

Richard A. Gill · Ingrid C. Burke

Ecosystem consequences of plant life form changes at three sites in the semiarid United States

Received: 30 March 1999 / Accepted: 11 August 1999

Abstract Many semiarid rangelands have recently experienced changes in dominant plant life form. Both woody plant expansion into grasslands and the invasion of annual grasses into shrublands have potential influence on regional carbon cycling. Soil carbon content, chemistry, and distribution may change following shifts in dominant plant life form because plant life forms differ in litter chemistry and patterns of detrital input. This study assesses the amount, quality, and distribution of soil C below woody vegetation and grasses at three rangelands in Texas, New Mexico, and Utah. At each of these sites there has been a well-documented shift in dominant plant life form. In Texas and New Mexico, woody plants have increased in grasslands, while grasses have invaded into former shrublands in Utah. We measured total soil carbon, particulate organic matter (POM) C, and the carbon isotopic composition of soil carbon beneath woody plants and grasses at each of these three sites. At the La Copita Research Area in south-central Texas there was significantly more soil C found beneath *Prosopis glandulosa*, the dominant woody plant, than was found beneath grasses. Mean soil C content to 1 m was 7.2 kg C m⁻² beneath *P. glandulosa* and 6.0 kg C m⁻² beneath grasses. There was also significantly more POM C beneath *P. glandulosa* than beneath grasses. Stable carbon isotopic composition indicated that the expansion of *P. glandulosa* in savannas in Texas first influences carbon cycling in surface soils, then deep soil C, and finally throughout the soil profile. At the Sevilleta National Wildlife Refuge in central

New Mexico, we found that there was significantly more soil C in the upper 10 cm of the soil profile beneath *Larrea tridentata* than was found beneath *Bouteloua* spp. Stable carbon isotopic composition indicated that the expansion of *L. tridentata* influenced C cycling throughout the soil profile. At Curlew Valley in northern Utah, we found no significant differences in total profile soil C beneath different plant life forms. However, there was significantly more soil C found at the soil surface beneath woody plants than was observed beneath annual grasses. There was significantly less POM C beneath annual grasses than was found beneath woody plants or perennial grasses. Based on stable carbon isotopic analyses, we concluded that the invasion of grasses into shrublands influenced only the upper 30 cm of the soil profile. We determined that following changes in plant life form dominance, the most consistent change in soil C was an alteration in content and distribution of POM C, a slowly cycling pool of soil C. While we failed to find a consistent change in total profile soil C with plant life form across our sites, the change in soil C chemistry may have important implications for long-term soil C storage in semiarid systems where there have been shifts in plant life form.

Key words Plant life form · Soil depth · Root distribution · Plant invasion · Soil carbon chemistry

Introduction

The distribution of woody and herbaceous vegetation in semiarid and arid regions has changed dramatically during the 20th century (Van Vegten 1983; Schlesinger et al. 1990; Skarpe 1991; D'Antonio and Vitousek 1992; Archer 1994). Woody vegetation has increased globally in grassland and savanna regions (reviewed in Archer 1994). At the same time, exotic grasses have expanded into areas previously dominated by woody vegetation (reviewed in D'Antonio and Vitousek 1992). Three of

R.A. Gill (✉)¹ · I.C. Burke
Department of Forest Sciences, Colorado State University,
Fort Collins, CO 80523, USA

I.C. Burke
Natural Resource Ecology Laboratory, Colorado State University,
Fort Collins, CO 80523

Present address:

¹Department of Botany, Duke University, Durham, NC 27708, USA,
e-mail: rgill@duke.edu,
Tel.: +1-919-6607400, Fax: +1-919-6607425

the important changes in plant life form in the semiarid United States are: (1) *Prosopis glandulosa* var. *glandulosa* Torr. (honey mesquite) expansion in thorn savannas and grasslands from Texas to Arizona (Glendening 1952; Archer 1994; Boutton et al. 1998); (2) *Larrea tridentata* (DC.) Coville (creosotebush) expansion in desert grasslands in New Mexico and Arizona (Grover and Musick 1990; Schlesinger et al. 1990; Kieft et al. 1998); and (3) *Bromus tectorum* L. (cheatgrass) invasion into Great Basin shrublands (Mack 1981; D'Antonio and Vitousek 1992; Knapp 1996). The increase of woody vegetation in grasslands and savannas has been implicated in desertification and decreased economic productivity of southwestern rangelands (Bogusch 1952; Glendening 1952; Schlesinger et al. 1990). The invasion of *B. tectorum* into the Great Basin has reduced forage quality for livestock and altered fire frequency (Young and Evans 1973; West 1988; Knapp 1996).

Many investigators have shown that because of differences in biomass allocation and litter chemistry, different plant life forms produce characteristic patterns of soil C and nutrient accumulation (Hook et al. 1991; Schlesinger et al. 1990, 1996; Trumbore et al. 1995; Burke et al. 1998). Soil C, N, and micronutrient concentrations are generally higher under savanna trees and shrubs than in the bare or grass-dominated interspaces, while there is also a concentration of soil nutrients below grasses relative to plant interspaces (Virginia 1986; Belsky et al. 1989; Schlesinger et al. 1990, 1996; Campbell et al. 1994; Scholes and Hall 1996; Burke et al. 1998; Kieft et al. 1998). Few studies, however, have explored how shifts in plant life form alter soil C dynamics, chemistry, and carbon storage vertically throughout a soil profile (Burke et al. 1987; Connin et al. 1997). Soil C kinetics are typically more rapid near the soil surface than at lower soil depths. Therefore, surface horizons are the most likely to be altered due to shifts in plant life form (Trumbore et al. 1995; Van Dam et al. 1997; Gill et al. 1999). However, evidence from tropical and sub-tropical systems shows that plant functional types may influence both surface and deep soil carbon dynamics (Nepstad et al. 1994; Trumbore et al. 1995; Boutton et al. 1998). Any alteration of deep soil C storage represents a long-term change in ecosystem C storage, due to the long turnover time of soil C in the lower soil profile (Trumbore et al. 1995; Van Dam et al. 1997).

Changes in the distribution of woody and herbaceous vegetation may potentially influence vertical patterns of ecosystem processes as well, since plant life forms differ in vertical biomass allocation patterns (Reynolds et al. 1997; Jackson 1999) and litter chemistry (Connin et al. 1997; Boutton et al. 1998). Two primary differences in biomass allocation between grasses and woody plants that may influence carbon, nutrient, and water cycling in semiarid systems are: (1) root distribution patterns, and (2) aboveground plant structure (Sala et al. 1997; Reynolds et al. 1997; Jackson 1999). Grasses and woody plants differ in C allocation to fine and coarse root biomass and in the depth-distribution of roots (Canadell

et al. 1996; Jackson et al. 1996, 1997). The expansion of *P. glandulosa* in both Texas and New Mexico is apparently shifting system-level rooting patterns from one dominated by fine, surface roots to one dominated by coarse roots concentrated deeper below shrub canopies (Heitschmidt et al. 1988; Connin et al. 1997; Boutton et al. 1998). Following *P. glandulosa* expansions in Texas, New Mexico, and Arizona, root biomass is higher below shrub canopies than in neighboring grasslands, while the contribution of fine roots to total biomass is decreasing (Virginia et al. 1992; McPherson et al. 1993; Boutton et al. 1998). Aboveground plant structure may affect ecosystem processes through airflow, albedo, and water percolation patterns (Haworth and McPherson 1995; Aguiar et al. 1996; Reynolds et al. 1997). Abiotic conditions differ sufficiently under shrub canopies relative to beneath grass canopies that decomposition, nutrient availability, and evaporation rates are reduced (Belsky et al. 1989; Jackson and Caldwell 1992; Campbell et al. 1994). Increased heterogeneity of soil C, nutrients, and soil water following shrub expansion in the Chihuahuan desert is likely due to changes in water infiltration patterns and erosional processes driven by canopy differences between shrubs and grasses (Schlesinger et al. 1990, 1996; Connin et al. 1997; Reynolds et al. 1997).

Previous studies have indicated that shifts in plant life form alter total-ecosystem litter chemistry (Scholes and Hall 1996; Connin et al. 1997). Litter chemistry, in turn, controls decomposition rates and soil organic matter quantity and quality (Melillo et al. 1982). Shrub litter is generally higher than grass litter in nutrient content and concentration, although differences may be species-specific (Vinton and Burke 1995; Scholes and Hall 1996; Connin et al. 1997; Kieft et al. 1998). However, litter from many savanna trees and shrubs contains high concentrations of lignin and secondary compounds that retard decomposition rates (Scholes and Walker 1993). In addition, the input of woody litter may have a role in increasing pools of slowly decomposing soil C (Boutton et al. 1998). Connin et al. (1997) determined that the most significant biogeochemical effect of *P. glandulosa* expansion in desert grasslands was an increase in pools of slowly cycling soil C, possibly caused by changes in litter quality.

In this study we examined the effects of changes in plant life form on the soil C content and chemistry, specifically focusing on the vertical distribution of soil C and particulate organic matter (POM) C in three semiarid rangelands. First, we hypothesized that the expansion of woody plants into grasslands would increase total soil C, with significant increases in soil C occurring in both surface and deep soils, and that conversely, grass invasion into shrublands would decrease total soil C, with the decrease primarily occurring at the soil surface. These changes would occur because of differences in plant litter quality, with shrub litter containing a fraction of lignin-rich, slowly decomposing material, because C in the upper soil profile cycles more rapidly than soil C in the

lower soil profile, and because of differences in root distribution among plant life forms. We used stable C isotopes to explicitly test where in the soil profile plant life forms have their greatest influence. Our hypothesis was that the soils under woody plants would have a higher proportion of slowly decomposing soil C than soils under grasses, and that the accumulation or loss of POM C would follow patterns of total soil C.

Materials and methods

Site descriptions and field sampling

We collected soil and vegetation samples from three sites in the semiarid United States that have experienced a change in the dominant vegetation within the past 120 years, and in each case the antecedent C₄ vegetation was replaced by C₃ vegetation. In addition, each site has a well-characterized invasion history (Archer 1995; Julio Betancourt, unpublished photographs; Neil West personal communication).

La Copita Research Area, Texas. We collected soil samples from the La Copita Research Area (LCRA) Texas Agricultural Experiment Station, which is 15 km from Alice, Texas (27°40'N, 98°12'W). The average annual rainfall at La Copita is 715 mm, with historical maxima in May and September. Mean annual temperature is 22.4°C (USDA 1979). Upland topographic positions are characterized by discrete clusters of woody plants within a continuous matrix of C₄ grasses (Whittaker et al. 1979). *Prosopis glandulosa* dominates La Copita woodlands. C₄ grasses, primarily *Paspalum setaceum* and *Setaria geniculata*, dominate the understorey and the shrub interspaces. In heavily grazed areas, *Aristida* spp. and *Bouteloua trifida* are the dominant grasses (Archer et al. 1988). Soil have previously been described in Archer (1995).

Woody vegetation at the LCRA in South Central Texas has expanded out of lowlands onto previously grass-dominated upland topographic positions (Archer et al. 1988; Archer 1995; Boutton et al. 1998). Archer et al. (1988) and Boutton et al. (1998) have extensively documented the *Prosopis glandulosa* expansion sequence at this site. The primary invasive species into the grassland matrix is *P. glandulosa*, which then facilitates the establishment of other woody species, creating shrub clusters (Brown and Archer 1989; Archer 1995). Shrub clusters, as defined by Archer et al. (1988), are groupings of two or more shrub species that are spatially separated from other woody vegetation. Where subsurface soils lack an argillic horizon, shrub clusters have expanded, coalescing into groves that have more than one dominant *P. glandulosa* overstorey tree. Recent research has indicated that the median age of *P. glandulosa* in clusters is 20 years and in groves is 45 years (Boutton et al. 1998). Canopy diameter for the dominant *P. glandulosa* individual is 6.5 m in clusters and 7.2 m in groves (Archer 1995). Thus, we considered the transition from individual shrubs, to clusters and the groves to be a chronosequence of shrub invasion, spanning approximately 45 years.

At three upland locations where humans had not directly manipulated shrub density, we collected soil samples from each of the three phases of the chronosequence, under *P. glandulosa* and adjacent grasses. These locations were separated by discrete drainages. At each location, we removed a single soil core (1 m long and 6.6 cm diameter) from under a randomly selected *P. glandulosa* individual, the dominant *P. glandulosa* in a discrete cluster, and under the largest *P. glandulosa* in a grove. Cores were taken from soils located at mid-canopy. We also collected soil cores from the adjacent grassland matrix 3 m from the canopy edge at each *P. glandulosa* sampling point. We collected soil in 10-cm increments from the soil surface to 50 cm, with two additional increments from 70 to 80 cm, and from 90 to 100 cm. The soils were refrigerated and taken to the laboratory for processing.

Sevilleta National Wildlife Refuge, New Mexico. Sevilleta National Wildlife Refuge (SEV), a Long-Term Ecological Research Site in central New Mexico, lies at the ecotone between Chihuahuan De-

sert vegetation and southern shortgrass steppe vegetation (34°3'N, 106°8'W) (Gosz 1993). Historical photographs show that since at least 1907, the ecotone between *Larrea tridentata* and grasslands dominated by *Bouteloua eriopoda* (Torr.) Torr. (black grama) and *B. gracilis* (H. B. K.) Lang. Ex Steud. (blue grama) has moved northward, increasing the extent of the area dominated by *L. tridentata* (Julio Betancourt, unpublished photographs). Average annual rainfall from 1989 to 1996 was 255 mm, mean monthly temperature ranged from 2.5°C to 25.1°C, and a mean annual temperature of 11.7°C (Kieft et al. 1998). Soils have been previously described by Kieft et al. (1998).

We collected soils from two randomly placed plots on either side of the ecotone between *L. tridentata* dominated shrublands and *B. eriopoda* and *B. gracilis* dominated grasslands. Samples were designated as either coming from the grass dominated side of the ecotone or from the shrub side of the ecotone. At each plot, we collected soil cores (6.6 cm diameter) from under randomly selected *L. tridentata* ($n=2$) and adjacent grasses ($n=2$). Samples were collected in 10-cm depth increments from the soil surface to the depth of the petricalcic layer. On the grass-dominated side of the ecotone, we sampled to a depth of 50 cm, while on the shrub side we sampled to 30 cm, the maximum depth to which we could manually extract cores. Samples were refrigerated and transported to the laboratory.

Curlew Valley, Utah. We collected soils from Curlew Valley (CV), Utah (41°52'N, 113°5'W), located 36 km southwest of Snowville, Utah. The CV site was an International Biological Program-Desert Biome site (Charley and West 1975). The United States Department of Agriculture Bureau of Land Management currently manages CV for cattle and sheep grazing. Long term average precipitation at the nearby Snowville United States Weather Bureau station is 244 mm, while mean annual temperature is 7.1°C (Caldwell et al. 1977). The climate is characterized by cool, wet winters and hot, dry summers (Caldwell et al. 1977). Historically this area was dominated by the shrubs *Artemisia tridentata* and *Atriplex confertifolia*, but following a series of fires in the late 1960s and early 1970s, large areas of the valley were either invaded by the exotic annual grass *Bromus tectorum* or seeded by the Bureau of Land Management with the exotic perennial bunchgrass *Agropyron cristatum* (L.) Gaertn. (N.E. West, personal communication). Dzurec et al. (1985) included a description of soil characteristics at CV.

We established two randomly placed transects across the boundary from pure stands of *Bromus tectorum* to *Atriplex confertifolia* (Torr. and Frem.) S. Wats. dominated sites and from pure *Agropyron cristatum* stands to *Atriplex confertifolia* dominated sites. Transects were 60 m long, with 30 m in each vegetation type. We collected 1-m-deep soil cores in 10-cm increments under the dominant plant at 30, 10, and 0 m from the boundary. Samples were refrigerated and transported to the laboratory.

Laboratory analyses

Soils from LCRA, SEV, and CV were processed using the same procedures. Each soil sample was passed through a 2-mm sieve to remove roots, coarse surface litter, and large cobble. Roots were retained for stable isotope determination. Roots were dried for 24 h, shaken to remove attached soil, and roots from soils containing significant amounts of CaCO₃ were washed with 0.5 M H₂SO₄+2% FeSO₄ to eliminate contamination by carbonates (Nelson and Sommers 1982). Due to lack of root material, roots from the same site, soil depth and vegetation type were composited before analysis, eliminating the possibility of performing statistical analyses on root data.

Soils were oven-dried at 55°C for 48 h. Sieved, dried whole soils were weighed and the weights used to calculate fine soil density based on the known volume of the soil core. Whole soils were homogenized and a 30-g subsample was used to determine particulate organic matter. A ~15-g subsample was ground using a ball grinder and used to determine total organic carbon and the natural abundance isotopic signature of the soil organic C. All soils found to contain carbonates were repeatedly washed with 0.5 M H₂SO₄+2% FeSO₄ to

remove carbonates (Nelson and Sommers 1982). Decalcification was not considered complete until soils failed to effervesce when the acid solution was added. All soils from SEV and CV, as well as soils from below 30 cm from LCRA contained significant concentrations of CaCO_3 .

Total soil carbon and nitrogen

We determined percent organic carbon (C) and percent organic nitrogen (N) using automated combustion analysis (LECO CHN-1000 Element Analyzer, St. Joseph, Mich., USA). These percentages were converted using the fine soil density to organic C and N content (g m^{-2}). We used this measure of organic C and N to determine whether plant life forms were associated with a consistent pattern in total soil C and N distributions.

POM fractionations

We used a method developed by Cambardella and Elliott (1992, 1993) for fractionation of POM. The fractionation of POM from whole soil involves both chemical and physical separation and isolates a fraction of soil C intended to correspond with the slow kinetic fraction in many ecosystem models (Cambardella and Elliott 1992). Theoretically, POM C includes a slowly decomposing fraction of organic matter that is physically but not chemically occluded. It consists of recently derived root fragments, as well as non-clay-occluded organic matter. Kelly et al. (1996) and Gill et al. (1999) have shown that POM C has a mean residence time of between 20 and 50 years in grassland soils and therefore is a likely a fraction that would respond at a temporal scale similar to plant life form changes in the semiarid United States.

A 30-g sample of whole soil was shaken in sodium hexametaphosphate for 18 h to disperse soil aggregates. This solution was then passed through 500- and 53- μm sieves. The organic C in the material remaining on the sieve was considered POM C. We converted percent C in the POM fraction to total POM C (g m^{-2}) using fine soil density and the proportion of soil mass within the POM size classes. We considered the amount of POM C under shrubs and grasses to be a measure of the influence of plant life form on soil C chemistry.

Stable isotope analyses

We used natural abundance isotopic techniques to assess where in the soil profile invasive vegetation production influenced soil C cycling, since the transition in dominant vegetation at all three sites represented a change in the primary photosynthetic pathway. The initial carboxylating enzyme in photosynthesis differs between photosynthetic pathways (C_3 vs. C_4). RuBP carboxylase in C_3 plants discriminates more strongly against $^{13}\text{CO}_2$ than PEP carboxylase in C_4 plants (Vogel 1980; O'Leary 1981). Consequently, C_3 and C_4 vegetation differ in their carbon isotopic composition. Measured relative to the international PDB standard, the $\delta^{13}\text{C}$ values of C_3 plants average -27% while C_4 vegetation averages -12% (Smith and Epstein 1971; Farquhar et al. 1989). Several researchers have shown that the early stages of decomposition slightly alter the isotopic signature of plant detritus during SOM formation, but the changes are small relative to differences between C_3 and C_4 vegetation (Balesdent et al. 1993; Wedin et al. 1995; Boutton et al. 1998).

Numerous studies have shown the value of using stable isotopes to monitor the influence of vegetation changes on soil C dynamics (Dzurec et al. 1985; Balesdent et al. 1988; McClaran and McPherson 1995; Boutton 1996; Connin et al. 1997; Boutton et al. 1998). The isotopic signature of soil C reflects the relative contribution of C_3 and C_4 production to soil C accumulation, and integrates over long time periods (Boutton 1996; Boutton et al. 1998). We interpreted differences in the isotopic signature of soil C beneath invasive and antecedent vegetation as the net effect of the invasive plant life form on soil C pools. Most of the grasses at

LCRA and SEV use the C_4 photosynthetic pathway, while *P. glandulosa* uses the C_3 pathway. At CV, *A. confertifolia*, the dominant shrub, uses the C_4 photosynthetic pathway, while both the perennial and annual grasses use the C_3 pathway. Our results are presented relative to the international standard PDB using a δ notation (Craig 1957) where

$$\delta^{13}\text{C}(\%) = \left[\frac{R_{\text{sample}}}{R_{\text{PDB}}} - 1 \right] \times 10^3$$

where R_{sample} was $^{13}\text{C}/^{12}\text{C}$ for the sample and R_{PDB} was $^{13}\text{C}/^{12}\text{C}$ for the standard. We analyzed CaCO_3 -free whole soil samples using a mass spectrometer (VG ISOGAS, Middlewich, UK) with a combustion elemental analyzer inlet (Fisons NA 1500, Carlo Erba Instrumentazione) to determine the soil C $\delta^{13}\text{C}$ value. We also calculated $\delta^{13}\text{C}$ values for root biomass under shrubs and grasses, which we used as endpoints in a two-pool mixing model to determine the relative contribution of C_3 or C_4 vegetation to soil C. We calculated an average $\delta^{13}\text{C}$ signature for grasses and for woody vegetation using the roots from each plant life form, averaged within site and depths. The variation in $\delta^{13}\text{C}$ among root samples from the same life form at each site was always within the range of resolution of the mass spectrometer ($\pm 0.2\%$). Percent C_3 -derived soil C was calculated using the equation (Boutton et al. 1998):

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

$\delta^{13}\text{C}_{\text{sample}}$ was the measured $\delta^{13}\text{C}$ value of whole soil, $\delta^{13}\text{C}_{\text{C}_3}$ was the $\delta^{13}\text{C}$ value of C_3 roots, and $\delta^{13}\text{C}_{\text{C}_4}$ was the $\delta^{13}\text{C}$ value of C_4 roots. We solved for x , which was the proportion of C_3 -derived soil C, while $1-x$ was the proportion of C_4 -derived soil C. We used these data to determine where in the soil profile changes in plant life form had the strongest influence on soil C cycling.

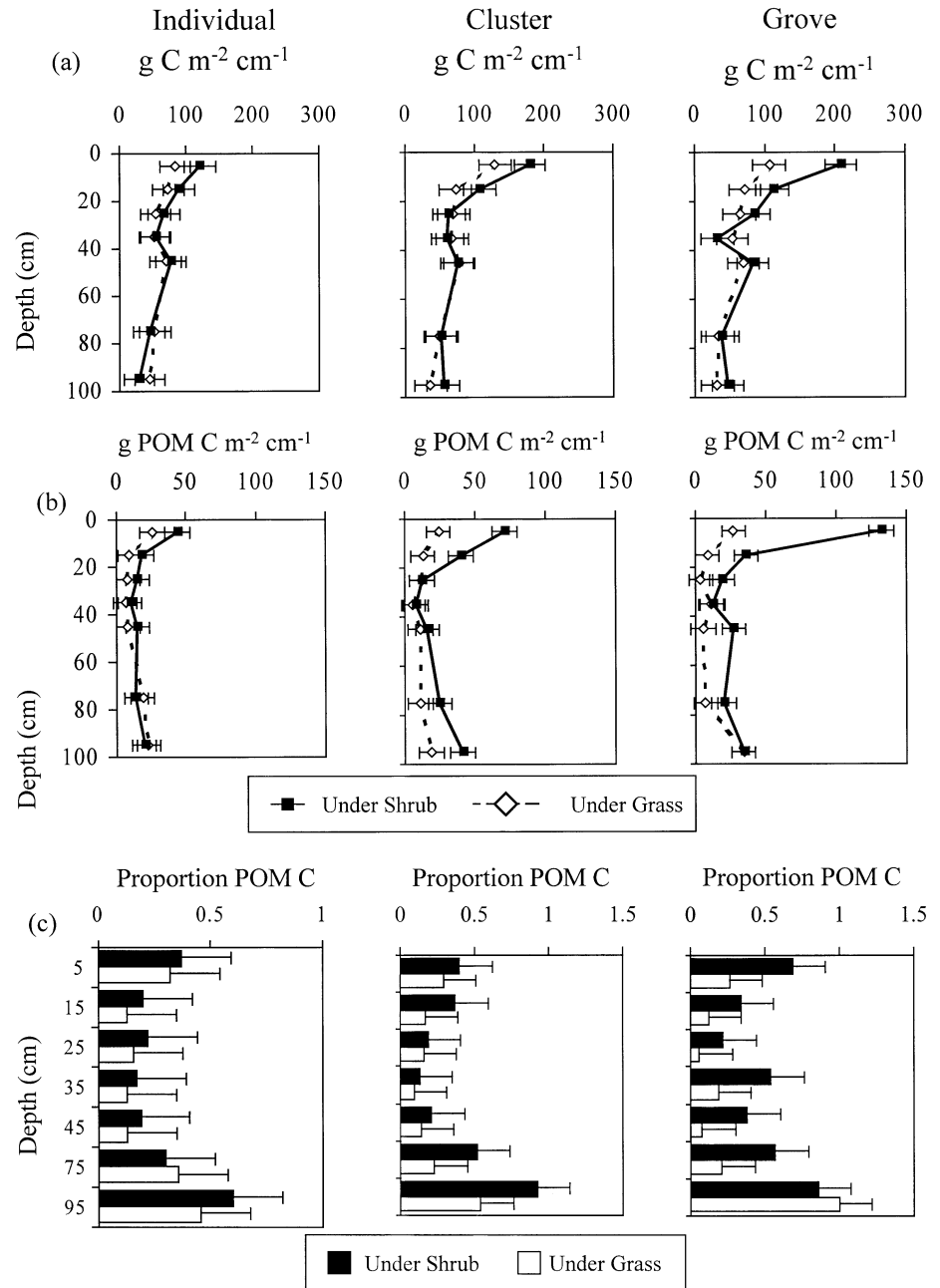
At each site, the plant life forms had distinct $\delta^{13}\text{C}$ signatures. At LCRA and SEV, roots from under woody vegetation clearly had a C_3 isotopic signature, with roots under *P. glandulosa* averaging -24.8% and roots under *L. tridentata* averaging -23.7% . The roots below grasses at these sites carried a C_4 isotopic signature, averaging -14.3% at LCRA and -13.9% at SEV. At CV, roots below *A. confertifolia* carried a C_4 signature, averaging -11.6% , while roots below *A. cristatum* and *B. tectorum* were C_3 , averaging -25.5% and -26.1% . Aboveground tissue may be an important input to soil organic matter, but we used roots as endpoints in the two-pool model because they are likely the most important input to SOC throughout the soil profile, and because the leaf litter $\delta^{13}\text{C}$ values reported by Boutton et al. (1998) were not markedly different from our measured root $\delta^{13}\text{C}$ values.

Statistics

Our study objective was to evaluate how shifts in plant life form influenced the amount, distribution, and quality of organic C and N stored in soils. To test the hypothesis that the expansion of woody vegetation increased total soil C storage, while grass invasion decreased total soil C storage, we summed total C for the entire soil profile, interpolating between depths, and performed an autoregressive analysis of variance for each site (ANOVA, SAS, SAS Institute Inc., Cary, N.C., USA). We performed the same analysis with total POM C under woody plants and grasses as the response variable to test whether plant life form influenced soil C chemistry. At LCRA, the fixed effects were plant life form (grass or shrub) and phase of the chronosequence (individual, cluster, grove). At SEV the fixed effects were plant life form (grass or shrub) and dominant vegetation (grassland, shrubland). At CV the fixed effects were plant life form (grass or shrub) and distance from boundary (0, 10, 30 m).

To test the hypothesis that plant life forms influence the depth distribution of soil C, POM C, and soil C cycling, we used an analysis of variance structure similar to the one previously used, except that we added depth as a fixed effect. For these analyses, total C, total N, POM C, or $\delta^{13}\text{C}$ at each soil depth were the response vari-

Fig. 1 Depth distribution of mean values of **a** soil C, **b** particulate organic matter (POM) C, and **c** the proportional contribution of POM C to total C at the La Copita Research Area. Error bars represent 95% confidence intervals determined using Tukey's least significant difference ($n=3$). **a, b** Filled squares and solid lines are mean values from soils beneath *Prosopis glandulosa* while open diamonds and broken lines are mean values taken from beneath grasses. **c** Solid bars are for soils taken beneath *P. glandulosa*; open bars are for soils taken beneath grasses. These graphs show the three-way interaction between plant life form, depth, and chronosequence



ables. Soil core was treated as a random effect. We considered samples within a single core as repeated measure, since within a core, data are not independent with depth. We therefore specified that the covariance structure should be calculated using a first-order autoregressive process (Repeated Measures AR(1), SAS, SAS Institute Inc., Cary, N.C., USA). To determine whether soils from the same depth increment under shrubs or under grasses were significantly different, we used Tukey's test for least significant differences, with $P < 0.05$ as a threshold for significant differences.

Results

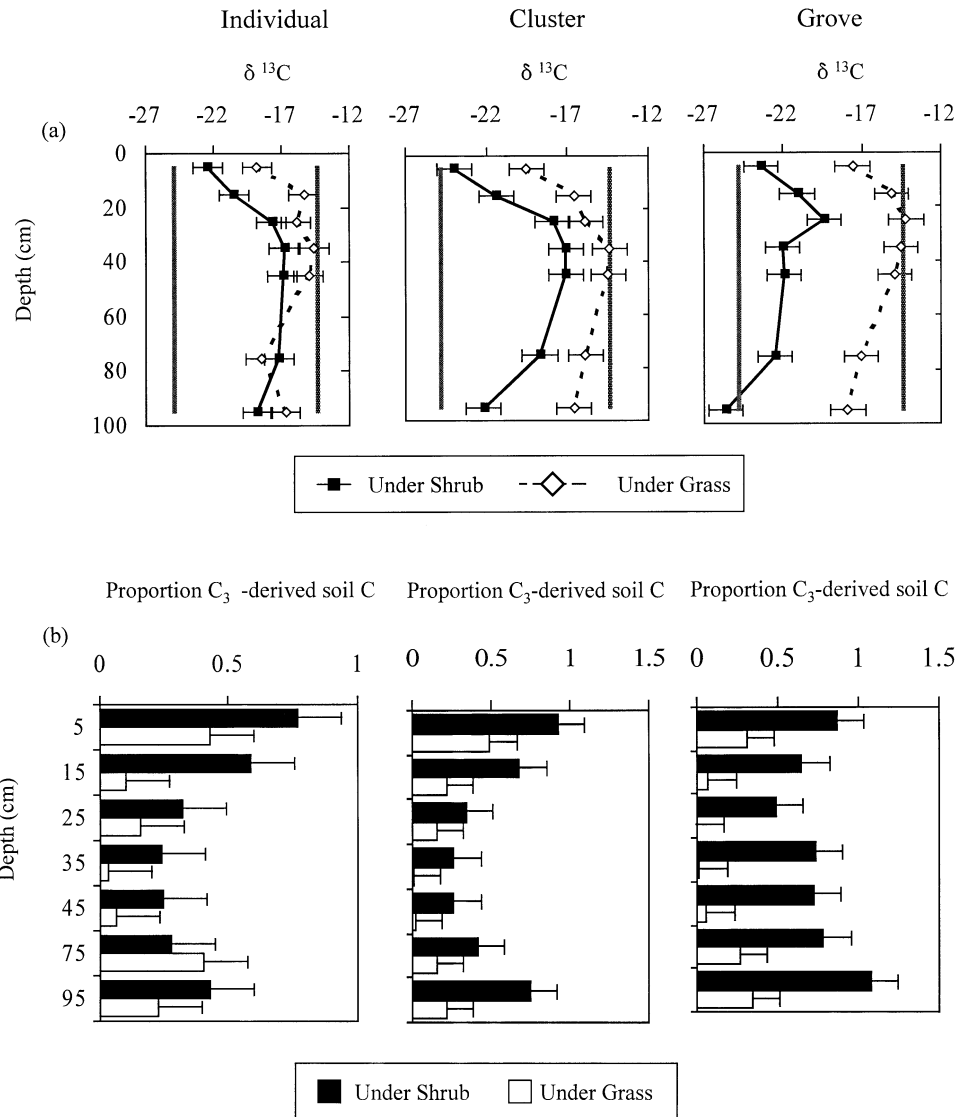
La Copita Research Area, Texas

Soil profiles beneath *P. glandulosa* had significantly more soil C, N, and POM C than soils beneath adjacent

grasslands (Fig. 1a). Total C under *P. glandulosa*, to a depth of 1 m, averaged 7.3 kg C m^{-2} , and under grass locations averaged 6.0 kg C m^{-2} ($P < 0.001$). There was a significant interaction between life form and soil depth, indicating that plant life form influenced the depth distribution of soil C ($P < 0.001$). There was significantly more soil C in the upper 20 cm of the soil profile under *P. glandulosa* than under adjacent grasses ($P < 0.01$).

The interaction between plant life form and soil depth was a significant factor in explaining the distribution of total soil N ($P < 0.01$). Nitrogen enrichment under shrubs, relative to adjacent grasslands, occurred in the upper 10 cm and from 90 to 100 cm. Nitrogen declined from a profile maximum of $17.5 \text{ g N m}^{-2} \text{ cm}^{-1}$ at the soil surface to a profile minimum of $6 \text{ g N m}^{-2} \text{ cm}^{-1}$ from 30 to 40 cm,

Fig. 2 Depth distribution of **a** whole soil C $\delta^{13}\text{C}$ and **b** the relative contribution of C_3 -derived soil C. **a** Filled squares and solid lines are mean values from soils beneath *P. glandulosa* while open diamonds and broken lines are mean values taken from beneath shrubs. Vertical lines show the $\delta^{13}\text{C}$ values of roots taken from beneath *P. glandulosa* and grasses **b** Solid bars are for soils taken beneath *P. glandulosa*; open bars are for soils taken beneath grasses



and increased to $8.5 \text{ g N m}^{-2} \text{ cm}^{-1}$ from 90 to 100 cm. Under grasses, N declined from $9.3 \text{ g N m}^{-2} \text{ cm}^{-1}$ from 0 to 10 cm to a profile minimum of $4 \text{ g N m}^{-2} \text{ cm}^{-1}$ from 90 to 100 cm. There were no significant differences in total N within the whole soil profile beneath grasses and *P. glandulosa*.

Of all the response variables, phase of chronosequence most dramatically influenced POM C (Fig. 1b,c). Soils beneath *P. glandulosa* had more POM C than soils beneath grasses, and the distribution of POM C through the soil profile was different between plant life forms. In addition, unlike total C and N, phase of chronosequence was a significant main effect in determining variation in POM distribution ($P < 0.001$). Beneath grasses, POM C was not significantly different between cores taken adjacent to individual *P. glandulosa*, clusters, or groves, and averaged $1.37 \text{ kg POM C m}^{-2}$ to a depth of 1 m. POM C under shrubs increased along the invasion chronosequence from $1.80 \text{ kg POM C m}^{-2}$ under an individual to $3.55 \text{ kg POM C m}^{-2}$ under grove vegetation. There was a

significant three-way interaction among plant life form, phase of chronosequence, and depth. Under individual shrubs, there was significantly more POM C from 0 to 10 cm than in the surface soils of adjacent grasslands (Fig. 1b). Within cluster vegetation, there was significantly more POM C in the surface 20 cm, and in the 90- to 100-cm layer under shrubs than under grasses. There was significantly more POM C under grove vegetation than adjacent grasslands from 0 to 30 cm and from 40 to 50 cm (Fig. 1b). Carbon in POM was a significantly higher proportion of total C under *P. glandulosa* than under grasses ($P < 0.02$); POM C was 40% of total C under *P. glandulosa* and 25% of total C under grasses (Fig. 1c). For the proportional contribution of POM C to total C, there was no significant interaction between plant life form and depth or the three-way interaction between plant life form, depth, and phase of chronosequence.

Under *P. glandulosa*, average soil $\delta^{13}\text{C}$ values decreased from -18.6‰ under individual shrubs in the youngest phase of the chronosequence, to -22.3‰ un-

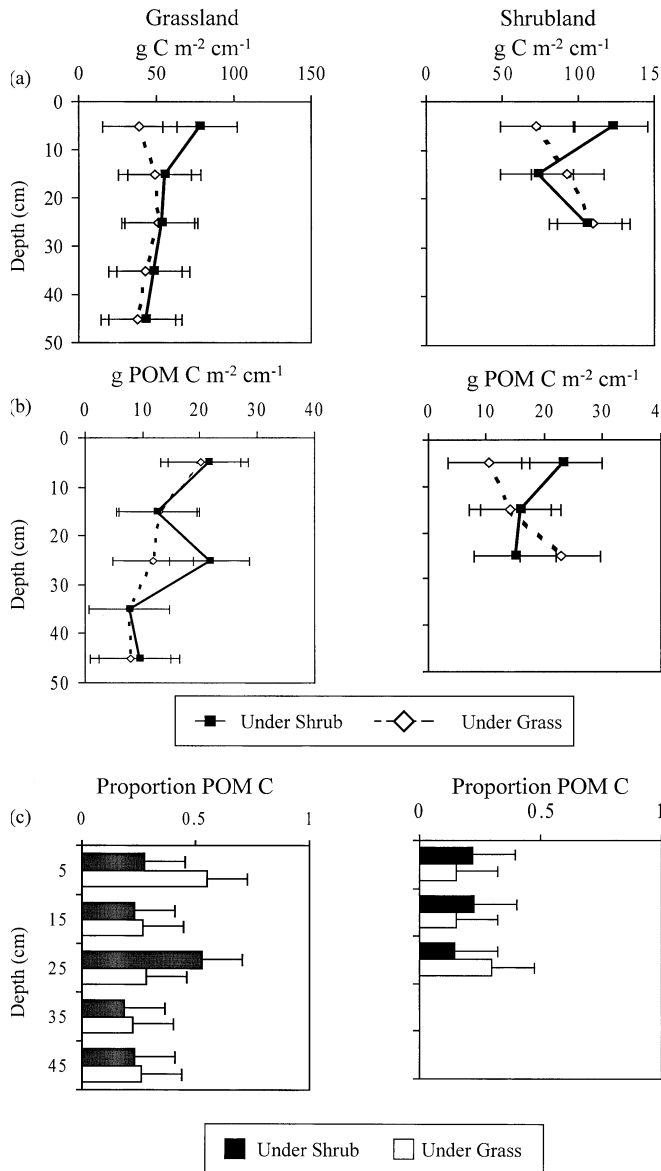


Fig. 3 Depth distribution of mean values of **a** soil C, **b** particulate organic matter C, and **c** the proportional contribution of POM C to total C at Sevilleta National Wildlife Refuge. Error bars represent 95% confidence intervals determined using Tukey's least significant difference ($n=4$). **a**, **b** Filled squares and solid lines are mean values from soils beneath *Larrea tridentata* while open diamonds and broken lines are mean values taken from beneath *Bouteloua* spp. **c** Solid bars are for soils taken beneath *L. tridentata*; open bars are for soils taken beneath *Bouteloua* spp.

der grove vegetation, the oldest phase. The $\delta^{13}\text{C}$ values for soil C under grasses did not vary significantly across the chronosequence. The average value under grasses for whole soil C was -16.6‰ . Under both shrubs and grasses, $\delta^{13}\text{C}$ values were low at the surface, increasing with depth to mid profile, and declining below 40 cm (Fig. 2a). Under shrub whole-soil $\delta^{13}\text{C}$ values followed a parabolic distribution, increasing from -23.3‰ at the soil surface to -18.3‰ at 20–30 cm, and decreasing to -22.2‰ from 90 to 100 cm. Under grass $\delta^{13}\text{C}$ values followed a similar pattern to under shrub

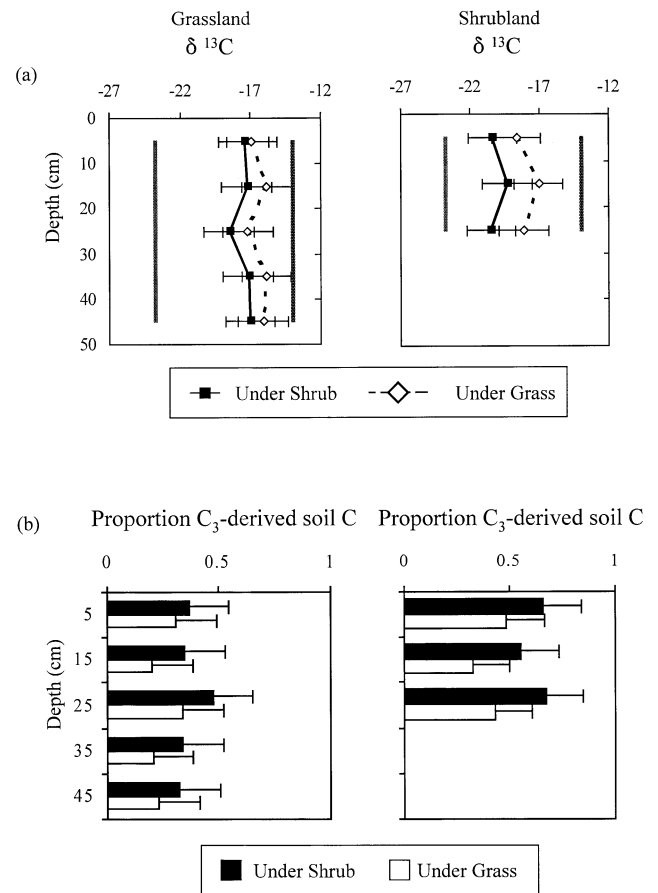


Fig. 4 Depth distribution of **a** whole soil C $\delta^{13}\text{C}$ and **b** the relative contribution of C_3 -derived soil C. **a** Filled squares and solid lines are mean values from soils beneath *L. tridentata* while open diamonds and broken lines are mean values taken from beneath *Bouteloua* spp. Vertical lines show the $\delta^{13}\text{C}$ values of roots taken from beneath *L. tridentata* and *Bouteloua* spp. **b** Solid bars are for soils taken beneath *L. tridentata*; open bars are for soils taken beneath *Bouteloua* spp.

soils, increasing from -18.6‰ at the soil surface to -14.4‰ at 30–40 cm, decreasing to -17.5‰ at 90–100 cm. The $\delta^{13}\text{C}$ values were significantly lower under *P. glandulosa* individuals in the upper 20-cm of the soil profile than under grasses, significantly lower from 0 to 20 and from 30 to 100 cm under cluster shrubs (intermediate phase) relative to grasses, and significantly lower at all depths below groves relative to adjacent grasses (Fig. 2a).

There was significantly more C_3 -derived soil C under *P. glandulosa* than under grasses ($P<0.001$). Soil C beneath *P. glandulosa* was 56% C_3 -derived, while soil C beneath grasses was 18% C_3 -derived (Fig. 2b). There was a significant interaction between life form and phase of chronosequence. C_3 -derived soil C increased from 41% under *P. glandulosa* individuals to 76% under grove vegetation. There were no significant differences between the relative contribution of C_3 -derived soil C under grasses along the shrub development chronosequence.

There were no significant differences in total profile C storage between plant life forms at the SEV site, although the surface 10 cm of the soil profile under shrubs contained significantly more soil C than soils under grasses (Fig. 3a). We compared the surface 30 cm, due to constraints on sampling below 30 cm in the shrubland. There was a significant two-way interaction between plant life form and soil depth in explaining variation in total soil C. Below 10 cm there were no significant differences in soil C storage under shrubs or grasses.

Organic N values were small and quite variable at SEV. None of the fixed effects were significant in explaining variation in organic N. Soils on the grassland side of the ecotone averaged $10.0 \text{ g N m}^{-2} \text{ cm}^{-1}$, while soils on the shrubland side contained $9.3 \text{ g N m}^{-2} \text{ cm}^{-1}$. Soils under shrubs on both sides of the ecotone were consistently higher in N than soils under grasses, although these differences were not significant. Beneath shrubs, soils averaged $11.0 \text{ g N m}^{-2} \text{ cm}^{-1}$ versus $9 \text{ g N m}^{-2} \text{ cm}^{-1}$ under grasses.

POM C ranged from 55% of total C in the surface 10 cm under grasses in grasslands to 15% of total C from 20 to 30 cm under shrubs in the shrubland (Fig. 3c). The highest measured POM C content was found at the soil surface under shrubs on the shrubland side of the ecotone ($23 \text{ g POM C m}^{-2} \text{ cm}^{-1}$) and under grasses on the grassland side ($20 \text{ g POM C m}^{-2} \text{ cm}^{-1}$). There was a significant three-way interaction among plant life form, dominant vegetation, and soil depth ($P < 0.01$).

We found that the whole-profile $\delta^{13}\text{C}$ values in the shrubland were significantly more negative than those in the grassland (Fig. 4a, $P < 0.056$). Average $\delta^{13}\text{C}$ values were -16.9‰ in grasslands and -19.0‰ in shrublands. Soil C $\delta^{13}\text{C}$ values beneath *L. tridentata* were significantly more negative than soil C $\delta^{13}\text{C}$ beneath *Bouteloua* spp. ($P < 0.001$). Shrub soils averaged -18.4‰ , while soils beneath grasses averaged -16.9‰ . There were no significant interactions among plant life form, dominant vegetation, or depth.

Under *L. tridentata*, 43% of soil C was C_3 -derived. The highest proportion of C_3 -derived soil C was beneath *L. tridentata* on the shrubland side of the ecotone (Fig. 4b). The surface 10 cm contained 66% C_3 -derived soil C, while soil C in the 20- to 30-cm depth increment below *L. tridentata* contained 67% C_3 -derived soil C. The lowest relative contribution of C_3 -derived soil C was under *Bouteloua* spp. on the grassland side of the ecotone, where between 20 and 30% of soil C originated from C_3 sources. The only significant differences were between plant life form, where significantly more soil C was C_3 -derived below *L. tridentata* than below *Bouteloua* spp.

Curlew Valley, Utah

There were no significant differences in total profile soil C among soils collected from beneath *Bromus tectorum*,

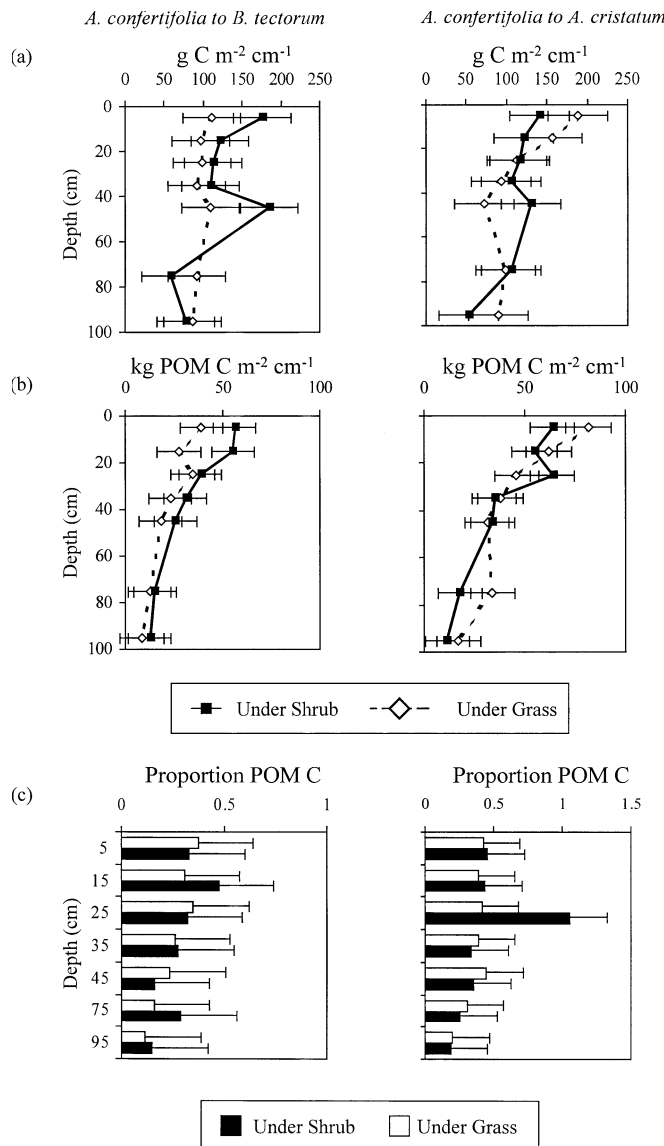


Fig. 5 Depth distribution of mean values of **a** soil C, **b** POM C, and **c** the proportional contribution of POM C to total C at Curlew Valley. Error bars represent 95% confidence intervals determined using Tukey's least significant difference ($n=6$). **a**, Filled squares and solid lines are mean values from soils beneath *Atriplex confertifolia* while open diamonds and broken lines are mean values taken from beneath grasses. **c** Solid bars are from soils taken beneath *A. confertifolia*; open bars are for soils taken beneath grasses (*Bromus tectorum*, *Agropyron cristatum*)

Atriplex confertifolia, or *Agropyron cristatum* ($P < 0.19$). Mean soil C beneath *Atriplex confertifolia*, *Agropyron cristatum*, and *B. tectorum* was 10.2 kg C m^{-2} , 8.9 kg C m^{-2} , and 8.0 kg C m^{-2} , respectively. At CV, the interaction between plant life form and soil depth explained variation in soil C ($P < 0.01$). There were no significant differences in soil C storage at any depths among plant life forms. Under annual grasses, soil C declined from 1.11 kg C m^{-2} at the surface 10 cm to 0.87 kg C m^{-2} at 90–100 cm (Fig. 5a). Under *A. cristatum*, soil C decreased from 1.88 kg C m^{-2} in the surface 10 cm to a profile minimum

of 0.95 kg C m⁻² at 90–100 cm. The distribution of soil C beneath *Atriplex confertifolia* decreased from 1.76 kg C m⁻² at the surface 10 cm to 0.65 kg C m⁻² at 90–100 cm, while there is possible evidence of a buried soil profile indicated by a peak in soil C of 1.85 kg C m⁻² at 40–50 cm.

There was a trend of N content being greatest under shrubs to a depth of 1 m (10.17 g N m⁻²), followed by perennial grasses (9.98 g N m⁻²) and annual grasses (5.73 g N m⁻²), although these differences were not significant. Organic N values were highly variable at CV, and neither fixed effects nor interactions were significant in explaining the distribution. The maximum N concentration in surface soils was found under *Agropyron cristatum*, which averaged 0.20 g N m⁻² cm⁻¹ at the surface 10 cm, while surface soils under *B. tectorum* and *Atriplex confertifolia* averaged 0.11 g N m⁻² cm⁻¹ and 0.14 g N m⁻² cm⁻¹.

At CV, POM C ranged from 37% under *Agropyron cristatum* to 23% under *B. tectorum* (Fig. 5c). The highest measured POM concentration was 81 g POM C m⁻² cm⁻¹ in surface soils beneath *A. cristatum*. The highest POM content was below *A. cristatum* (3.6 kg POM C m⁻²), which was not significantly different from *Atriplex confertifolia* (2.92 kg POM C m⁻²). The soils beneath *B. tectorum* had significantly less POM C than soils beneath *A. confertifolia* ($P < 0.02$). In addition, there were significant two and three-way interactions among plant type, distance from the ecotone boundary, and soil depth. POM C content increased under *A. confertifolia* toward the boundary, while POM C increased away from the boundary under both grasses. At the boundary between *Agropyron cristatum* and *Atriplex confertifolia*, there was significantly more POM C beneath *A. confertifolia* than beneath *Agropyron cristatum* ($P < 0.02$).

There were significant interactions between plant type and depth, plant type and distance from ecotone, and the three-way interaction between plant type, depth, and distance from ecotone. Average $\delta^{13}\text{C}$ values for the upper 50 cm of soil ranged from -16.8‰ under *Atriplex confertifolia* to -19.2‰ under *Agropyron cristatum*. The $\delta^{13}\text{C}$ values for soil C under *B. tectorum* averaged -18.3‰ . The soil C $\delta^{13}\text{C}$ values in the surface 10 cm beneath *A. cristatum* were significantly more negative than soil C $\delta^{13}\text{C}$ values beneath *Atriplex confertifolia*. Under both *Agropyron cristatum* and *B. tectorum*, soil C $\delta^{13}\text{C}$ values were consistently more negative in the upper half meter than soil C $\delta^{13}\text{C}$ values beneath *Atriplex confertifolia*, although these differences are not significant.

A large proportion of soil C beneath *A. confertifolia* was C₃-derived (Fig. 6b). The upper 50 cm of the soil profile beneath *A. confertifolia* were approximately 40% C₃-derived, increasing to over 70% C₃-derived at 1 meter. Relative to *A. confertifolia*, a higher proportion of soil C under *B. tectorum* and *Agropyron cristatum* was C₃ derived. Approximately 50% of soil C in the upper 50 cm under *B. tectorum* was C₃-derived. Almost 60% of soil C under *A. cristatum* was C₃-derived. The only statistically significant increase in C₃-derived soil C, relative to *Atriplex confertifolia*, occurred in the surface

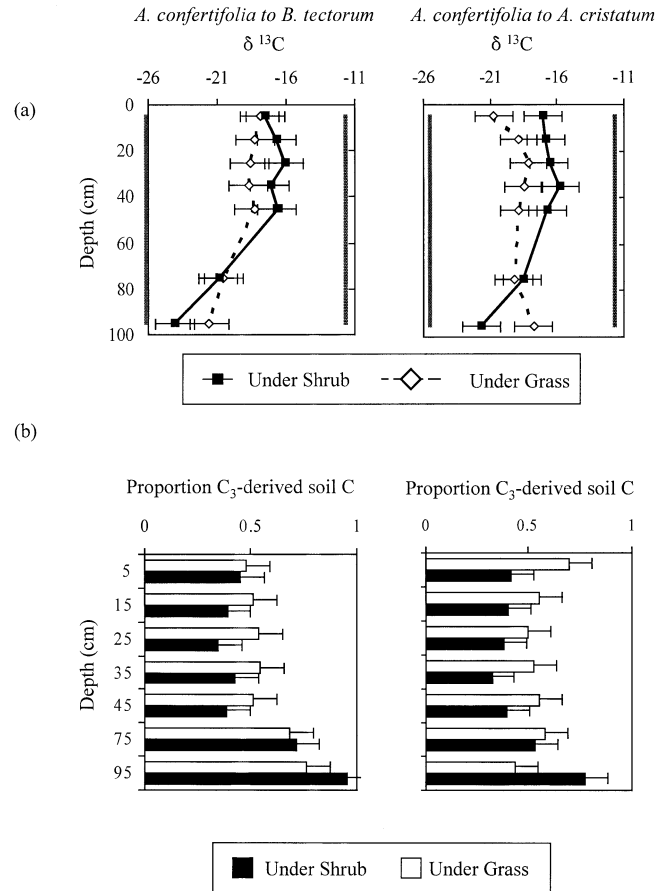


Fig. 6 Depth distribution of **a** whole soil C $\delta^{13}\text{C}$ and **b** the relative contribution of C₃-derived soil C. **a** Filled squares and solid lines are mean values from soils beneath *A. confertifolia* while open diamonds and broken lines are mean values taken from beneath grasses. Vertical lines show the $\delta^{13}\text{C}$ values of roots taken from beneath *A. confertifolia* and grasses **b** Solid bars are from soils taken beneath *A. confertifolia*; open bars are from soils taken beneath grasses

10 cm of the soil profile under *Agropyron cristatum* ($P < 0.05$).

Discussion

Several researchers have suggested that land cover changes may be one of the most significant ways that humans influence ecosystem properties (Vitousek 1994; Uitto and Ono 1996). The results of this study indicate that plant life forms influence the content, quality, and depth distribution of soil C across a range of environments. Our initial hypothesis was that expansion of woody plants into grasslands would increase soil C, with the largest changes observed in both surface and deep horizons, while grass invasion into shrublands would decrease total soil C exclusively in surface horizons. We found that surface layers beneath *Prosopis glandulosa* groves in thorn savannas at LCRA contained nearly twice the soil C found beneath adjacent grasses. At SEV, the surface 10 cm of soils beneath shrubs was enriched in C relative to soils beneath grasses. While there were

no significant differences in soil C storage beneath the different plant life forms in Utah, the invasion has occurred more recently than the other sites, and the trends in soil C storage are consistent with our initial hypothesis.

Along the invasion chronosequence at LCRA, *P. glandulosa* individuals significantly altered soil C dynamics in the surface 20 cm, shrub clusters altered the surface 20 cm and below 30 cm, and shrub groves altered the entire soil profile to 1 m. At SEV, the systematic decrease in $\delta^{13}\text{C}$ under *Larrea tridentata* relative to adjacent *Bouteloua* spp. showed that shrubs had uniformly affected the soil C cycle with depth, although increased accumulation of soil C relative to grasses occurred only in the surface 10 cm. At CV, stable isotopes suggest that both grass species may have influenced soil C cycling in the surface 50 cm of the soil profile, with the perennial grass having the largest alteration in soil C isotopic signature, relative to the shrub. While we did not have sufficient root data to explicitly test the relationship between root biomass and soil C, many other studies have shown that woody plants are almost always more deeply rooted than grasses. Jackson et al. (1996) synthesized data from the literature showing patterns of root distribution for different plant life forms. Grasses generally have <10% of root biomass below 50 cm, while shrubs have >40% below 50 cm. Numerous studies have determined that soil C kinetics are more rapid at the soil surface than at depth, and therefore, soil C $\delta^{13}\text{C}$ values most quickly equilibrate with current vegetation in the upper soil profile (Balesdent et al. 1988; Elzein and Balesdent 1995; Van Dam et al. 1997; Boutton et al. 1998).

At both LCRA and CV, $\delta^{13}\text{C}$ values decreased below 30 cm beneath the dominant C_4 plants. Decreasing $\delta^{13}\text{C}$ values may indicate that the assumption that the grasses at LCRA and the shrubs at CV have been the dominant vegetation for centuries to millennia may not be valid. Boutton et al. (1998) used radiocarbon dating at LCRA to determine the age of soil organic matter. They found that soil organic matter at 1 m was between 1500 and 2500 years old, which would be sufficient time for changes in vegetation. However, the differences that we observed in deep soil horizons between adjacent woody and herbaceous vegetation may indicate that changes in current vegetation is altering soil C dynamics in a soil region that has very long mean residence times. The increased proportion of C_3 -derived C in the lower soil profile relative to surface horizons suggests that LCRA and CV historically had a higher proportion of C_3 plants than was observed prior to the current invasions.

Our second hypothesis was that shifts in plant life form would alter the amount and distribution of POM C. The invasion chronosequence at LCRA showed a clear trend – POM C storage increased with *P. glandulosa* age. At SEV there was more POM C in soils under shrubs than in soils beneath grasses. Soils beneath *Bromus tectorum* at CV were depleted in POM C relative to *Atriplex confertifolia* stands, although there were no significant differences in POM C beneath *A. confertifolia*

and the perennial bunchgrass *Agropyron cristatum*. The higher content of POM C under shrubs relative to most grasses at all three sites indicates that soil C quality may be determined in large measure by the relative abundance of woody and herbaceous plants. Campbell et al. (1994) and Connin et al. (1997) also showed that woody plants altered soil C chemistry by increasing the relative contribution of slowly decomposing fractions of soil C.

Schimel et al. (1995) proposed that increased soil C beneath trees and shrubs in south Texas is a by-product of increases in net primary production following woody vegetation expansion. They used a simulation model to suggest that the increased storage of soil C under trees in savanna ecosystems was primarily due to N fixation by *P. glandulosa*, and additional N increased net primary production in the simulation. Vitousek et al. (1987) observed similar increases in soil C when an N-fixing tree invaded ecosystems in Hawaii. However, the higher content of POM C under non-N fixing shrubs at SEV and CV relative to grasses indicates that higher C content under shrubs may be controlled primarily by differences in plant litter chemistry.

In addition to changes in productivity, litter chemistry, and allocation patterns associated with shifts in plant life form, alteration in hydrology may influence rates of C cycling. Several researchers have demonstrated distinct differences in hydrological patterns between grasses and shrubs. These patterns affect water storage, evapotranspiration, water-use efficiency, and use of water from different soil layers (Walter 1971; Walker and Noy-Meir 1982; Knoop and Walker 1985; Sala et al. 1989; Joffre and Rambal 1993; LeRoux et al. 1995). The presence of deep-rooted species also may induce hydraulic lift, pumping deep soil water to the soil surface (Richards and Caldwell 1987). Any alteration in hydrology in semiarid systems influences carbon cycling, since both production and decomposition are tied to water availability and respond positively to increased soil moisture (Burke et al. 1989). Virginia (1986) found that woody plants altered soil characteristics primarily by changing site hydrology.

Other below-canopy changes in microenvironment may occur following changes in plant life form (Stark 1994). Shading under woody vegetation reduces evaporative demand from the soil surface and in many cases enhances water storage (Belsky 1994; Haworth and McPherson 1995; Scholes and Archer 1997). Stark (1994) found that soils beneath woody vegetation contained plant available water much later in the growing season than soils in grass dominated areas, presumably due to decreased evaporation. Since soils beneath tree canopies are typically cooler than grassland soils, decomposition may be constrained at these lower temperatures (Belsky 1994).

Our study design did not account for changes in interspaces between plants, limiting our ability to scale up from our results and interpret what may be occurring at a stand level. In semiarid systems with discontinuous plant cover, the relative importance of plant interspaces varies

between plant life forms and is important in determining stand level biogeochemistry (Vinton and Burke 1995; Connin et al. 1997; Burke et al. 1998; Burke, in press). In this study, we did not determine if there were any changes in total C associated with plant interspace soils. Connin et al. (1997) found that soils beneath *P. glandulosa* in southern New Mexico were enriched in soil C, but these increases were offset by decreases in soil C in shrub interspaces. Consequently, there was no net increase in soil C storage at a landscape scale following *P. glandulosa* invasion in southern New Mexico. M.R. Aguiar, I.C. Burke, W.K. Lauenroth, and J.E. Anderson (unpublished work) found that scaling up from individual plants to a stand level reduced or eliminated the significant influence of plant life forms on soil properties.

The results from all three sites collectively demonstrate how difficult it is to define plant functional types in order to predict the influence of vegetation change on the distribution of soil C. Evidence from LCRA and CV showed that the depth distribution of soil C may be largely controlled by root distributions and soil C kinetics. However, there were not significant plant life form-induced changes in the depth distribution of soil C at SEV, except at the soil surface. In addition, this study did not explicitly control for differences in physiological and life history characteristics. The largest observed response in C storage occurred beneath *P. glandulosa*, an N-fixing species. Both annual and perennial grasses, with unique life history characteristics, had distinct influences on C cycling. At CV, perennial grasses stabilized the same amount of soil C and POM C as shrubs, while soils beneath annual grasses contained less total C and POM C than adjacent shrublands.

Discussions concerning the development of plant functional types have focused attention on differences between woody plants and grasses (Barkman 1988; Reynolds et al. 1997; Sala et al. 1997; Lauenroth et al. 1997; and many others). Some, such as Barkman (1988) and Shmida and Burgess (1988), have focused on above-ground morphology to explain differences in the ecosystem functions of photosynthesis and soil hydrology. Others, notably Jackson et al. (1996) and Sala et al. (1997), have evaluated how rooting patterns within certain groups influenced and were influenced by ecosystem hydrological patterns, feeding back to primary production. We determined that following changes in plant life form dominance, the most consistent change in soil C was an alteration in content and distribution of POM C, a slowly cycling pool of soil C. While we failed to find a consistent increase or decrease in total soil C across our sites, the POM C and stable isotopes serve as sensitive indicators demonstrating that vegetation changes may have important implications for local and regional C storage and cycling.

Acknowledgments We appreciate the willingness of Texas A & M University, the US Fish and Wildlife Service, and the US Bureau of Land Management to let us collect samples from lands they manage. Richard Arthur, John Barrett, Mary Booth, Ken Murphy, and Sharman Tullis provided valuable assistance in the

field. Bill Lauenroth, Daniel Milchunas, Gene Kelly and two anonymous reviewers provided valuable comments on earlier versions of this paper. This project was supported by the National Science Foundation grant BSR-8114822 to ICB.

References

- Aguiar MR, Paruelo JM, Sala OE, Lauenroth WK (1996) Ecosystem responses to changes in plant functional type composition: an example from the Patagonian steppe. *J Veg Sci* 7:381–390
- Archer SA (1994) Woody plant encroachment into SW grasslands and savannas: rates, patterns and proximate causes. In: Vavra M, Laycock W, Pieper R (eds) Ecological implications of livestock herbivory in the West. Society for Range Management, Denver, pp 13–68
- Archer SA (1995) Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstructing the past and predicting the future. *Ecoscience* 2:83–99
- Archer SA, Scifres C, 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 carbon-13 natural abundances. *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
- Barkman JJ (1988) New systems of plant growth forms and phenological plant types. In: Werger MJA, Aart PMJ van der, During HJ, Verhoeven JTA (eds) Plant form and vegetation structure. SPB Academic, The Hague, pp 9–44
- Belsky AJ (1994) Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. *Ecology* 75: 922–932
- Belsky AJ, Amundson RG, Duxbury JM, Riha SJ, Ali AR, Mwonga SM (1989) The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. *J Appl Ecol* 26:1005–1024
- Bogusch ER (1952) Brush invasion of the Rio Grande Plains of Texas. *Tx J Sci* 4:85–91
- Boutton TW (1996) Stable carbon isotope ratios of soil organic matter and their use as indicators of vegetation and climate change. In: Boutton TW, Yamasaki S (eds) Mass spectrometry of soils. Marcel Dekker, New York, pp 47–82
- Boutton TW, Archer SR, Midwood AJ, Zitzer SF, Bol R (1998) $\delta^{13}\text{C}$ values of soil organic carbon and their use in documenting vegetation change in a subtropical savanna ecosystem. *Geoderma* 82:5–41
- Brown JR, Archer SA (1989) Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. *Oecologia* 80:19–26
- Burke IC (in press) Landscape and regional biogeochemistry: approaches. In: Sala OE (ed) Methods in ecosystem science. Springer, Berlin Heidelberg New York
- Burke IC, Reiners WA, Sturges DL, Matson PA (1987) Herbicide treatment effects on properties of mountain big sagebrush soils after fourteen years. *Soil Sci Soc Am J* 51:1337–1343
- Burke IC, Yonker CM, Parton WJ, Cole CV, Flach K, Schimel DS (1989) Texture, climate, and cultivation effects on soil organic matter content in US grassland soils. *Soil Sci Soc Am J* 53: 800–805
- Burke IC, Lauenroth WK, Vinton MA, Hook PB, Kelly RH, Epstein HE, Aguiar MR, Robles MD, Aguilera MO, Murphy KL, Gill RA (1998) Plant-soil interactions in temperate grasslands. *Biogeochemistry* 42:121–43
- Caldwell MM, White RS, Moore RT, Camp LB (1977) Carbon balance, productivity, and water use of cold-winter desert shrub communities dominated by C_3 and C_4 species. *Oecologia* 29:275–300

- Cambardella CA, Elliott ET (1992) Particulate soil organic-matter changes across a grassland cultivation sequence. *Soil Sci Soc Am J* 56:777–783
- Cambardella CA, Elliott ET (1993) Carbon and nitrogen distribution in aggregates from cultivated and native grassland soils. *Soil Sci Soc Am J* 57:1071–1076
- Campbell BM, Frost P, King JA, Mawanza M, Mhlanga L (1994) The influence of trees on soil fertility on two contrasting semi-arid soil types at Matopos, Zimbabwe. *Agrofor Syst* 28:159–172
- Canadell J, Jackson RB, Ehleringer JR, Mooney HA, Sala OE, Schulze E-D (1996) Maximum rooting depth for vegetation types at the global scale. *Oecologia* 108:583–595
- Charley JL, West NE (1975) Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. *J Ecol* 63:945–963
- Connin SL, Virginia RA, Chamberlain CP (1997) Carbon isotopes reveal soil organic matter dynamics following arid land shrub expansion. *Oecologia* 110:374–386
- Craig H (1957) Isotopic standards for carbon and oxygen and correlation factors for mass spectrometric analysis of carbon dioxide. *Geochem Cosmochim Acta* 42:59–62
- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu Rev Ecol Syst* 23:63–87
- 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 Curlew Valley, Utah. *Oecologia* 66:17–24
- Elzein A, Balesdent J (1995) Mechanistic simulation of vertical distribution of carbon concentrations and residence times in soils. *Soil Sci Soc Am J* 59:1328–1335
- Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. *Annu Rev Plant Physiol Plant Mol Biol* 40:503–537
- Gill RA, Burke IC, Lauenroth WK, Milchunas DG (1999) Relationship between root biomass and soil organic matter pools in the shortgrass steppe of eastern Colorado. *Ecosystems* 2:226–236
- Glendening GE (1952) Some quantitative data on the increase of *P. glandulosa* and cactus on a desert grassland range in southern Arizona. *Ecology* 33:319–328
- Gosz JR (1993) Ecotone hierarchies. *Ecol Appl* 3:369–376
- Grover HD, Musick HB (1990) Shrubland encroachment in southern New Mexico, U.S.A.: an analysis of desertification processes in the American Southwest. *Clim Change* 16:165–190
- Haworth K, McPherson GR (1995) Effects of *Quercus emoryi* trees on precipitation distribution and microclimate in a semi-arid savanna. *J Arid Environ* 31:153–170
- Heitschmidt RK, Ansley RJ, Dowhower PW, Jacoby PW, Price DL (1988) Some observations from excavation of honey *P. glandulosa* root systems. *J Range Manage* 41:227–231
- Hook PB, Burke IC, Lauenroth WK (1991) Heterogeneity of soil and plant N and C associated with individual plants and openings in North American shortgrass steppe. *Plant Soil* 138:247–256
- Jackson RB (1999) The importance of root distributions for hydrology, biogeochemistry, and ecosystem functioning. In: Tenhunen J, Kabat P (eds) Integrating hydrology, ecosystem dynamics, and biogeochemistry in complex landscapes (Dahlem Conference). Wiley, Chichester, pp 219–240
- Jackson RB, Caldwell MM (1992) Shading and the capture of localized soil nutrients: nutrient contents, carbohydrates, and root uptake kinetics of a perennial tussock grass. *Oecologia* 91:457–462
- Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze E-D (1996) A global analysis of root distributions for terrestrial biomes. *Oecologia* 108:389–411
- Jackson RB, Mooney HA, Schulze E-D (1997) A global budget for fine root biomass, surface area, and nutrient contents. *Proc Natl Acad Sci* 94:7362–7366
- Kelly RH, Burke IC, Lauenroth WK (1996) Soil organic matter and nutrient availability responses to reduced plant inputs in shortgrass steppe. *Ecology* 77:2516–2527
- Joffre R, Rambal S (1993) How tree cover influences the water balance of Mediterranean rangelands. *Ecology* 74:570–582
- Kieft TL, White CS, Loftin SR, Aguilar R, Craig JA, Skaar DA (1998) Temporal dynamics in soil carbon and nitrogen resources at a grassland-shrubland ecotone. *Ecology* 79:671–683
- Knapp PA (1996) Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin Desert. *Global Environ Change* 6:37–52
- Knoop WT, Walker BH (1985) Interactions of woody and herbaceous vegetation in a southern African savanna. *J Ecol* 73:235–253
- Lauenroth WK, Coffin DP, Burke IC, Virginia RA (1997) Interactions between demographic and ecosystem processes in semi-arid and arid grasslands: a challenge for plant functional types. In: Smith TM, Shugart HH, Woodward IF (eds) Plant functional types. Cambridge University Press, Cambridge, pp 234–254
- LeRoux X, Bariac T, Mariotti A (1995) Spatial partitioning of the soil water resource between grass and shrub components in a West African humid savanna. *Oecologia* 104:147–155
- Mack RN (1981) Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agroecosystems* 7:145–165
- McClaran MP, McPherson GR (1995) Can soil organic carbon isotopes be used to describe grass-tree dynamics at a savanna-grassland ecotone and within the savanna? *J Veg Sci* 6:857–862
- 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
- Melillo JM, Aber JD, Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63:621–626
- Nelson DW, Sommers LE (1982) Total carbon, organic carbon, and organic matter. In: Page AL, Miller RH, Keeney DR (eds) Methods of soil analysis, 2nd edn. Soil Science Society of America, Madison, pp 539–580
- Nepstad DC, Carvalho CR de, Davidson EA, Jipp PH, Lefebvre PA, Negreiros GH, Silva ED da, Stone TA, Trumbore SE, Vieira S (1994) The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature* 372:666–669
- O'Leary M (1981) Carbon isotope fractionation in plants. *Phytochemistry* 20:553–567
- Reynolds JF, Virginia RA, Schlesinger WH (1997) Defining functional types for models of desertification. In: Smith TM, Shugart HH, Woodward FI (eds) Plant functional types. Cambridge University Press, Cambridge, pp 195–216
- Richards JH, Caldwell MM (1987) Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* 73:486–489
- Sala OE, Golluscio RA, Lauenroth WK, Soriano A (1989) Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia* 81:501–505
- Sala OE, Lauenroth WK, Golluscio RA (1997) Plant functional types in temperate semi-arid regions. In: Smith TM, Shugart HH, Woodward FI (eds) Plant functional types. Cambridge University Press, Cambridge, pp 217–33
- Schimel DS, Brown VB, Hibbard KA, Lund CP, Archer SA (1995) Aggregation of species properties for biogeochemical modeling: empirical results. In: Jones CG, Lawton JH (eds) Linking species and ecosystems. Chapman and Hall, New York, pp 209–214
- Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG (1990) Biological feedbacks in global desertification. *Science* 247:1043–1048
- Schlesinger WH, Raikes JA, Hartley AE, Cross AF (1996) On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77:364–374

- Scholes RJ, Archer SA (1997) Tree-grass interactions in savannas. *Annu Rev Ecol Syst* 28:517–544
- Scholes RJ, Hall DO (1996) The carbon budget of tropical savannas, woodlands and grasslands. In: Breyer AI, Hall DO, Melillo JM, Ågren GI (eds) *Global change: effects on coniferous forests and grasslands*. Wiley, New York, pp 69–100
- Scholes RJ, Walker BH (1993) *An African savanna: synthesis of the Nylsvley study*. Cambridge University Press, Cambridge
- Shmida A, Burgess TL (1988) Plant growth form strategies and vegetation types in arid environments. In: Werger MJA, Aart PJM van der, During HJ, Verhoeven JTA (eds) *Plant form and vegetation structure*. SPB Academic, The Hague, pp 211–242
- Skarpe C (1991) Impact of grazing in savanna ecosystems. *Ambio* 20:351–356
- Smith BN, Epstein S (1971) Two categories of $^{13}\text{C}/^{12}\text{C}$ ratios for higher plants. *Plant Physiol* 47:380–384
- Stark J (1994) Causes of soil nutrient heterogeneity at different scales. In: Caldwell MM, Pearcy RW (eds) *Exploitation of environmental heterogeneity by plants*. Academic Press, San Diego, pp 255–284
- Trumbore SE, Davidson EA, Camargo PB de, Nepstad DC, Martinelli LA (1995) Belowground cycling of carbon in forests and pastures of eastern Amazonia. *Global Biogeochem Cycl* 9:515–528
- Uitto JI, Ono A (1996) *Population, land management, and environmental change*. The United Nations University, Tokyo
- USDA (United States Department of Agriculture) (1979) *Soil survey of Jim Wells County, Texas*. United States Department of Agriculture/Soil Conservation Service, Washington, D.C.
- Van Dam D, Veldkamp E, Van Breemen N (1997) Soil organic carbon dynamics: Variability with depth in forested and deforested soils under pasture in Costa Rica. *Biogeochemistry* 39:343–375
- Van Vegten JA (1983) Thornbush invasion in a savanna ecosystem in eastern Botswana. *Vegetatio* 56:3–7
- Vinton MA, Burke IC (1995) Interactions between individual plant species and soil nutrient status in shortgrass steppe. *Ecology* 76:1116–1133
- Virginia RA (1986) Soil development under legume tree canopies. *For Ecol Manage* 16:69–79
- Virginia RA, Jarrel 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
- Vitousek PM (1994) Beyond global warming: ecology and global change. *Ecology* 75:1861–1876
- Vitousek PM, Walker LR, Whiteaker LD, Mueller-Dombois D, Matson PA (1987) Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* 233:802–804
- Vogel JC (1980) *Fractionation of the carbon isotopes during photosynthesis*. Springer, Berlin Heidelberg New York
- Walker BH, Noy-Meir I (1982) Aspects of the stability and resilience of savanna ecosystems. In: Huntley BJ, Walker BH (eds) *Ecology of tropical savannas*. Springer, Berlin Heidelberg New York, pp 556–590
- Walter H (1971) *Ecology of tropical and subtropical vegetation*. Van Nostrand Reinhold, New York
- Wedin DA, Tieszen LL, Dewey B, Pastor J (1995) Carbon isotope dynamics during grass decomposition and soil organic matter formation. *Ecology* 76:1383–1392
- West NE (1988) Intermountain deserts, shrub steppes, and woodlands. In: Barbour MG, Billings WD (eds) *North American terrestrial vegetation*. Cambridge University Press, New York, pp 209–230
- Whittaker RH, Gilbert LR, Connell JH (1979) Analysis of a two-phase pattern in a mesquite grassland. *Tx J Ecol* 67:935–952
- Young JA, Evans RA (1973) Downy brome: intruder in the plant succession of big sagebrush communities in the Great Basin. *J Range Manag* 26:410–415