1988). Similarly, mesquite roots (<2 mm) were collected within dune profiles to identify any systematic $\delta^{13}\text{C}$ variations in tissues, related to rooting depth, which might influence $\delta^{13}\text{C}$ values of associated litter.

Sample preparation and analyses

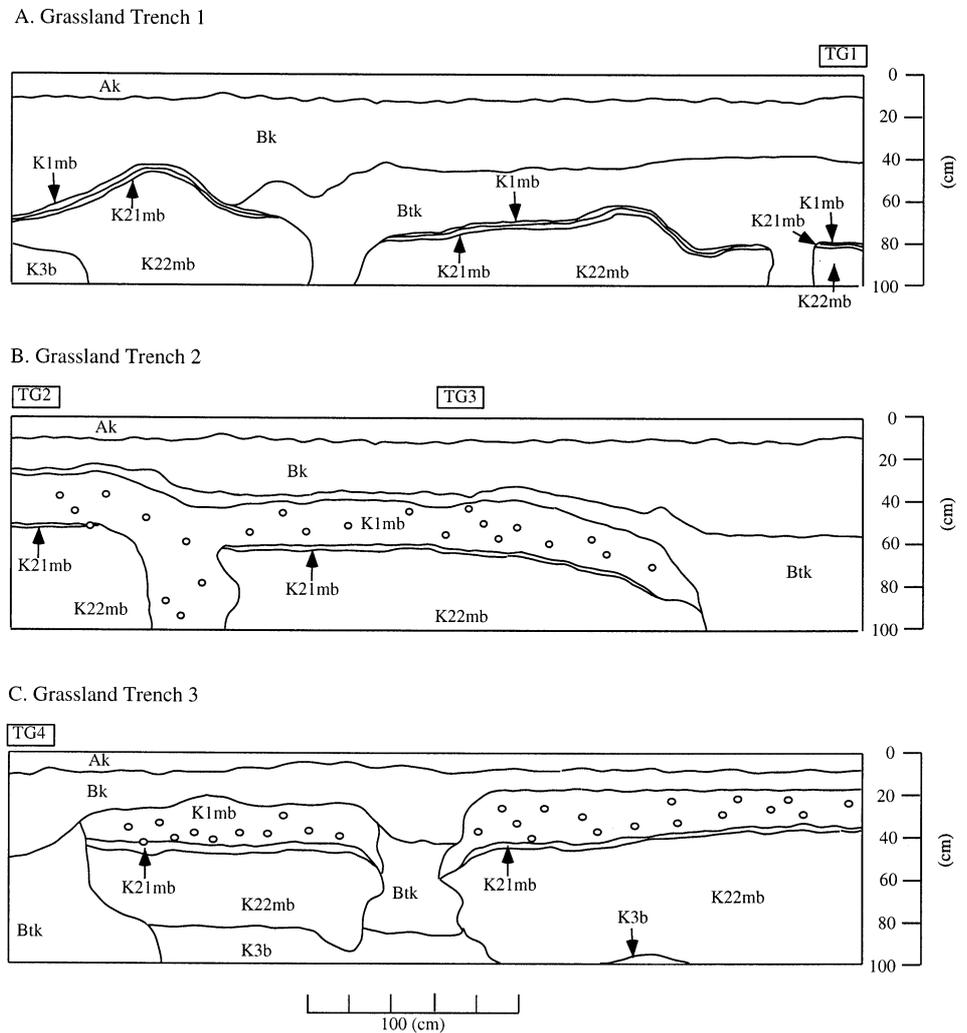
Plant tissues were dried overnight at 55° C, ground to <0.4 mm diameter in a mixing mill, homogenized, and stored. Soils were passed through a 2-mm sieve; organic litter and roots >2 mm were removed by hand and stored separately. Light and heavy SOM (Stevenson and Elliott 1989) were separated from soil subsamples

(~30 g) by flotation in a 1.2 g·cm⁻³ NaCl solution following the methods of Strickland and Sollins (1987). Together, LFC and HFC represent labile and stable detrital pools, respectively (Sollins et al. 1984; Hsieh 1992). The LFC was treated with 1 M HCl to remove CaCO_3 , then rinsed with deionized water, oven dried at ~60° C, and homogenized prior to analysis. The HFC was treated three times with 1 M HCl and then washed three times with deionized water. The carbonate-free soils were then dried and homogenized. Inspection of the treated soils under a microscope (at 300 \times) and by SEM imagery indicated that carbonate and LFC removals were complete.

Carbon isotope ratios of plant tissue and SOM were determined by stable isotope ratio mass spectrometry measured from cryogenically purified CO_2 following combustion at 900° C (Boutton 1991). $^{13}\text{C}/^{12}\text{C}$ ratios were measured on a Finnigan delta E gas source mass spectrometer at the Dartmouth college D-LITE laboratory. All results are expressed in delta notation ($\delta^{13}\text{C}$) where: $\delta^{13}\text{C} = (R_{\text{sample}}/R_{\text{std}} - 1) \times 1000$; R_{sample} and R_{std} are the absolute $^{13}\text{C}/^{12}\text{C}$ ratios of sample and standard, respectively. $\delta^{13}\text{C}$ values are reported in parts per thousand (‰) relative to the Vienna Pee Dee Belemnite (VPDB) standard (Coplen 1994). Sample precision (± 1 SD), for bulk plant tissue and SOM depends largely upon sample heterogeneity. At a given location and soil depth, LFC and HFC $\delta^{13}\text{C}$ values varied by $\pm 0.2\text{‰}$ and $\pm 0.3\text{‰}$, respectively, similar to plant litter collected at individual locations ($\pm 0.2\text{‰}$).

Percent organic C was determined by dry combustion on a Carlo Erba CHN analyzer following soil pretreatment with 1 M HCl to remove CaCO_3 (Pella and Colombo 1973). Attempts to acidify soils within sample cups (e.g., Nieuwenhuize et al. 1994) were unsuccessful, due to material loss during the dissociation of

Fig. 2A–C Soil profile characteristics in three grassland trenches. *Numbered boxes* refer to sample locations. Capital letters *A*, *B*, and *K* represent master horizons. We use the *K* horizon to designate a zone of maximum CaCO_3 accumulation (Gile et al. 1965). Intra-horizon subdivisions are represented by number. *Lower case letters* (used as suffixes) represent specific kinds of master horizons: *t* accumulation of silicate clay, *k* accumulation of carbonates, *m* indurated, *b* buried



CaCO_3 . Therefore, soils (~50 g) were acid-pretreated in 250-ml glass beakers, rinsed with deionized water, oven dried at ~60°C, and homogenized. Organic C was then measured in samples of the carbonate-free sediment. Percent C in HFC was measured on soils pretreated to remove LFC; percent C in LFC was then calculated as the difference between total organic C and HFC. Results for all organic C fractions are reported as a proportion of total soil weight using percent total C (measured on untreated soils) to correct for CaCO_3 loss during pretreatment. Repeated C analyses ($n=10$) of individual soils yielded a precision of 0.02%. Comparisons of organic C pools by horizon between grassland profiles and mesquite dunes were made by a student's t-test with equal variance using the SAS statistical package (SAS 1987).

Selected LFC, HFC, and pedogenic CaCO_3 samples were sent to Beta Analytic (Miami, Fla.) for ^{14}C dating by Accelerator Mass Spectrometry (e.g., Trumbore et al. 1989). Isotopic $^{14}\text{C}/^{12}\text{C}$ ratios of graphite targets made from the samples were measured using AMS facilities at the Lawrence Livermore National Laboratory (USA). Relative ^{14}C specific activities were normalized to a fixed $\delta^{13}\text{C}$ value of -25.0‰ and expressed as a percentage of a modern standard, which is 95% of the activity of National Bureau of Standards' oxalic acid.

Calculations

Soil organic matter was partitioned into shrub (shrub-C) and grass (grass-C) source as follows: $\delta_1 = \chi \times \delta_0 + (1 - \chi) \times \delta_2$; where δ_1 is the $\delta^{13}\text{C}$ of bulk SOM, δ_0 is the $\delta^{13}\text{C}$ of grass-C, δ_2 is the $\delta^{13}\text{C}$ of

shrub-C, and χ is the proportion of grass-C remaining in the soil (Martin et al. 1990). The loss of grass-C from shrub HFC pools was calculated, assuming bulk densities of equivalent grass/dune soil horizons are similar (Gile and Grossman 1979), as: $C_4^- \text{ loss} = \chi_1 - \chi_2 (H_2/H_1)$; where χ_1 and χ_2 are the percentage of grass-C in HFC pools from grass and dunes soils (respectively), and H_1 and H_2 are percentage of HFC (by weight) in grass and dunes soils, respectively. In this context, the mean residence time (MRT) of HFC can be estimated assuming exponential decay: $\text{MRT} = k \{ -(\ln[C_t/C_0]) / \Delta t \}$; where k is the mean decay constant, C_t is the percentage of grass-C at some time t after shrub establishment, C_0 is the percentage of grass-C just before shrub establishment (t_0), and $\Delta t = t - t_0$ (Jenkinson and Rayner 1977).

We derived MRT values for LFC pools using a decomposition model that relates annual variations in atmospheric ^{14}C levels and residue bomb C to the ^{14}C activity and MRT of active SOM (Hsieh 1993). This model has the following form:

$$A_a = \sum_{i=b}^p \exp[-k(p-i)] \times {}^{14}\text{C}_i \exp[-(p-i)/8268] / \sum_{i=b}^p [- (p-i) / \text{MRT}]$$

where A_a is the specific ^{14}C activity of an active SOM pool, k is a first order decay constant, p is the year when the soil was sampled, ${}^{14}\text{C}_i$ is the specific activity in the atmosphere of the year i , and 8268 years is the MRT of ^{14}C . Assuming steady-state turnover for LFC pools and that ^{14}C sources to these pools are equilibrated with atmospheric ^{14}C , MRTs in the range of 1–80 years can be calculated (Hsieh 1993).

Results

Root distributions

Mesquite encroachment caused fundamental changes in the size, density, and distribution of root biomass (Figs. 3 and 4). In grassland trenches, fine root (<3 mm diameter) abundance was greatest in the top 40 cm, but fine roots occurred at depths up to 1 m. Under mesquite, fine roots occurred at depth (up to 2 m) and were present in interdune soils. Overall, fine root densities were lower in the dune profiles than in the grassland profiles. Coarse roots in 3- to 10- and >10-mm size classes were absent in grassland profiles, but appeared in both dunes, reflecting a shift in belowground biomass toward larger and deeper woody roots. The largest roots (>10 mm) occurred directly beneath mesquite canopies due to strong taproot development, which is characteristic of this species (Ludwig 1977). Roots in the 3- to 10-mm size class were present well beyond shrub canopies, at depths up to 80 cm.

Fig. 3 Rooting densities in sample grids (20 cm²) along three grassland trenches. The number of fine root (<3 mm diam.) intersections are represented by *grid pattern*

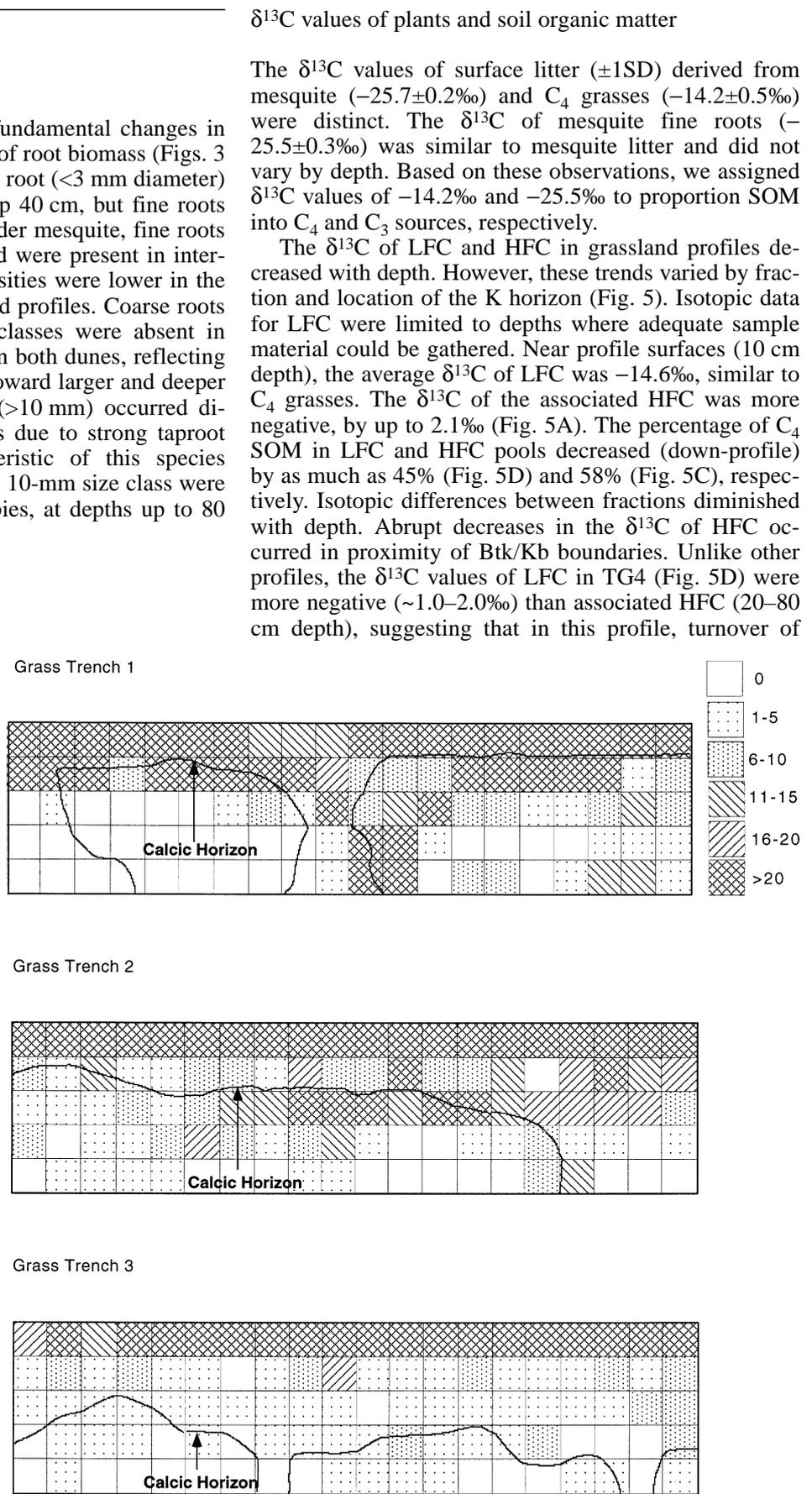
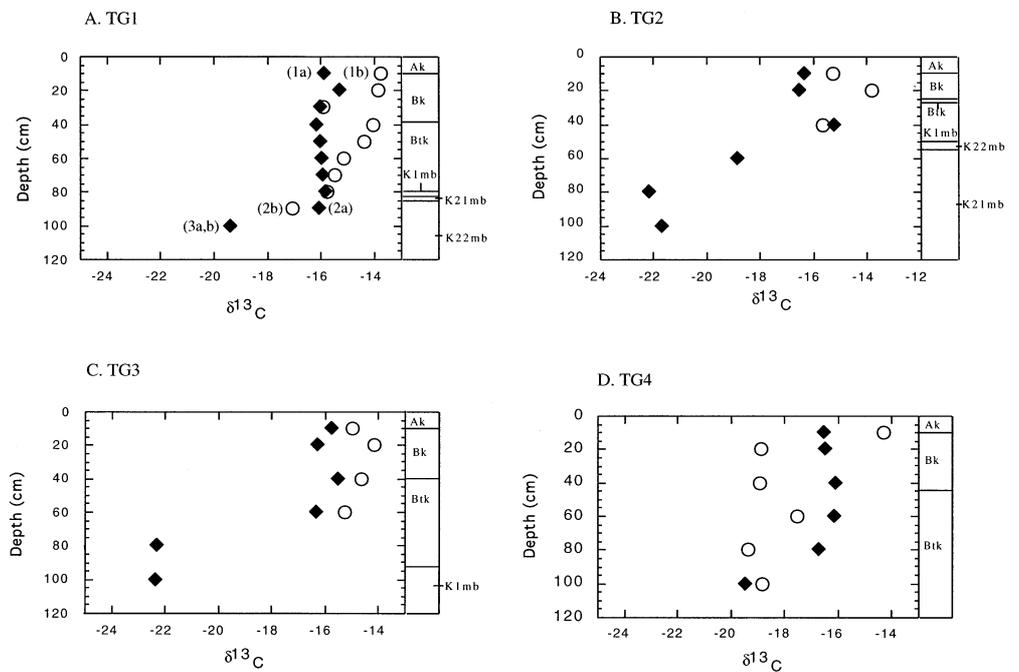


Fig. 4A, B Rooting densities in sample grids (20 cm²) along two mesquite dune trenches. The number of fine root (<3 mm diam.) intersections are represented by *grid pattern*. Root counts in 3–10 and >10 mm diam. size classes (when present) are *numbered*, respectively



Fig. 5A–D $\delta^{13}\text{C}$ values of light (*open circles*) and heavy (*shaded diamonds*) soil organic matter fractions in four grassland profiles. *Numbered* data points refer to ¹⁴C ages listed in Table 2

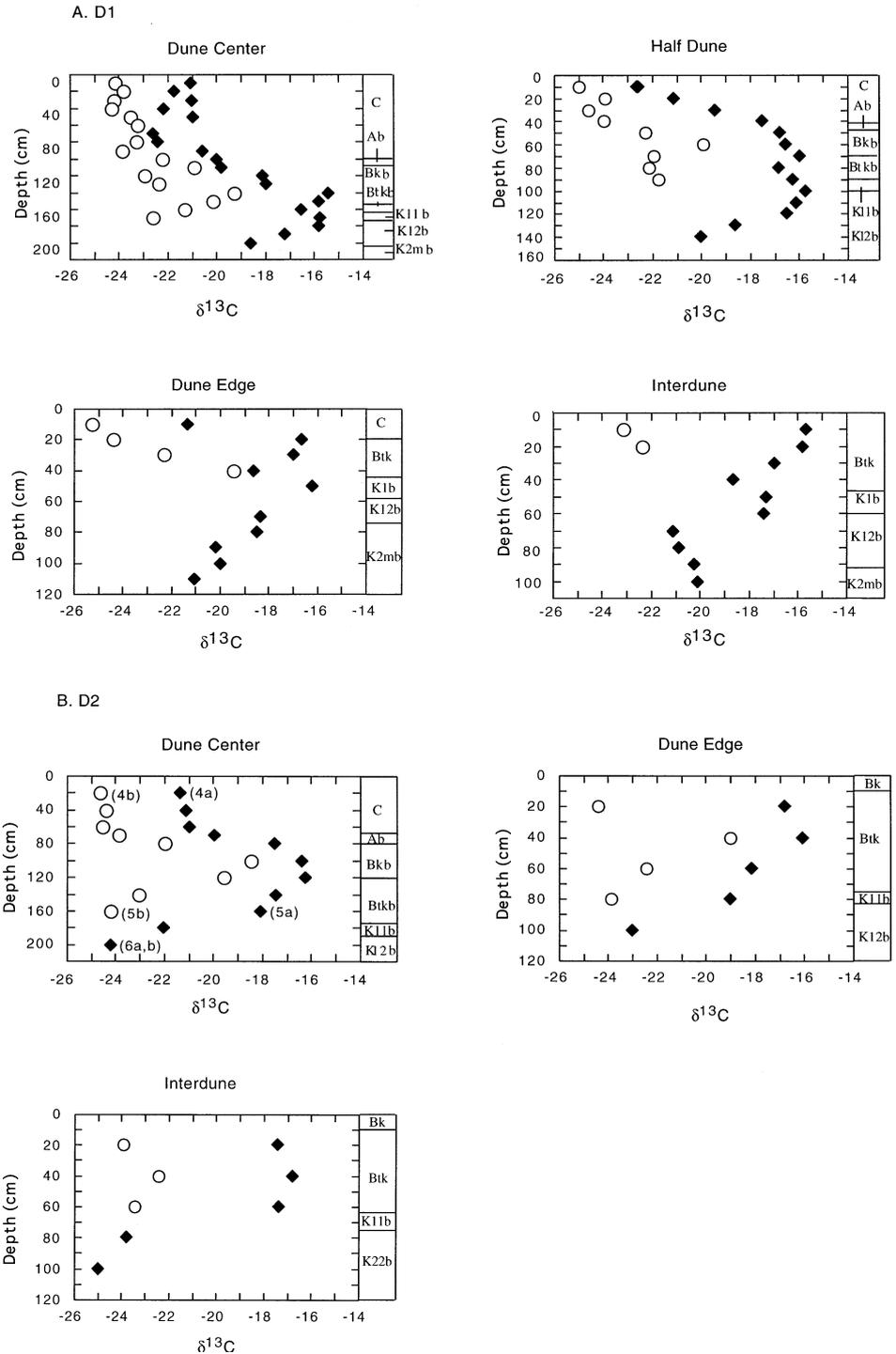


LFC is slower than HFC. More likely, these results reflect an accumulation of shrub-C from a nearby mesquite (~7 m distance) which may be rooting into the soil pipe (i.e., vertical extension of Btk horizon) that this profile bisects (Fig. 2). Ludwig (1977) suggests that Jornada

shrubs concentrate roots within soil pipes to access accumulating soil moisture.

Modern shrub-C can be discerned from “inherited” grass-C from the $\delta^{13}\text{C}$ profiles of SOM in mesquite dunes (Fig. 6). In general, mesquite contribution to SOM

Fig. 6 $\delta^{13}\text{C}$ values of light (*open circles*) and heavy (*shaded diamonds*) soil organic matter fractions in **A** dune 1 (*D1*) and **B** dune 2 (*D2*). Numbered data points refer to ^{14}C ages listed in Table 2



pools decreased with increasing depth and distance from dune center. At the center of D1 (Fig. 6A), the $\delta^{13}\text{C}$ of HFC increased down-profile from -21.9‰ to -15.4‰ between 10 and 140 cm, then decreased to -18.6‰ at 200 cm. The $\delta^{13}\text{C}$ of LFC was relatively constant between 10–90 cm ($\sim -21.3\text{‰}$) but varied irregularly between 100 and 170 cm. The $\delta^{13}\text{C}$ of LFC was consistently less than associated HFC, by an average of 2.8‰.

Variation of $\delta^{13}\text{C}$ values between LFC and HFC pools and soil depth were consistent between dune and inter-

dune profiles. However, erosion of A and Bk horizons in interdune soils effectively removed the upper portion of the HFC $\delta^{13}\text{C}$ profile. Similarly, LFC was limited to the surface 40 cm due to substrate loss above Kb horizons. The distribution of SOM $\delta^{13}\text{C}$ values was similar between D1 (Fig. 6A) and D2 (Fig. 6B), when compared by horizon. However, $\delta^{13}\text{C}$ values of LFC within interdune soils of D2 were more negative (up to 2‰). The lowest HFC $\delta^{13}\text{C}$ value (-24.9‰) of any soil profile occurred in the K2b horizon of D2.

Table 1 Comparison of C pools with equivalent grassland and mesquite dune soil horizons. Values were derived from sample measurements composited across profiles and by horizon within each site. Numbers within parentheses indicate ± 1 SD. Values for

carbon fractions in Dune C horizons were compared to values for equivalent pools from grassland Ak and Bk horizons combined. All C concentrations reported with respect to total soil weight

Horizon	Sample Number (n)	Total C (% by wt.)	Organic C (% by wt.)	Light fraction ^a (% by wt.)	Heavy fraction (% by wt.)	C ₄ carbon ^b Heavy fraction (%)	C ₄ carbon ^b Light fraction (%)
Composite Grassland Profile							
Ak	4	0.66 (0.25)	0.15 (0.02)	0.01 (0.02)	0.14 (0.02)	83 (4.0)	96 (4.0)
Bk	7	0.82 (0.42)	0.13 (0.05)	0.03 (0.03)	0.10 (0.03)	83 (4.0)	86 (20.0)
Btk	7	3.00 (0.88)	0.05 (0.01)	0.01 (0.01)	0.04 (0.01)	79 (12.0)	78 (17.0)
K1	4	11.19 (10.00)	0.04 (0.03)	--	0.04 (0.03)	80 (17.0)	0 --
K2	6	37.93 (13.51)	0.01 (0.01)	--	0.01 (0.01)	43 (22.0)	0 --
Composite Mesquite Dune Profile (Center)							
C	9	0.21 (0.08)	0.14 (0.05)	0.04 (0.03)	0.11 (0.03)	34 (6.0)***	14 (5.0)***
Ab	4	0.56 (0.22)	0.21 (0.04)*	0.07 (0.02)**	0.14 (0.03)	46 (3.0)***	28 (13.0)***
Bkb	5	1.19 (0.83)	0.12 (0.30)	0.03 (0.02)	0.08 (0.03)	76 (9.0)	42 (16.0)***
Btkb	6	1.99 (0.70)*	0.05 (0.02)	0.00 (0.01)	0.05 (0.02)	77 (9.0)	18 (14.0)***
K1	3	12.69 (2.65)	0.01 (0.01)	--	0.01 (0.01)	58 (39.0)	0 --
K2	2	43.87 (37.67)	0.01 (0.00)	--	0.01 (0.00)	48 (33.0)	0 --

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, *t*-test comparing soil parameters between equivalent grassland and dune soil horizons

^a Light fraction calculated as difference between total organic C and the heavy fraction

^b Percent C₄ derived within respective fractions

of D2 (76% and 26%, respectively; Fig. 7B); although shrub-C occurred to greater depth in D2. Similar levels of shrub-C (mean 64%) were detected in LFC pools beyond the boundaries of both dunes (Fig. 7A, B), but extended to a greater depth in D2. HFC pools contained higher levels of C₃-C in Kb horizons of D2, and to a lesser extent D1, relative to grassland Kb horizons. However, the absence of significant rooting activity or coexisting LFC suggests that such C₃-C existed prior to shrub establishment.

Soil organic matter: pools and chemistry

To assess direct effects of mesquite on SOM storage, we compared organic C pools in grassland and dune (center) soils (Table 1). Measurements were composited by site (due to the small number of samples) and compared across equivalent soil horizons. Overall, mesquite had little impact on SOM composition or storage. Total organic C and LFC increased in dune Ab horizons, relative to grasslands ($P > 0.05$ and 0.01, respectively), but were similar in all other horizons. No significant changes in HFC storage were detected ($P < 0.05$). However, relative amounts of C₄-C in both HFC (C-Ab horizons) and LFC (C-Btkb horizons) pools decreased beneath mesquite ($P > 0.001$). Changes in total soil C were limited to dune Btkb horizons, where a slight decrease occurred ($P > 0.05$).

Although the amount and proportion of HFC and LFC were similar between grass and shrub sites, mesquite have altered the chemistry of litter contributing to SOM pools. C/N ratios of LFC in the dunes (16.0 ± 4.0 ; $n=27$) were, on average, 36% less than those in grassland profiles (25 ± 13.0 ; $n=28$). C/N ratios of HFC were similar, 13.0 ± 2.0 ; $n=21$ vs. 11.0 ± 1.0 ; $n=28$ (respectively) and in

Table 2 Relative ¹⁴C specific activity and age of carbon fractions in a grassland and mesquite dune soil profile

Sample number	Depth (cm)	Carbon ^b fraction	¹⁴ C (% of modern ± 1 SD)	¹⁴ C age (yr BP ± 1 SD)
Grassland: profile TG1				
1a	10	HFC	94.1 \pm 0.6	490 \pm 60
1b	10	LFC	119.0 \pm 0.8	Modern
2a	90	HFC	76.9 \pm 0.5	2100 \pm (50)
2b	90	LFC	103.8 \pm 0.7	Modern
3a	100	HFC	30.6 \pm 0.2	9,510 \pm (60)
3b	100	CaCO ₃	8.0 \pm 0.08	20,270 \pm (80)
Mesquite: profile D2-Center				
4a	20	HFC	86.4 \pm 0.54	1,170 \pm (60)
4b	20	LFC	122.1 \pm 0.8	Modern
5a	160	HFC	53.6 \pm 0.34	5,010 \pm (60)
5b	160	LFC	103.0 \pm 0.7	Modern
6a	200	HFC	30.7 \pm 0.2	9,480 \pm (60)
6b	200	CaCO ₃	6.9 \pm 0.08	21,450 \pm (90)

^a Refer to Figs. 5 and 6

^b HFC and LFC refer to heavy and light soil organic matter fractions, respectively. CaCO₃ refers to pedogenic carbonate

general, less variable than those of LFC, consistent with previous SOM studies (e.g., Sollins et al. 1984).

Soil organic matter: ¹⁴C ages

The ¹⁴C ages of HFC increased with soil depth (to ~9.5 Ka BP) and exceeded those of coexisting LFC by ~100 years to 9.5 Ka (Table 2). In addition, specific ¹⁴C activities of LFC pools exceeded 100% (due to incorporation of bomb C), which is indicative of both rapid turnover and/or recent incorporation of plant litter (Jenkinson and Rayner 1977). HFC entrained in Kb horizons post-dates

the surrounding carbonate by ~10 Ka. Gile and Grossman (1979) reported similar "contamination" in pedogenic carbonates from the Jornada. Within both grass and mesquite soils, an unconformity at Btk/K1mb boundaries demarcates the position of an ancient erosional surface. As a result, we can only place the prehistoric C₃- to C₄ transition sometime between 9.5 and 5.0 Ka BP – assuming fairly uniform rates of organic input and turnover.

Soil organic matter turnover

Vegetation surveys indicate that mesquite rapidly colonized the coppice dune study area 80–95 years ago (Hennessey et al. 1983; Gibbens and Beck 1985). Within that time, the proportion of C₄-C in HFC from Ab and Bkb horizons decreased ~37% and 6% (respectively), relative to grassland soils (Table 1). These differences are consistent with turnover rates of 136–161 years (Ab horizon) and 257–305 years (Bkb horizon). We did not detect any losses of C₄-C within lower horizons.

The proportion of C₄-C in LFC increased in dune Ab horizons (~476%), relative to grassland profiles, due to higher amounts of total LFC in the former. This may result from an initial stimulatory effect of shrubs on grass production beneath shrub canopies (Scanlan 1992; Tiszler and R. Virginia unpublished work). In contrast, the proportion of C₄-C in LFC decreased in dune Bkb (~44%) and Btkb (~18%) horizons. Concentrations of LFC in Kb horizons were too low to estimate changes in C₄-C (Table 1).

We calculated turnover rates for LFC in profiles TG1 (10 cm depth) and D2 (20 cm depth) based on the specific ¹⁴C activity of these materials (Table 2). Both samples were gathered near the surface and have δ¹³C values (TG1=-13.8‰; D2=-24.7‰), similar to grass and mesquite litter (respectively), suggesting that each pool has attained a steady state in C turnover. Two possible MRT values for TG1 (7 and 40 years) and D2 (11 and 28 years) were thus derived (Hsieh 1993).

Discussion

We find evidence of both modern shrub expansion and earlier plant community changes from δ¹³C values of SOM in the Jornada. The δ¹³C of LFC and HFC in grassland soils decreased with depth by as much as 4.6‰ (Fig. 5D) and 6.6‰ (Fig. 5C), respectively. In plant communities where relative C₃/C₄ biomass has been stable over long periods of time, the δ¹³C of SOM often increases with depth by ~2–3‰ (e.g., Nadelhoffer and Fry 1988). This pattern has been attributed to fractionation by decomposers, preservation of isotopically distinct biochemical fractions, and/or variations in the ¹³C content of atmospheric CO₂ over the past century (Friedli et al. 1986; Nadelhoffer and Fry 1988; Baldesdent et al. 1993). Our data indicate that C₃ plant biomass was great-

er prehistorically and that SOM pools are in a state of transition, not fully reflecting the δ¹³C of the present C₄ grasses.

The δ¹³C values of HFC in grassland soils reveal a post-glacial shift to C₄ dominance which is generally consistent with regional paleoecological reconstruction's. During the late-Pleistocene, southern New Mexico was cooler (Brakenridge 1978) and moister than at present (Wells 1966; Marion et al. 1985), providing an environment favorable to C₃ species (Van Devender and Spaulding 1979). Expansion of C₄ grasses during the mid-Holocene (c. 8 Ka BP) occurred throughout southwest, largely in response to climatic warming (Neilson 1986). In the Jornada Basin, however, isotope data indicate a shift from C₄ to C₃ plant dominance (c. 7–9 Ka BP), as evidenced by decreased δ¹³C values in pedogenic carbonate and SOM from alluvial surfaces (Cole and Monger 1994). Fossil pollen and carbonate isotope studies on alluvial and basin deposits in the Jornada do suggest a partial recovery of C₄ grasses c. 5–4 Ka BP (Freeman 1972, Buck 1996). The absence of a C₄-to-C₃ isotopic shift (c. 7–9 Ka BP) in our profiles probably results from soil truncation, prior to this transition.

Mesquite have produced recent changes in the vertical distribution of root biomass and SOM that facilitate the formation of shrub resource islands (e.g., Garcia-Moya and McKell 1970). These changes are evident in the down-profile increase in δ¹³C values of SOM in coppice dunes (e.g., Tieszen and Archer 1990). McPherson et al. (1993) attributed an increase of SOM δ¹³C values (~6.0‰) beneath mesquite (*Prosopis juliflora* (Swartz) DC) in southern Arizona to recent shrub expansion. However, the specific timing of shrub establishment was not known. Our data suggest that mesquite have produced substantial changes in SOM δ¹³C values in less than 100 years.

The most important biogeochemical consequence of mesquite expansion may be the production of woody biomass below the rooting zone of perennial grasses. We found significant numbers of both coarse and fine roots up to 2 m beneath dune surface and to at least 1 m depth in soils between dunes. Jenkins et al. (1988) identified mesquite roots in Jornada dunes at depths of up to 6 m. In comparison, desert grasses generally concentrate roots in the upper 15 cm of soil (Cable 1969). We found only fine root biomass in our grassland profiles, most of which was concentrated between 0 and 40 cm depth. Consequently, both total and deep root biomass may have increased following shrub establishment.

Mesquite should enhance long-term soil C sequestration by creating a net C sink in root litter (McPherson et al. 1993; Fisher et al. 1994; Nepstad et al. 1994). The presence of modern shrub-C in LFC pools beneath mesquite (to at least 160 cm depth) indicates that root litter is an important source of soil C at depth. Like HFC, specific ¹⁴C activities of LFC increase downprofile, due perhaps to slower turnover and/or litter input in lower soil horizons. Significantly, ¹⁴C activities of LFC lower in TG1 (90 cm=103.8%) and M2 (160 cm=103.0%) reveal

the presence of C which is not actively cycling (Hsieh 1993), i.e., MRT > 80 years (Table 2).

Connin et al. (in press) recently evaluated community-level changes in net C balance associated with shrub expansion in the Jornada Basin. On an area weighted basis, aboveground biomass and NPP of grass and mesquite dune habitats were similar (L.F. Huenneke, unpublished data). However, SOM contents were ~15% less (to 1 m depth) in mesquite communities relative to grasslands, despite a corresponding increase (~45%) in root biomass (Connin et al., in press). They attributed the loss of SOM in mesquite communities to soil erosion between shrubs. Thus, despite dramatic changes in plant distribution and structure, total ecosystem C has not changed, only its distribution between biomass and soils.

The influence of litter quality on short-term SOM turnover and its effect on net soil C storage should also be considered in the context of shrub expansion. In our study, C/N ratios of LFC in mesquite soils were ~36% lower than in grassland soils, evidently due to differences in litter quality between black gamma (C/N \approx 38) and mesquite (C/N \approx 16) (Schaefer et al. 1985; Cepeda-Pizarro and Whitford 1990). Decreasing C/N ratios of LFC beneath mesquite should enhance N availability and stimulate SOM turnover relative to grassland soils (Moorhead and Reynolds 1991; Sollins et al. 1984), causing a decline in LFC. Recent work indicates that N mineralization potentials are greater under mesquite than adjacent grasses in the Jornada (J. Tizler and R. Virginia, unpublished data). However, we found few differences in C storage between equivalent grass and mesquite soil horizons, indicating that changes in root distribution and LFC litter quality have had little impact on C storage thus far.

Direct estimates of SOM turnover within grass and mesquite habitats are necessary to predict the ultimate impacts of shrub expansion on nutrient availability and SOM storage. Active SOM pools generally turn over on a decadal scale (Jenkinson and Rayner 1977; Trumbore et al. 1989; Hsieh 1993) and LFC turnover rates are generally faster than that of bulk SOM. For example, Gregorich et al. (1995) used $\delta^{13}\text{C}$ values to calculate a ~35 year MRT for bulk soil (0–30 cm) and a ~12 year MRT for associated LFC in cultivated soils from Canada. Trumbore et al. (1996) reported turnover times for low-density SOM (τ =6–8 years) in California at a mean annual temperature (~17.8°C) similar to the Jornada. These data suggest that the lower MRT values calculated for LFC in our grass (τ =7 years) and mesquite (τ =11 years) soils are the most appropriate. It is possible that MRTs of LFC have increased beneath mesquite relative to grasses, which is consistent with Cepeda-Pizarro and Whitford (1990), who reported greater biomass loss in black grama litter over time than in mesquite litter. However, it is important to note that slight inclusion of older grass-C in the mesquite sample could produce the differences in LFC turnover measured between our sites.

The MRTs of HFC under mesquite decreased with depth from an average of ~150 to 280 years in Ab to Bkb horizons, respectively. These estimates are lower than

MRTs of stable C calculated from $\delta^{13}\text{C}$ values in cultivated soils (0–20 cm depth; τ \approx 400–1400 years) (Balesdent et al. 1988) but higher than in a forest-savanna (0–10 cm depth; τ \approx 40 years) (Martin et al. 1990). These variations probably reflect site-related differences in climate, soil properties, and/or the specific SOM fraction measured. Estimates of stable SOM turnover based on ^{14}C models also exceed our values. Hsieh (1992) calculated MRTs for stable SOM from two prairie soils in Missouri and Illinois of 853 and 2973 years, respectively. In comparison, Trumbore (1993) calculated younger MRTs for dense (i.e., stable) SOM fractions in temperate (τ =470) and tropical soils (τ =990 years).

Sub-surface decomposition is rapid in arid land environments (Whitford et al. 1988), which is consistent with the relatively low MRTs calculated for HFC in our study. Assuming, that $\text{C}_4\text{-C}$ comprises ~80% of HFC beneath mesquite (Table 1), and assuming a MRT of 280 years, we calculate that HFC in the Bkb horizon will equilibrate isotopically (with mesquite litter inputs) in ~2.5 Ka. However, a steady-state in C turnover for these HFC pools may be achieved in less time.

In summary, Schlesinger et al. (1990) define desertification in the context of the redistribution of soil resources and suggest that changes in soil properties and their spatial variation may alter functional properties of arid land environments. Despite an increase in the spatial heterogeneity of soil resources and plant cover following shrub expansion in the Jornada, we found few significant changes in total SOM when grass and shrub soils were compared by horizon. However, the source, distribution, and quality of root litter and SOM is changing. These changes may influence C storage and soil N mineralization rates which depend upon the relative amounts and C/N ratios of LFC and HFC pools (Sollins et al. 1984). Since N limits NPP in arid lands (Schlesinger et al. 1990), desertified shrub communities may exhibit patterns of resilience and resistance that are distinct from the grasslands they have replaced (Reynolds et al. in press). We predict that changes in SOM production and cycling resulting from mesquite expansion in the Jornada Basin are characteristic of arid land grass-to-shrub vegetation changes worldwide and have important implications for ecosystem productivity and human use.

Acknowledgements We are grateful to John Anderson, Barbara Nolen, Amrita de Syoza, and Melody Brown for their logistical support and field assistance. We are particularly grateful to Kris Havstad, Director of the USDA Jornada Experimental Range for scientific contribution and for providing staff and equipment during trench excavation. We thank W.H. Schlesinger and three anonymous reviewers for constructive suggestions on early versions of this manuscript. Special thanks to L.H. Gile and R.P. Gibbens for sharing their invaluable knowledge of desert ecosystems. We also thank Y.P. Hsieh for providing assistance with MRT calculations and Mengchi Ho for assistance with soil analysis. This research was supported by a National Science Foundation Dissertation Improvement Grant DEB-9520743 and a National Science Foundation grant DEB-9006621 and it is a contribution to the National Science Foundation Jornada Basin Long Term Ecological Research Program. This study was also supported by the Earth, Ecosystem, and Ecological Science Graduate Program at Dartmouth College.

References

- Archer SR, Scifres CR, Bassham CR, Maggio R (1988) Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecol Monogr* 58:111–127
- Balesdent J, Wagner GH, Mariotti A (1988) Soil organic matter turnover in long-term field experiments as revealed by the carbon-13 natural abundance. *Soil Sci Soc Am J* 52:118–124
- Balesdent J, Girardin C, Mariotti A (1993) Site-related $\delta^{13}\text{C}$ of tree leaves and soil organic matter in a temperate forest. *Ecology* 74:1713–1721
- Bender MM (1968) Mass spectrometric studies of carbon-13 variations in corn and other grasses. *Radiocarbon* 10:468–472
- Boutton TW (1991) Stable carbon isotope ratios of natural materials. II. Atmospheric, terrestrial, marine, and freshwater environments. In: Colman D, Fry B (eds) *Carbon isotope techniques*. Academic Press, New York, pp 173–185
- Brakenridge RG (1978) Evidence for a cold, dry full-glacial climate in the American southwest. *Quat Res* 9:22–40
- Brown JR, Archer S (1990) Water relations of a perennial grass and seedling vs adult woody plants in a subtropical savanna, Texas. *Oikos* 57:366–374
- Buck BJ (1996) Late Quaternary landscape evolution, paleoclimate, and geoarchaeology, southern New Mexico and west Texas. Ph D thesis, New Mexico State University, Las Cruces
- Buffington LC, Herbel CH (1965) Vegetation changes on a semi-desert grassland range from 1958–1963. *Ecol Monogr* 35:139–164
- Cable DR (1969) Competition in the semidesert grass-shrub type as influenced by root systems, growth habits, and soil moisture extraction. *Ecology* 50:27–38
- Cepeda-Pizarro JG, Whitford WG (1990) Decomposition patterns of surface leaf litter of six plant species along a Chihuahuan Desert watershed. *Am Midl Nat* 123:319–330
- Cole DR, Monger CH (1994) Influence of atmospheric CO_2 on the decline of C_4 plants during the last deglaciation. *Nature* 368:533–536
- Connin SL, Virginia RA, Chamberlain CP, Huenneke LF, Harrison K, Schlesinger WH (in press) Dynamics of carbon storage in degraded arid land environments: a case study from the Jornada Experimental Range, New Mexico (USA). In: Squires VR, Glenn EP, Ayoub AT (eds) *Drylands and global change in the twenty-first century*. University of Arizona Press, Arizona
- Cheng H, Molina J (1995) In search of the bioreactive soil organic carbon: the fractionation approaches. In: Kimble LR, Levine E, Stewart BA (eds) *Soils and global change*. CRC, Boca Raton, pp 343–350
- Coplen TB (1994) Reporting of stable hydrogen, carbon, and oxygen isotopic abundances. *Pure Appl Chem* 66:272–276
- Dzurec RS, Boutton TW, Caldwell MM, Smith BN (1985) Carbon isotope ratios of soil organic matter and their use in assessing community composition changes in Curley Valley, Utah. *Oecologia* 66:17–24
- Ehleringer JR, Cooper TA (1988) Correlations between carbon isotope ratio and microhabitat in desert plants. *Oecologia* 76:562–566
- Fisher MJ, Rao IM, Ayarza MA, Lascano CE, Sanz JI, Thomas RJ, Very RR (1994) Carbon storage by introduced deep-rooted grasses in South American savannas. *Nature* 371:236–238
- Freeman CE (1972) Pollen study of some Holocene alluvial deposits in Dona Ana County, Southern New Mexico. *Tex J Sci* 24:203–220
- Friedli H, Lotscher H, Oeschge H, Siegenthaler U, Stauffer B (1986) Ice core record of the $^{13}\text{C}/^{12}\text{C}$ ratios of atmospheric CO_2 in the past two centuries. *Nature* 324:237–238
- Garcia-Moya E, McKell CM (1970) Contribution of shrubs to the nitrogen ecology of a desert wash community. *Ecology* 51:81–88
- Gibbens RP, Beck RF (1985) Changes in grass basal area and forb densities over a 64-year period on grassland types of the Jornada Experimental Range. *J Range Manage* 41:186–192
- Gibbens RP, Tromble JM, Hennessy JT, Cardenas M (1983) Soil movement in mesquite dunelands and former grasslands of southern New Mexico from 1933 to 1980. *J Range Manage* 36:145–148
- Gile LH (1966) Coppice dunes and the Rotura soil. *Soil Sci Soc Am Proc* 30:657–660
- Gile LH, Grossman RB (1979) *The desert project soil monograph*. Soil Conservation Service, United States Department of Agriculture, Washington
- Gile LH, Peterson FF, Grossman RB (1965) The K horizon: a master soil horizon of carbonate accumulation. *Soil Sci* 99:74–82
- Goldberg DE, Turner RM (1986) Vegetation change and plant demography in permanent plots in the Sonoran Desert. *Ecology* 67:695–712
- Gregorich EG, Ellert BH, Monreal CM (1995) Turnover of soil organic matter and storage of corn residue carbon estimates from natural ^{13}C abundance. *Can J Soil Sci* 75:161–167
- Heitschmidt RK, Ansely RJ, Dowhower PW, Jacoby PW, Price DL (1988) Some observations from excavation of honey mesquite root systems. *J Range Manage* 41:227–231
- Hennessy JT, Gibbens RP, Tromble JM, Cardenas M (1983) Vegetation changes from 1935 to 1980 in mesquite dunelands and former grasslands of southern New Mexico. *J Range Manage* 36:370–374
- Hennessy JT, Gibbens JM, Tromble JM, Cardenas M (1985) Mesquite (*Prosopis glandulosa* Torr.) dunes and interdunes in southern New Mexico: a study of soil properties and soil water relations. *J Arid Environ* 9:27–38
- Houghton FE (1972) *Climatic guide*, New Mexico State University, Las Cruces, New Mexico, 1851–1971. *Agric Stn Res Rep* 230:1–20
- Hsieh YP (1992) Pool size and mean age of stable organic carbon in cropland. *Soil Sci Soc Am J* 56:460–464
- Hsieh YP (1993) Radiocarbon signatures of turnover rates in active soil organic carbon pools. *Soil Sci Soc Am J* 57:1020–1022
- Janzen HH, Cambell CA, Brandt SA, Lafond GP, Townley-Smith L (1992) Light-fraction organic matter in soils from long-term crop rotation. *Soil Sci Soc Am J* 56:1799–1806
- Jenkins MB, Virginia RA, Jarrell WM (1988) Depth distribution and seasonal populations of mesquite-nodulating rhizobia in warm desert ecosystems. *Soil Sci Soc Am J* 52:1644–1650
- Jenkinson DS, Rayner JH (1977) The turnover of soil organic matter in some of the Rothamsted classical experiments. *Soil Sci* 76:297–304
- Kelly RD, Walker BH (1976) The effects of different forms of land use on the ecology of a semi-arid region of southeastern Rhodesia. *J Ecol* 64:553–576
- Ludlow M, Troughton J, Jones R (1976) A technique for determining the proportion of C_3 and C_4 species in plant samples using stable natural isotopes of carbon. *J Agric Sci* 87:625–632
- Ludwig JA (1977) Distributional adaptations of root systems in desert environments. In: Marshall JK (ed) *The belowground ecosystem: a synthesis of plant-associated processes*. Colorado State University, Fort Collins, pp 85–91
- Marion GN, Schlesinger WH, Fonteyn PJ (1985) CALDEP: a regional model for soil CaCO_3 (caliche) deposition in southwestern deserts. *Soil Sci* 139:468–481
- Mariotti A, Peterschmidt E (1994) Forest savanna ecotone dynamics in India as revealed by carbon isotope ratios of soil organic matter. *Oecologia* 97:475–480
- Martin A, Mariotti A, Balesdent J, Lavelle P, Vuattoux R (1990) Estimate of organic matter turnover rate in a savanna soil by ^{13}C natural abundance measurements. *Soil Biol Biochem* 22:517–523
- McPherson GR, Boutton TW, Midwood AJ (1993) Stable carbon isotope analysis of soil organic matter illustrates vegetation change at the grassland/woodland boundary in southeastern Arizona, USA. *Oecologia* 93:95–101
- Moorhead DL, Reynolds JF (1991) A general model of litter decomposition in the northern Chihuahuan Desert. *Ecol Model* 56:197–219

- Nadelhoffer KJ, Fry B (1988) Controls on natural nitrogen-15 and carbon-13 abundance's in forest soil organic matter. *Soil Sci Soc Am J* 52:1633–1640
- Neilson RP (1986) High-resolution climatic analysis and south-west biogeography. *Science* 232:27–34
- Nepstad DC, Carvalho CR, Davidson EE, Jipp PH, Levebvre PA, Negreiros GH, da Silva ED, Stone TA, Trumbone SE, Vieira S (1994) The role of deep roots in hydrological and carbon cycles of Amazonian forests and pastures. *Nature* 372:666–669
- Nieuwenhuize J, Maas Y, Middelburg JJ (1994) Rapid analysis of organic carbon and nitrogen in particulate materials. *Mar Chem* 45:217–224
- Pella E, Colombo B (1973) Study of carbon, hydrogen, and nitrogen determination by combustion-gas chromatography. *Mikrochim Acta* 1973:697–719
- Reynolds JF, Virginia RA, Schlesinger WH (in press) Defining functional types for models of desertification. In: Smith TM, Shugart HH, Woodward FI (eds) *Plant functional types. Their relevance to ecosystem properties and global change* (International Geosphere-Biosphere Programme Book Series 1). Cambridge University Press, Cambridge
- SAS (1987) *SAS/STAT Guide for personal computers*, version 6 edn. SAS Institute, Cary
- Scanlan JC (1992) A model of woody-herbaceous biomass relationships in eucalyptus and mesquite communities. *J Range Manage* 45:75–80
- Schaefer D, Steinberger Y, Whitford WG (1985) The failure of nitrogen and lignin control of decomposition in a North American desert. *Oecologia* 65:382–386
- Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrall WM, Virginia RA, Whitford WG (1990) Biological feedbacks in global desertification. *Science* 247:1043–1048
- Smith BN, Epstein S (1971) Two categories of $^{13}\text{C}/^{12}\text{C}$ ratios for higher plants. *Plant Physiol* 47:380–384
- Sollins P, Spycher G, Glassman CA (1984) Net nitrogen mineralization from light- and heavy-fraction forest soil organic matter. *Soil Biol Biochem* 16:31–37
- Spycher G, Sollins P, Rose S (1983) Carbon and nitrogen in the light fraction of a forest soil: vertical distribution and seasonal patterns. *Soil Sci* 135:79–87
- Stevenson FJ, Elliott ET (1989) Methodologies for assessing the quantity and quality of soil organic matter. In: Colman DC, Oades JM, Uehara G (eds) *Dynamics of soil organic matter in tropical ecosystems*. University of Hawaii Press, Hawaii, pp 173–199
- Strickland TC, Sollins P (1987) Improved method for separating light- and heavy-fraction organic material from soil. *Soil Sci Soc Am J* 51:1390–1393
- Tieszen LL, Archer S (1990) Isotopic assessment of vegetation changes in grassland and woodland systems. In: Osmond CB, Pitelka LF, Hidy GM (eds) *Plant biology of the basin and range*. Springer-Verlag, Berlin Heidelberg New York, pp 293–321
- Trumbore SE (1993) Comparison of carbon dynamics in tropical and temperate soils using radiocarbon measurements. *Global Biogeochem Cycles* 7:275–290
- Trumbore SE, Vogel JS, Southon JR (1989) AMS ^{14}C measurements of fractionated soil organic matter: an approach to deciphering the soil carbon cycle. *Radiocarbon* 31:644–654
- Trumbore SE, Chadwick OA, Amundson R (1996) Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. *Science* 272:393–395
- Van Devender TR, Spaulding GW (1979) Development of vegetation and climate in the southwestern United States. *Science* 204:701–710
- Van Vegten JA (1983) Thornbush invasion in a savanna ecosystem in eastern Botswana. *Vegetatio* 56:3–7
- Virginia RA, Jarrell WM (1983) Soil properties in a mesquite-dominated Sonoran Desert ecosystem. *Soil Sci Soc Am J* 47:138–144
- Virginia RA, Jarrell WM, Whitford WG, Freckman DW (1992) Soil biota and soil properties in the surface rooting zone of mesquite (*Prosopis glandulosa*) in historical and recently desertified Chihuahuan Desert habitats. *Biol Fertil Soil* 13:90–98
- Wells PV (1966) Late Pleistocene vegetation and degree of pluvial climatic change in the Chihuahuan Desert. *Science* 153:970–975
- Whitford WG, Stinnet K, Anderson J (1988) Decomposition of roots in a Chihuahuan Desert ecosystem. *Oecologia* 75:8–11