Oecologia (1993) 93:95–101

Oecologia

Stable carbon isotope analysis of soil organic matter illustrates vegetation change at the grassland/woodland boundary in southeastern Arizona, USA

G.R. McPherson[1], T.W. Boutton[2], A.J. Midwood[2,]*

[1] Forest-Watershed Sciences Program, School of Renewable Natural Resources, University of Arizona, Tucson, AZ 85721, USA
[2] Department of Rangeland Ecology and Management, Texas A & M University, College Station, TX 77843, USA

Received: 14 May 1992 / Accepted: 8 September 1992

Abstract. In southeastern Arizona, *Prosopis juliflora* (Swartz) DC. and *Quercus emoryi* Torr. are the dominant woody species at grassland/woodland boundaries. The stability of the grassland/woodland boundary in this region has been questioned, although there is no direct evidence to confirm that woodland is encroaching into grassland or vice versa. We used stable carbon isotope analysis of soil organic matter to investigate the direction and magnitude of vegetation change along this ecotone. $\delta^{13}C$ values of soil organic matter and roots along the ecotone indicated that both dominant woody species (C_3) are recent components of former grasslands (C_4), consistent with other reports of recent increases in woody plant abundance in grasslands and savannas throughout the world. Data on root biomass and soil organic matter suggest that this increase in woody plant abundance in grasslands and savannas may increase carbon storage in these ecosystems, with implications for the global carbon cycle.

Key words: $\delta^{13}C$ values – Life-form shifts – *Prosopis juliflora* – *Quercus emoryi* – Savanna

Woody plant abundance has increased substantially during the last 50 to 300 years in many of the world's grasslands (Archer et al. 1988). Examples have been documented in Africa (Kelly and Walker 1976; van Vegton 1983), Australia (Harrington et al. 1984), India (Singh and Joshi 1979), South America (Schofield and Bucher 1986; Bucher 1987), and North America (Buffington and Herbel 1965; Blackburn and Tueller 1970; Smeins 1983; Archer et al. 1988). Increased woody plant abundance in North American grasslands has been attributed to climate change (Hastings and Turner 1965; Neilson 1986), reduced fire frequency (Sauer 1950; Stewart 1951), increased cattle grazing (Bogusch 1952; Bahre 1977), or combinations of these factors (Humphrey 1958; Wright and Bailey 1982). Although encroachment of woody plants into grasslands has been reported widely, the rates and patterns of the process have seldom been quantified (Archer et al. 1988). Furthermore, Bahre (1991) concluded that woody plants have always been present in most North American grasslands, and cautioned against interpreting increased woody plant dominance as evidence of range expansion of woodlands.

It has been suggested that the world's grasslands may become increasingly susceptible to succession toward woodland as a consequence of anticipated global climatic changes (Emanuel et al. 1985). Conversely, global warming may cause communities to shift upslope, with grasslands expanding into woodlands. In general, post-Pleistocene shifts in mid-latitude woody plant communities have been found to reflect the latter phenomenon (e.g., Betancourt et al. 1990).

Prosopis juliflora (Swartz) DC. and *Quercus emoryi* Torr. represent the primary woody species at grassland/woodland boundaries in southeastern Arizona. Evidence from historical sources (Humphrey 1958; Hastings and Turner 1965; Bahre 1977; Bahre 1991) indicates that *Prosopis juliflora* has increased in density and/or stature in desert grasslands of southeastern Arizona. These studies have relied on historical accounts or photographs, and have been largely anecdotal in nature. Research on a closely-related species (*Prosopis glandulosa* Torr.) documented increased density and abundance of *Prosopis* during the past 100–200 years, and demonstrated facilitation of recruitment of other woody plants by that species, in grasslands of southern Texas (Archer et al. 1988; Archer 1990).

Research on distribution patterns of other woody species in the southwestern United States has been even less definitive than the work on *Prosopis*. Hastings and Turner (1965), relying on historic photographs, concluded that grasslands have replaced *Quercus* woodlands as the latter communities receded upslope in the last century. They attributed *Quercus* die-off at the wood-

---

* *Present address:* Macaulay Land Use Research Institute, Craigiebuckler, Aberdeen AB92QJ, Scotland

Correspondence to: G.R. McPherson

land-grassland boundary to an increasingly xeric climate. Cooke and Reeves (1976) questioned this interpretation, primarily because the amount and distribution of precipitation have not changed significantly in the last 100 years. Bahre (1977) indicated that regeneration of *Quercus* spp. decreased with grazing, but later concluded that the distribution of *Quercus* woodlands has been stable since the 1860's (Bahre 1991).

Prosopis juliflora and *Quercus emoryi* are C_3 plants, whereas dominant grasses in this region (i.e., *Bouteloua* spp., *Aristida* spp., *Eragrostis* spp.) are C_4 plants. C_3 plants have average $\delta^{13}C$ values of about $-27‰$, while C_4 plants have average $\delta^{13}C$ values near $-12‰$ (Boutton 1991b). Because the $\delta^{13}C$ value of soil organic matter (SOM) is approximately equal to that of the plant material from which it originates (Nadelhoffer and Fry 1988; Melillo et al. 1989; Boutton 1991b), the isotopic composition of SOM can be used to indicate where vegetation has shifted from dominance by one photosynthetic pathway type to the other (Stout et al. 1981). $\delta^{13}C$ values of SOM have been used previously to document shifts in community composition and distribution (e.g., Dzurec et al. 1985; Schwartz et al. 1986; Volkoff and Cerri 1987; Tieszen and Archer 1990; Ambrose and Sikes 1991).

We hypothesized that warm season (C_4) grasses have been displaced by woody plants (C_3) at the woodland/grassland boundary in southeastern Arizona. If this hypothesis is correct, then there should be a discrepancy between the $\delta^{13}C$ of woody vegetation and associated SOM. Analysis of stable carbon isotope values will provide direct chemical evidence which will allow acceptance or rejection of the hypothesis that woody plants have replaced grasses in southeastern Arizona. If woody plant species have been a long-term component of these landscapes, then the $\delta^{13}C$ values of SOM beneath trees should bear a C_3-like isotope signature. However, if woody species have encroached recently on C_4 grasslands, then the $\delta^{13}C$ of the SOM should still bear a C_4-like value similar to that found in the grassland matrix.

Methods

Study areas

Research was conducted at two sites in southeastern Arizona, USA: Fort Huachuca Military Reservation (FHMR) (31° 34′ N, 110° 26′ W, in the Huachuca Mountains) and the Appleton-Whittell Audubon Society Research Ranch (RR) (31° 36′ N, 110° 30′ W, in Canelo Hills). Elevation of areas sampled ranged from 1480 to 1570 m. Livestock grazing has been excluded from these sites since about 1950 and 1969, respectively. On both sites, mean annual precipitation is approximately 500 mm, with 70% falling in summer (July–October) and 20% in winter (December–March). Study areas had soils of the White House series (loamy, thermic, Ustollic Haplargids). These soils are formed in old alluvium weathered from andesite, rhyolite, dacite, granite, and tuffaceous rock material, on piedmont slopes (Richardson et al. 1985).

Sampling was conducted in *Prosopis juliflora* and *Quercus emoryi* savannas (hereafter, *Prosopis* savannas and *Quercus* savannas) on each site. *Quercus* savannas at both study sites are transitional between closed-canopy *Quercus* woodlands (at higher elevations) and semi-desert grasslands (at lower elevations), forming a band typically less than 250 m wide. *Prosopis* savannas are located within semi-desert grasslands (Research Ranch site) or are transitional between these grasslands (at locally higher elevations) and bottomland *Prosopis* bosques (at locally lower elevations) (Fort Huachuca site). Typical woody plants in these savannas are 4–5 m tall and distributed sparsely. Herbaceous vegetation in all savannas sampled is comprised almost exclusively of warm-season (C_4) perennial grasses with few cool-season (C_3) herbs (Wentworth 1983; Gurevitch 1986). Dominant herbaceous species on all sites were *Bouteloua curtipendula* (Michx.) Torr., *B. hirsuta* Lag., *B. gracilis* (H.B.K.) Lag. ex Steud., *Eragrostis lehmanniana* Nees, *E. intermedia* Hitchc., and *Aristida* spp. *Prosopis* trees, which have winter-deciduous, relatively open canopies, have more understory biomass than evergreen, closed-canopy *Quercus* trees (personal observation).

Procedures

Within each site and community, 2 threes were selected at random with the following restrictions: selected trees were 3–6 m tall, and were at least 5 m from the nearest neighboring tree. Thus, the sampled trees were similar, in size and distribution, to others in the savannas. Soil and litter samples were collected within 0.5 m of the base of trees and in the herbaceous zones between trees (at least 5 m from the nearest tree). Field sampling was conducted in February 1990.

At each sample point (i.e., under each tree and in herbaceous zones), litter was collected from a 0.5 m^2 plot, and a soil core (10-cm diameter) was extracted and divided into 10-cm depth intervals. Core depth was limited to 40–50 cm at all sites by the presence of consolidated parent material. Large roots were separated from bulk soil by sifting through a 2 mm sieve. Small roots and particulate organic matter (the "light fraction", Stevenson and Elliott 1989) were removed by flotation in saturated NaCl solution (density = $1.2 \text{ g} \cdot \text{cm}^{-3}$). Root and soil samples were washed several times in distilled water to remove excess salt. Litter, root, and soil samples were oven-dried at 70° C, weighed, pulverized to a fine powder, and homogenized thoroughly with a mixer mill (Brinkmann Model MM2, Brinkmann Instruments Co., Westbury, NY, USA). These soils did not contain carbonates (H.L. Bohn, pers. comm.): soils were not effervescent, and pH varied from 5.4 to 6.4 (mean = 6.0). Soil organic carbon and total nitrogen were determined by an automated Dumas combustion procedure (Pella and Colombo 1973) using a Carlo Erba NA–1500 elemental analyzer. Repeated measurement ($n = 5$) of a soil standard (Leco 502–062, Leco Corp., St. Joseph, MI, USA) yielded a precision of $0.15 \text{ g} \cdot \text{kg}^{-1}$ for carbon and $0.02 \text{ g} \cdot \text{kg}^{-1}$ for nitrogen.

Samples were combusted to CO_2 following Boutton (1991a), and the isotopic composition of the CO_2 determined on a dual-inlet, triple collector gas isotope ratio mass spectrometer (VG–903, Middlewich, UK). Results are expressed in $\delta^{13}C$ notation:

$$\delta^{13}C \text{ ‰} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$$

where R = mass 45/mass 44 of sample or standard CO_2 (Craig 1957). All samples are reported relative to the international PDB standard. Repeated measurement ($n = 5$) of a soil standard yielded a precision (1 SD) of 0.1‰.

Data were tested for normality with the Wilk-Shapiro W-statistic (Shapiro and Wilk 1965). Data were distributed normally ($P < 0.05$), and were analyzed subsequently with analysis of variance. We tested responses of soil organic carbon, total nitrogen, root mass, and $\delta^{13}C$ values to the main effects of study site (FHMR, RR), species *(Quercus emoryi, Prosopis juliflora)*, sampling location (tree, herbaceous zone), and depth (0–10, 10–20, 20–30, 30–40, 40–50 cm), and their interactions.

Results

Root mass was not affected ($P > 0.05$) by 2-, 3-, or 4-way interactions between study site, species, sampling location, and depth. Furthermore, only sampling location and depth influenced ($P < 0.05$) root mass. The mass of roots under trees was approximately twice that under grassland at all depths sampled (Fig. 1). Root mass decreased markedly with increased soil depth; roots at the 40–50 cm depth contributed about 8% to the cumulative root mass to that depth.

Carbon and nitrogen were characterized by three-way interactions ($P < 0.05$) between study site, species, and sampling location. Because of the interaction, and since we were primarily interested in the effects of sampling location and depth on soil elements, subsequent analyses were restricted to effects of sampling location and depth within study sites and species. Under *Prosopis* trees, carbon and nitrogen were not affected ($P > 0.15$) by interactions or main effects of sampling location and depth on either site. Under *Quercus* trees, interactions between sampling location and depth were not evident ($P > 0.15$) on either site. However, carbon and nitrogen levels under *Quercus* trees decreased ($P < 0.05$) with increased sampling depth on both sites (Fig. 2). In addition, carbon and nitrogen levels were higher ($P < 0.05$) under trees than in herbaceous zones at RR and tended to be higher ($P = 0.16$ for both elements) under trees at FHMR.

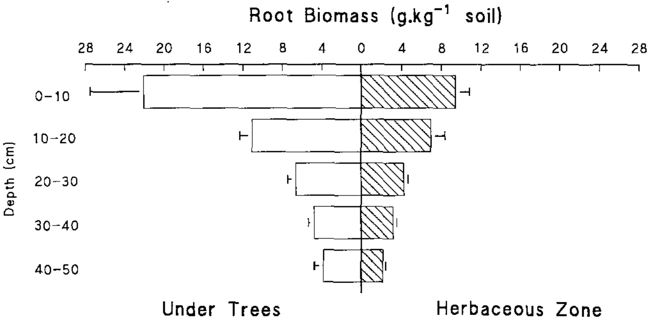

Fig. 1. Mean root mass (g · kg^{-1} soil) under trees and in herbaceous zones in semi-arid *Quercus* and *Prosopis* savannas, southern Arizona, USA. Small horizontal lines are standard error bars

$\delta^{13}C$ values for SOM were characterized by an interaction ($P < 0.05$) between study site and species, and main effects of sampling location and depth. The site × species interaction was most apparent for *Prosopis* trees, under which $\delta^{13}C$ values at 0–10 cm were over 4‰ higher at FHMR than RR (Figs. 3, 4). By contrast, $\delta^{13}C$ values under *Quercus* trees were higher at RR than FHMR throughout the soil profile. SOM had a strong C_4-like signature in all herbaceous zone profiles. $\delta^{13}C$ values for SOM samples were generally larger than $\delta^{13}C$ values for the accompanying root samples.

Despite a clear influence of C_3 trees on $\delta^{13}C$ values of litter under both tree species, SOM $\delta^{13}C$ values under trees increased with increasing depth for each species and

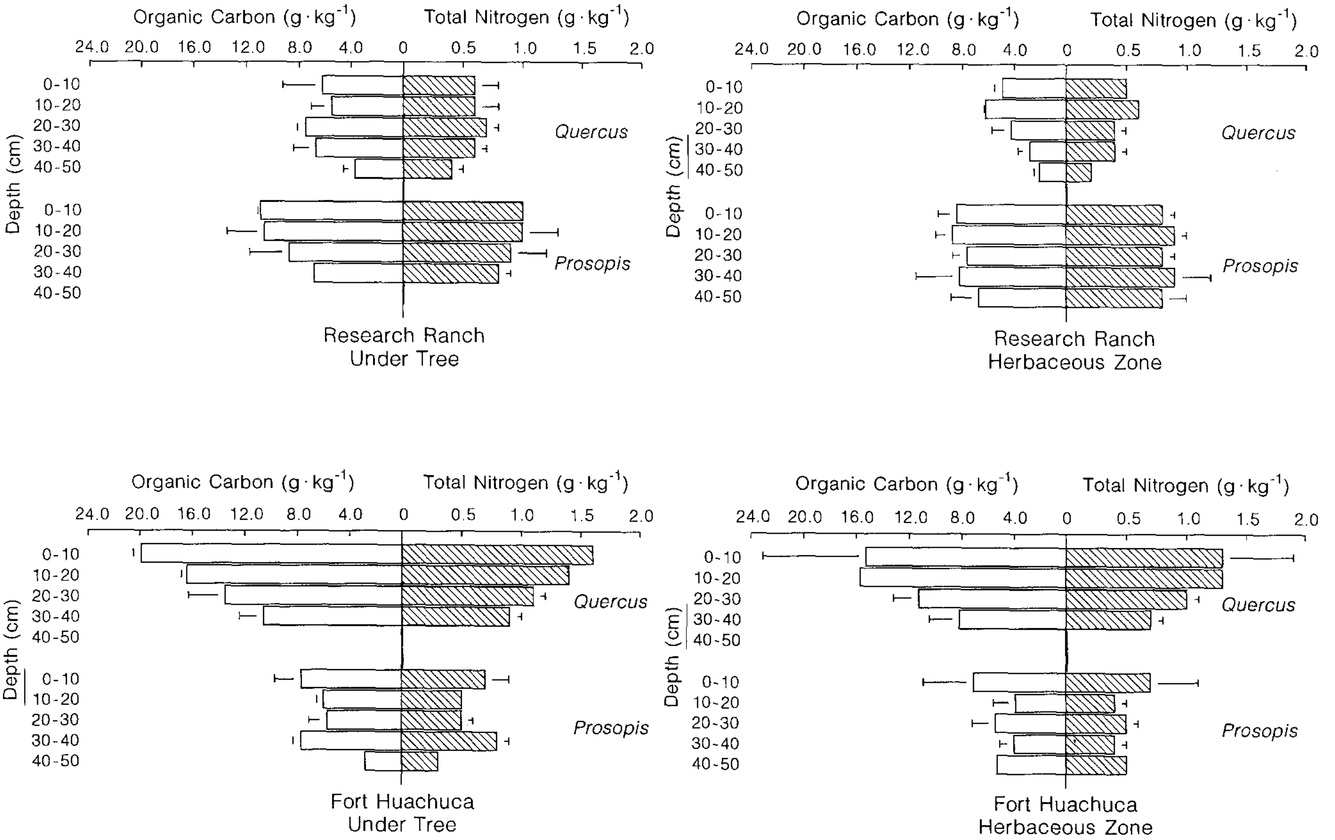

Fig. 2. Mean organic carbon and total nitrogen (g · kg^{-1} soil) under trees and in herbaceous zones in semi-arid *Quercus* and *Prosopis* savannas, southern Arizona, USA. Small horizontal lines are standard error bars

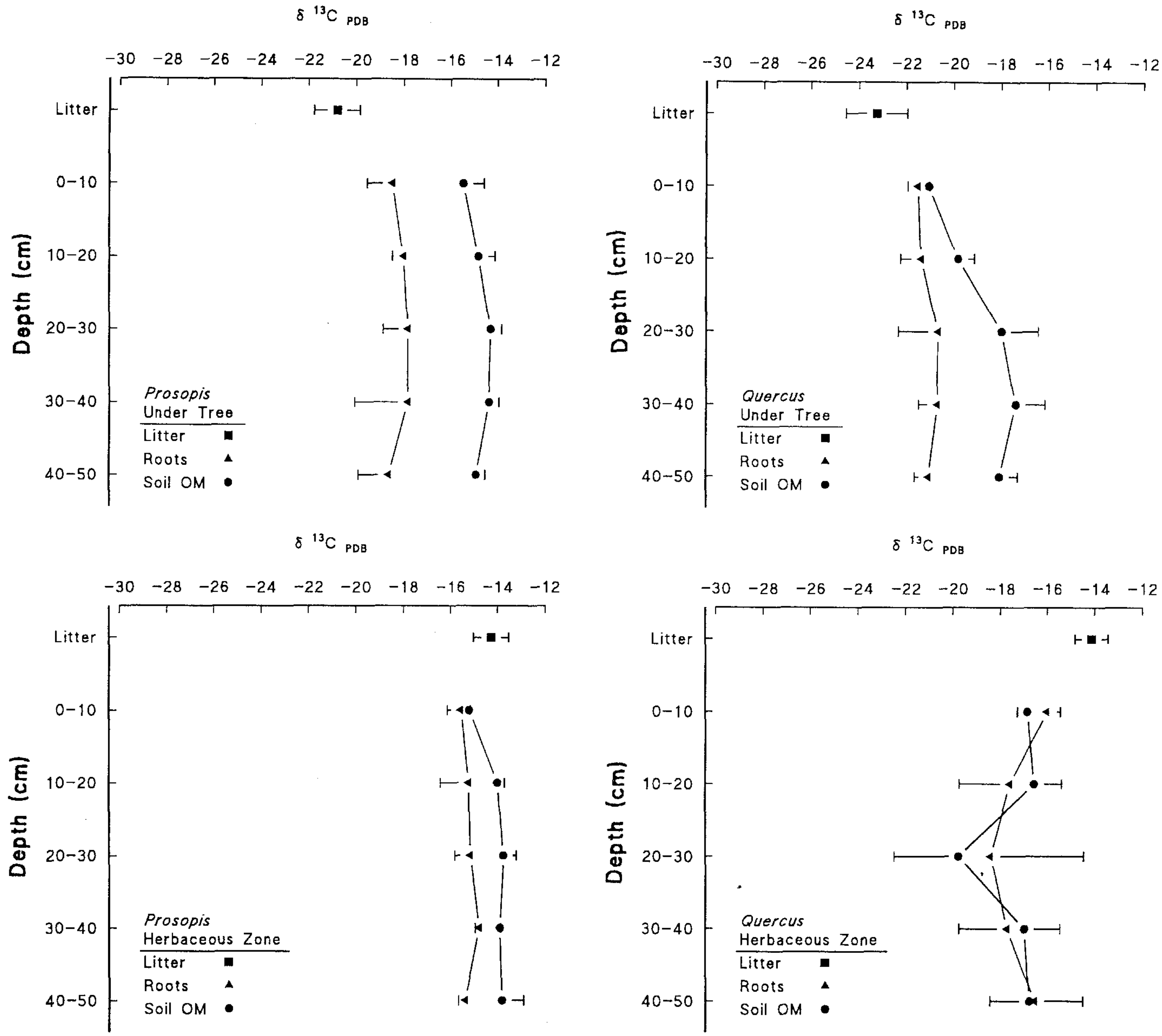

Fig. 3. Mean $\delta^{13}C$ values of roots, litter, and SOM under trees and in herbaceous zones in semi-arid *Quercus* and *Prosopis* savannas at the Research Ranch study site, southern Arizona, USA. Small horizontal lines are standard error bars

site. $\delta^{13}C$ values of SOM and roots were similar throughout herbaceous zone profiles, but diverged with increasing depth under trees. However, rate and magnitude of changes in $\delta^{13}C$ values of SOM differed between species and study sites. For example, $\delta^{13}C$ values under *Prosopis* trees increased from −19.9 to −15.8‰ at FHMR, but varied only from −15.5 to −14.9‰ at RR. $\delta^{13}C$ values of SOM under *Quercus* trees were similar to values under *Prosopis* trees at FHMR, but were lower throughout the profile at RR. Litter $\delta^{13}C$ values were higher under *Prosopis* trees than under *Quercus* trees at both study sites.

Discussion

The tendency for roots to be concentrated in upper soil layers has been reported for several biomes (Richards 1986 and references therein). Root biomass under trees and in grassland areas in this study declined in a negative exponential manner, similar to patterns reported previously for grasslands (Dahlman and Kucera 1965; Okali et al. 1973; Sims and Singh 1978; Melgoza and Nowak 1991), temperate forests (McClaugherty et al. 1982), tropical forests (Huttel 1975), tundra (Dennis 1977), and estuarine marsh (Curtis et al. 1990). By contrast, root distributions in savannas usually exhibit a pattern of increased root biomass with increased depth to 20–30 cm, then decreased root biomass with greater

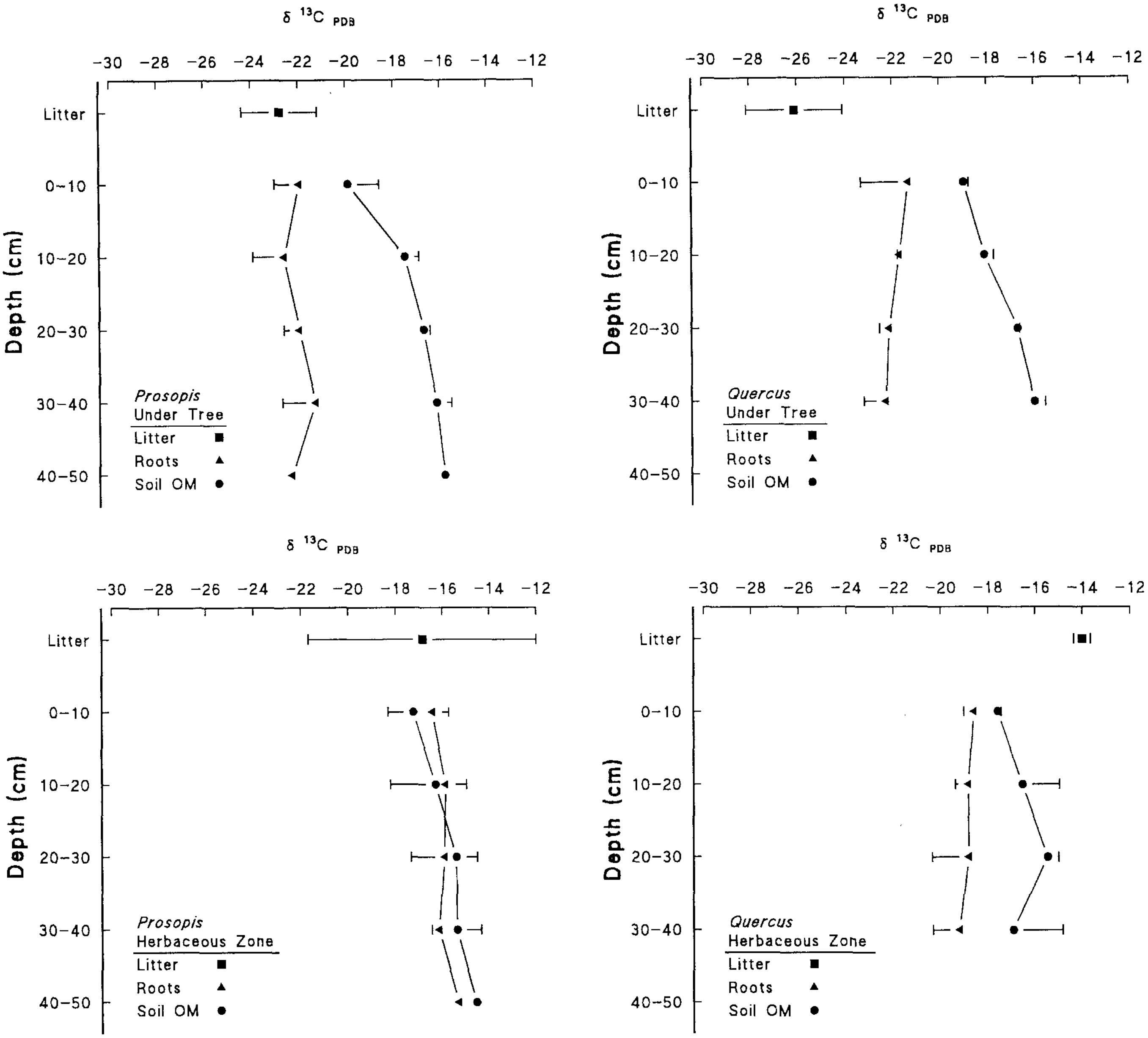

Fig. 4. Mean $\delta^{13}C$ values of roots, litter, and SOM under trees and in herbaceous zones in semi-arid *Quercus* and *Prosopis* savannas at the Fort Huachuca Military Reservation study site, southern Arizona, USA. Small horizontal lines are standard error bars

soil depth (Lawson et al. 1968; Soriano and Sala 1983; Knoop and Walker 1985). This pattern is consistent with Walter's (1971) two-layer hypothesis of savanna stability if woody plants account for the increased root biomass in the subsurface layer.

Root distributions in our *Quercus* and *Prosopis* savannas follow a pattern similar to that reported for other biomes, but atypical for savannas. Furthermore, root distribution patterns did not differ under trees of different species, and a similar pattern (though with lower root mass) was found in open grassland. Although *Quercus* and *Prosopis* trees have obvious architectural differences above ground, they appear to be similar with respect to distribution of root mass.

Increased carbon and nitrogen under *Quercus* trees is consistent with other studies documenting enhanced fertility beneath woody plants in grasslands and deserts (Virginia and Jarrell 1983; Jackson et al. 1990; Schlesinger et al. 1990). In contrast to results reported previously in *Prosopis* savannas of southern Arizona (Tiedemann and Klemmedson 1973a, 1973b, 1986, Klemmedson and Tiedemann 1986), we did not find greater concentrations of carbon or nitrogen under *Prosopis* trees. *Prosopis* may have colonized our study sites so recently that soil nutrient levels have not had time to increase.

Increased root mass (under both tree species) and soil carbon *(Quercus)* under trees may have important implications for the global carbon cycle. Specifically, increased woody plant biomass in grasslands and savannas throughout the world may be an important carbon sink.

Given the large land area undergoing this physiognomic conversion (see introduction), increased carbon storage in the root mass and soil organic carbon beneath woody plants could be a significant phenomenon.

$\delta^{13}C$ values support the hypothesis that these savannas are transitional, and are changing from grassland to woodland. All herbaceous zone profiles had $\delta^{13}C$ values of SOM which were in equilibrium with $\delta^{13}C$ values of roots and extant vegetation. By contrast, $\delta^{13}C$ values under trees of both species indicated that trees are recent occupants of former grassland sites: $\delta^{13}C$ values for SOM increased with increasing soil depth, and were higher than (i.e., lagged behind) $\delta^{13}C$ values of roots. Although sample size in this study is admittedly small, it is clear that all trees sampled are recent occupants of former grassland sites, and that all herbaceous zones have been dominated by C_4 grasses throughout the period. This interpretation is consistent with many studies which have documented recent physiognomic shifts from grassland or savanna to woodland throughout the world (e.g., Tieszen and Archer 1990 and references therein). Empirical studies are supported further by a recent model (Menaut et al. 1990), which found no conditions in which savannas were stable-they succeeded quickly to closed-canopy woodlands except under extremely frequent fire regimes, when they reverted to grasslands.

An alternative interpretation of our data is that the intermittent tree cover of these savannas varies from place to place over time, with individual trees establishing in herbaceous zones concomitant with the death of other individuals (i.e., within-savanna redistribution of trees). However, we found no evidence that trees formerly occurred in any of the herbaceous zones we sampled, and this hypothesis is not consistent with the model of Menaut et al. (1990) or other empirical studies.

Our findings for *Prosopis* savannas are supported locally by interpretations of historical evidence and photographs. In reviews of historical evidence, Hastings and Turner (1965) and Bahre (1991) concluded that *Prosopis* has recently increased in abundance in former grasslands in southeastern Arizona.

Our conclusion that *Quercus* trees are recent components of former grasslands is not consistent with previous interpretations of grassland/woodland boundary dynamics in this region. Hastings and Turner (1965) concluded that *Quercus* woodlands are receding at the grassland/woodland boundary, and Bahre (1991) concluded that the boundary is stable. However, these studies relied heavily on historic ground photography of disturbed sites, nearly all of which were taken a decade or more after sites were disturbed in the 1860's. Furthermore, the field of view in ground photographs is usually oblique and narrow, which limits their usefulness for determining changes in plant distribution (Bahre 1991). Data from the current study represent the first direct evidence of life-form shifts at the grassland/woodland boundary in the southwestern United States, with results that are consistent with a global pattern of increased woody plant abundance in grasslands and savannas. Examples in the United States, documented with stable isotope methodology, have been reported by Tieszen and Archer (1990) and Steuter et al. (1990).

Results of this study are contrary to those expected from changes in global climate alone: global warming and drying since the Pleistocene has generally caused woody plant communities to shift upslope (Betancourt et al. 1990). The recent establishment of *Quercus* trees into former grasslands below oak woodlands apparently results from factors other than post-Pleistocene warming and drying. Livestock grazing, altered fire frequency, and increased atmospheric CO_2 (Mayeux et al. 1991) may be among the factors influencing this successional pattern.

Acknowledgements. Kelly Brown, Kathryn Haworth, Justine McNeil, Roy Pollisco, Daniel Watts, and Xin Wang provided field and laboratory assistance. The U.S. Army and the Audubon Society graciously allowed access to study sites. Funding was provided by the University of Arizona Foundation and the Office of the Vice President for Research under the University of Arizona Small Grants Program, and Texas Agricultural Experiment Station Project H-6945.

References

Ambrose SH, Sikes NE (1991) Soil carbon isotope evidence for Holocene habitat change in the Kenya Rift Valley. Science 253:1402–1405

Archer S (1990) Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas, U.S.A. J Biogeog 17:453–462

Archer S, Scifres C, Bassham CR (1988) Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecol Monogr 58:111–127

Bahre CJ (1977) Land-use history of the Research Ranch, Elgin, Arizona. J Ariz Acad Sci 12 [Suppl 2]: 1–32

Bahre CJ (1991) A Legacy of Change: Historic Human Impact on Vegetation in the Arizona Borderlands. University of Arizona Press, Tucson, 231 p

Betancourt JL, Van Devender TR, Martin PS (1990) Packrat Middens: The Last 40,000 Years of Biotic Change. University of Arizona Press, Tucson, 467 p

Blackburn WH, Tueller PT (1970) Pinyon and juniper invasion in black sagebrush communities in east-central Nevada. Ecology 51:841–848

Bogusch ER (1952) Brush invasion on the Rio Grande Plains of Texas. Texas J Sci 4:85–90

Boutton, TW (1991a) Stable carbon isotope ratios of natural materials: I. Sample preparation and mass spectrometric analysis. In: Coleman DC, Fry B (eds) Carbon Isotope Techniques. Academic Press, New York, pp 155–171

Boutton, TW (1991b) Stable carbon isotope ratios of natural materials: II. Atmospheric, terrestrial, marine, and freshwater environments. In: Coleman DC, Fry B (eds) Carbon Isotope Techniques. Academic Press, New York, pp 173–185

Bucher EH (1987) Herbivory in arid and semi-arid regions of Argentina. Revista Chilenda de Historia Natural 608:265–273

Buffington LC, Herbel CH (1965) Vegetational changes on a semidesert grassland range from 1858 to 1963. Ecol Monogr 35:139–164

Cooke RU, Reeves RW (1976) Arroyos and environmental change in the American south-west. Clarendon Press, Oxford

Craig H (1957) Isotopic standards for carbon and oxygen and correction factors for mass spectrometric analysis of carbon dioxide. Geochim Cosmochim Acta 12:133–149

Curtis PS, Balduman LM, Drake BG, Whigman DF (1990) Elevated atmospheric CO_2 effects on belowground processes in C_3 and C_4 estuarine marsh communities. Ecology 71:2001–2006

Dahlman RG, Kucera CL (1965) Root productivity and turnover in native prairie. Ecology 46:84–89

Dennis JG (1977) Distribution patterns of belowground standing crop in arctic tundra at Barrow, Alaska. In: Marshall JK (ed) The Belowground Ecosystem: A Synthesis of Plant-Associated

Processes. Range Science Department, Colorado State Univ, Fort Collins, pp 53–62

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

Emanuel WR, Shugart HH, Stevenson M (1985) Climatic change and the broad-scale distribution of terrestrial ecosystem complexes. Climatic Change 7:29–43

Gurevitch J (1986) Competition and the local distribution of the grass *Stipa neomexicana*. Ecology 67:46–57

Harrington GN, Wilson AD, Young MD (1984) Management of Australia's Rangelands. CSIRO, Melbourne

Hastings JR, Turner RM (1965) The Changing Mile. University of Arizona Press, Tucson, 317 p

Humphrey RR (1958) The desert grasslands: a history of vegetational change and an analysis of causes. Bot Rev 24:193–252

Huttel C (1975) Root distribution and biomass in three Ivory Coast rain forest plots. In: Golley FB, Medina E (eds) Tropical Ecological Systems: Trends in Terrestrial and Aquatic Research. Springer-Verlag, New York, pp 123–130

Jackson LE, Strauss RB, Firestone MK, Bartolome JW (1990) Influence of tree canopies on grassland productivity and nitrogen dynamics in deciduous oak savanna. Agric Ecosyst Environ 32:89–105

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

Klemmedson JO, Tiedemann AR (1986) Long-term effects of mesquite removal on soil characteristics: II. Nutrient availability. Soil Sci Soc Am J 50:476–480

Knoop WT, Walker BH (1985) Interactions of woody and herbaceous vegetation in a southern African savanna. J Ecol 73:235–253

Lawson GW, Jenik J, Armstrong-Mensah KO (1968) A study of a vegetation catena in Guinea savanna at Mole Game Reserve (Ghana). J Ecol 56:505–522

Mayeux HS, Johnson HB, Polley HW (1991) Global change and vegetation dynamics. In: James LF, Evans JO, Ralphs MH, Child RD (eds) Noxious Range Weeds. Westview Press, Boulder, CO, pp 62–74

McClaugherty CA, Aber JD, Melillo JM (1982) The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. Ecology 63:1481–1490

Melgoza G, Nowak RS (1991) Competition between cheatgrass and two native species after fire: implications from observations and measurements of root distribution. J Range Man 44:27–33

Mellilo JM, Aber JD, Linkins AE, Ricca A, Fry B, Nadelhoffer KJ (1989) Carbon and nitrogen dynamics along the decay continuum: plant litter to soil organic matter. In: Clarholm M, Bergstrom L (eds) Ecology of Arable Land. Kluwer Academic Publ, Dordrecht, Netherlands, pp 53–62

Menaut JC, Gignoux J, Prado C, Globert J (1990) Tree community dynamics in a humid savanna of the Cote-d'Ivoire: modelling the effects of fire and competition with grass and neighbours. J Biogeog 17:471–481

Nadelhoffer, KJ, Fry B (1988) Controls on natural nitrogen–15 and carbon–13 abundances in forest soil organic matter. Soil Sci Soc Am J 52:1633–1640

Neilson RP (1986) High resolution climatic analysis and southwest biogeography. Science 232:27–34

Okali DUU, Hall JB, Lawson GW (1973) Root distribution under a thicket clump on the Accra plains, Ghana: its relevance to clump localization and water relations. J Ecol 61:439–454

Pella E, Colombo B (1973) Study of carbon, hydrogen, and nitrogen determination by combustion-gas chromatography. Mikrochim Acta 1973:697–719

Richards JH (1986) Root form and depth distribution in several biomes. In: Carlisle D, Berry WL, Kaplan IR, Watterson JR (eds) Mineral Exploration: Biological Systems and Organic Matter, Prentice-Hall, Englewood Cliffs, New Jersey, pp 83–97

Richardson ML, Clemmons SD, Walker JC (1979) Soil survey of Santa Cruz and parts of Cochise and Pima counties, Arizona. United States Department of Agriculture Soil Conservation Service and Forest Service, 100 p

Sauer CO (1950) Grassland climax, fire and man. J Range Man 3:16–21

Schlesinger WH, Reynolds, JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG (1990) Biological feedbacks in global desertification. Science 247:1043–1048

Schofield CJ, Bucher EH (1986) Industrial contributions to desertification in South America. Trends Ecol Evol 1:78–80

Schwartz D, Mariotti A, Lanfranchi R, Guillet B (1986) $^{13}C/^{12}C$ ratios of soil organic matter as indicators of vegetation changes in the Congo. Geoderma 39:97–103

Shapiro SS, Wilk MB (1965) An analysis of variance test for normality (complete samples). Biometrika 52:591–611

Sims PL, Singh JS (1978) The structure and function of ten western North American grasslands. J Ecol 66:547–572

Singh JS, Joshi MC (1979) Ecology of the semi-arid regions of India with emphasis on land-use. In: Walker BH (ed) Management of Semi-arid Ecosystems, Elsevier, Amsterdam, pp 243–273

Smeins FE (1983) Origin of the brush problem–a geographical and ecological perspective of contemporary distributions. In: McDaniel KC (ed) Brush Management Symposium, Texas Tech Press, Lubbock, pp 5–16

Soriano A, Sala O (1983) Ecological strategies in a Patagonian steppe. Vegetatio 56:9–15

Steuter AA, Jasch B, Ihnen J, Tieszen LL (1990) Woodland/grassland boundary changes in the middle Niobrara Valley of Nebraska identified by $\delta^{13}C$ values of soil organic matter. Am Midl Nat 124:301–308

Stevenson FJ, Elliott ET (1989) Methodologies for assessing the quantity and quality of soil organic matter. In: Coleman DC, Oades JM, Uehara G (eds) Dynamics of Soil Organic Matter in Tropical Ecosystems, NifTAL Project, Dept Agronomy and Soil Science, University of Hawaii, pp 173–199

Stewart OC (1951) Burning and natural vegetation in the United States. Geog Rev 41:317–320

Stout JD, Goh KM, Rafter TA (1981) Chemistry and turnover of naturally occurring resistant organic compounds in soil. In: Paul EA, Ladd JN (eds) Soil Biochemistry, vol 5, Marcel Dekker, New York, pp 1–73

Tiedemann AR, Klemmedson JO (1973a) Nutrient availability in desert grassland soils under mesquite *(Prosopis juliflora)* trees and adjacent open areas. Soil Sci Soc Am Proc 37:107–110

Tiedemann AR, Klemmedson JO (1973b) Effects of mesquite on physical and chemical properties of the soil. J Range Manage 26:27–29

Tiedemann AR, Klemmedson JO (1986) Long-term effects of mesquite removal on soil characteristics: I. Nutrients and bulk density. Soil Sci Soc Am Proc 50:472–475

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, Ecological Studies Series, Vol 80, Springer–Verlag, Heidelberg, pp 293–321

van Vegten JA (1983) Thornbrush 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

Volkoff B, Cerri CC (1987) Carbon isotope fractionation in subtropical Brazilian grassland soils: comparison with tropical forest soils. Plant Soil 102:27–31

Walter H (1971) Ecology of tropical and subtropical vegetation. Burnett JH (ed), Translated by Mueller-Dombois D. Oliver and Boyd, Edinburgh

Wentworth TR (1983) Distributions of C_4 plants along environmental and compositional gradients in southeastern Arizona. Vegetatio 52:21–34

Wright HA, Bailey AW (1982) Fire Ecology: United States and Southern Canada. John Wiley & Sons, New York, 501 p