

## INTERRELATIONSHIPS AMONG SHRUB ENCROACHMENT, LAND MANAGEMENT, AND LITTER DECOMPOSITION IN A SEMIDESERT GRASSLAND

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**Abstract.** Encroachment of woody plants into grasslands, and subsequent brush management, are among the most prominent changes to occur in arid and semiarid systems over the past century. Despite the resulting widespread changes in landcover, substantial uncertainty about the biogeochemical impacts of woody proliferation and brush management exists. We explored the role of shrub encroachment and brush management on leaf litter decomposition in a semidesert grassland where velvet mesquite (*Prosopis velutina*) abundance has increased over the past 100 years. This change in physiognomy may affect decomposition directly, through altered litter quality or quantity, and indirectly through altered canopy structure. To assess the direct and indirect impacts of shrubs on decomposition, we quantified changes in mass, nitrogen, and carbon in litterbags deployed under mesquite canopies and in intercanopy zones. Litterbags contained foliage from mesquite and Lehmann lovegrass (*Eragrostis lehmanniana*), a widespread, nonnative grass in southern Arizona. To explore short- and long-term influences of brush management on the initial stages of decomposition, litterbags were deployed at sites where mesquite canopies were removed three weeks, 45 years, or 70 years prior to study initiation.

Mesquite litter decomposed more rapidly than lovegrass, but negative indirect influences of mesquite canopies counteracted positive direct effects. Decomposition was positively correlated with soil infiltration into litterbags, which varied with microsite placement, and was lowest under canopies. Low under-canopy decomposition was ostensibly due to decreased soil movement associated with high under-canopy herbaceous biomass. Decomposition rates where canopies were removed three weeks prior to study initiation were comparable to those beneath intact canopies, suggesting that decomposition was driven by mesquite legacy effects on herbaceous cover-soil movement linkages. Decomposition rates where shrubs were removed 45 and 70 years prior to study initiation were comparable to intercanopy rates, suggesting that legacy effects persist less than 45 years.

Accurate decomposition modeling has proved challenging in arid and semiarid systems but is critical to understanding biogeochemical responses to woody encroachment and brush management. Predicting brush-management effects on decomposition will require information on shrub–grass interactions and herbaceous biomass influences on soil movement at decadal timescales. Inclusion of microsite factors controlling soil accumulation on litter would improve the predictive capability of decomposition models.

**Key words:** brush management; decay constant; decomposition; desert grassland; *Eragrostis*; field experiment, southern Arizona, USA; land-cover change; leaf litter; *Prosopis*; shrubland; soil movement; woody-plant encroachment.

### INTRODUCTION

Decomposition of organic material is a crucial component in biogeochemical cycles that, at the local level, exerts strong control over soil fertility, affects the fate and residence time of carbon and nutrients in soil pools, and can ultimately influence plant community composition and production (Hobbie 1992, Aerts 1997, Wardle et al. 1998). Short-term decomposition dynamics

may have a particularly strong influence on biogeochemical fluxes in drylands because of the relatively small size of litter, soil organic matter, and available mineral nutrient pools in these systems (Moorhead and Reynolds 1991). Decomposition dynamics may, in turn, be strongly influenced by land-cover changes involving alterations in plant growth-form composition (Zhang and Zak 1995, Salimon et al. 2004).

One of the most prominent global land-cover changes over the past century has been a proliferation of woody vegetation in grassland and savanna systems (Archer et al. 1995). While considerable research has focused on the causes and patterns of woody encroachment (van Auken 2000), there is little consensus on the biogeochemical

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consequences of this shift in land cover (Wessman et al. 2004). Furthermore, because woody-plant encroachment often has undesirable effects on livestock production and wildlife habitat, management interventions aimed at reversing tree and shrub proliferation are common (Scifres 1980, Valentine 1989, Bovey 2001, Hamilton et al. 2004). The ecological consequences of such activities are largely unknown, and their extensive spatial and temporal variability may account for a sizeable portion of current uncertainty in how woody encroachment affects biogeochemical pools and processes (Asner et al. 2003, Houghton 2003). To address these uncertainties, we assessed the influence of vegetative cover type and “brush management” on short-term C and N dynamics during leaf-litter decomposition in a semidesert grassland where woody-plant encroachment has been ongoing since the early 1900s. While C in leaves accounts for only a small portion of system-wide C, the relatively rapid turnover of the pool makes leaf-litter decomposition a key component of the C cycle (Aerts 1997). Hence, we used this as an indicator of how biogeochemical processes may be influenced by woody encroachment and brush management.

Vegetation exerts strong control over local decomposition rates through direct and indirect pathways, mediated by both biological and physical mechanisms. Direct effects are those associated with changes in litter quality or quantity (Melillo et al. 1982, Hobbie 2000), while indirect effects are associated with differences in plant structure, such as canopy influences on microclimate (Mack and D’Antonio 2003). Prior research suggests that direct effects of vegetation on decomposition may be comparatively less important in drylands than in mesic systems (Cepeda-Pizarro and Whitford 1990). This may be due, in part, to constraints on microbial response to changes in litter quality during frequent periods of high temperature and low moisture in drylands (Moorhead and Reynolds 1991). Although indirect effects may be particularly important in drylands when vegetation change includes shifts in physiognomy (e.g., grassland–shrubland transitions), they remain relatively poorly characterized in comparison to direct influences (Mack and D’Antonio 2003). Studies assessing the influence of canopy structure on decomposition rates have documented positive, negative, and neutral influences (Piene and van Cleve 1978, Edmonds 1979, Binkley 1984, Zhang and Zak 1995, Hope et al. 2003). This variation in response may be due to system-specific differences in the nature of canopy influences on microclimate and subsequent microbial activity. In dryland systems, woody-plant canopies may alter soil water availability by affecting canopy interception, stem flow, and throughfall, and also through their influence on evapotranspiration and hydraulic redistribution. Plant canopies can also decrease the intensity of solar radiation, including UV radiation, and alter soil-surface temperatures relative to intercanopy areas (Archer 1995, Breshears et al. 1997, Hester et al. 1997, Scholes and

Archer 1997, Schlesinger and Pilmanis 1998, Barnes et al. 2005, Zou et al. 2005) to influence decomposition dynamics.

Land-management practices that remove encroaching woody vegetation have the potential to decouple the direct and indirect influences of vegetation on decomposition. Brush-management approaches vary, but fall into three main categories: prescribed burning, chemical (herbicides), and mechanical (roller chopping, grubbing, chaining, etc.) (Valentine 1989, Bovey 2001, Hamilton et al. 2004). All three types of brush management will cause direct changes to the magnitude and pattern of litter inputs into the soil and simultaneously affect decomposition indirectly through altering canopy structure; however, the specific impacts of brush management on litter decomposition dynamics will vary depending on the type of treatment, treatment efficacy and the extent to which soils are disturbed. In addition to these immediate effects of brush management, canopy removal may also have long-term “legacy effects” in which decomposition rates are altered at the site of former shrub canopies. This is because enhanced herbaceous production and soil C and N pools on sites formerly occupied by shrubs may persist for several decades following canopy removal (Tiedemann and Klemmedson 1986, McClaran 2003). Plant removal may also affect decomposer communities (Wardle et al. 1999), although the duration of this impact in drylands is unknown. Skeletons of woody plants killed by herbicides may remain standing for decades in arid environments, potentially causing physical alterations to the decomposition environment. Trees dying of nonanthropogenic mortality may have similar influences on decomposition as trees killed by herbicides.

We developed a conceptual model for woody-encroachment and brush-management influences on rates of decomposition (Fig. 1) and tested this framework in a field experiment at a southern Arizona semidesert grassland. Our experiment explored the influences of *Prosopis velutina* Woot. (velvet mesquite) encroachment and brush management on loss rates of mass, C, and N from leaf litter during the initial stages of decomposition. By experimentally manipulating mesquite canopy cover, we sought to tease apart direct and indirect influences of this woody plant on decomposition. Space-for-time substitution was used to explore how short-term decomposition might respond several decades after brush management. We hypothesized that (1) encroaching mesquite would have direct, positive influences on rates of leaf-litter decomposition because of its higher litter-N content relative to grasses but (2) mesquite canopies would indirectly decelerate decomposition rates due to decreased under-canopy solar radiation and soil moisture. We further predicted that (3) removal of mesquite canopies (a proxy for brush management or natural mortality) would have an immediate, positive influence on decomposition dynamics; but (4) legacy effects on herbaceous, soil, and microbial pools would delay return

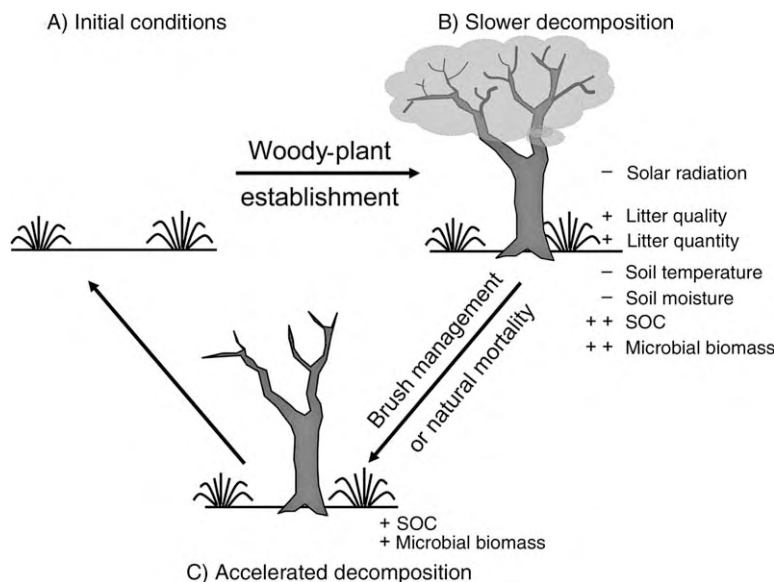


FIG. 1. Hypothesized direct and indirect influences of woody encroachment and subsequent brush management on decomposition rates in dryland systems. We predicted that woody-plant encroachment into former grasslands (A→B) would lead to a net decrease in decomposition rates with positive direct effects of woody plants being more than offset by their negative indirect effects. We further predicted that tree mortality from brush management or natural causes (B→C) would lead to an acceleration of decomposition because the negative indirect effects would no longer be at play, while the legacy of direct, positive influences would persist for some time. Legacy effects would eventually dwindle, and decomposition rates would return to initial conditions (C→A). SOC is soil organic carbon.

to pre-encroachment decomposition rates over decadal time scales. During the course of this study, a serendipitous discovery that soil movement into litterbags affected decomposition rates allowed us to explore the relationships between soil movement, land cover, and decomposition. Although this study assessed only specific mechanical and chemical brush-management treatments at very short (1-year) and long (40- and 70-year) timescales, we aimed to use these treatments to gain a mechanistic basis for constraining predictions of decomposition response to brush-management practices and natural shrub mortality.

#### METHODS

##### *Study site*

Leaf-litter decomposition rates were assessed at the Santa Rita Experimental Range (SRER), a 21 513-ha semidesert grassland research site ~80 km south of Tucson in Pima County, Arizona, USA (more information about SRER is *available online*).<sup>2</sup> Studies were conducted in Pasture 2S (110°53'4.32" W, 31°47'36.07" N) at an elevation of 1100 m. Vegetation and climate of the site have been described in detail by McClaran (2003). Mean annual precipitation (370 mm) is divided roughly equally between winter rains and late summer monsoons. The dominant ground cover is Lehmann lovegrass (*Eragrostis lehmanniana* Nees), a C<sub>4</sub> grass native to southern Africa and intentionally introduced

to the SRER in the 1930s (McClaran and Anable 1992). Lehmann lovegrass has displaced native perennial grasses and is now the dominant grass species in many parts of southern Arizona and western New Mexico (Schussman et al. 2006). Other common perennial species at the SRER include the grasses Arizona cottontop (*Digitaria californica* Benth.) and bush muhly (*Muhlenbergia porteri* Scribn. ex Beal); burroweed (*Haplopappus tenuisectus* Greene), a suffruticose shrub; and cholla cactus (*Opuntia* spp.) Site records have documented increases in woody-plant cover, primarily velvet mesquite (*Prosopis velutina* Woot.; a summer-green, leguminous shrub), since the early 1900s (McClaran et al. 2003). Current land cover at the study site is ~55% herbaceous, ~30% woody plant, and ~15% bare ground (D. Browning, S. Archer, G. Asner, M. McClaran, and C. Wessman, *unpublished manuscript*).

##### *Litter collection and litterbag construction*

Mesquite leaves were collected on 25 November 2003, after leaf drop had commenced. Lack of a synchronous leaf drop in mesquite at this subtropical site necessitated gently removing senescing leaves from trees in order to obtain a uniform decomposition substrate. Lehmann lovegrass material was collected by clipping quiescent plants on 4 December 2003. In order to maintain a consistent leaf:culm ratio, collections were standardized to include 8-cm segments that began 4 cm above the ground. Plant material not clearly produced from the current-year's growth was discarded. After collection, all

<sup>2</sup> (<http://ag.arizona.edu/SRER/>)

plant material was dried at 30°C for 4–7 days. This temperature is well below maximum temperatures experienced by plants in the field and thus should not have affected tissue chemistry. Litterbags (10 × 10 cm) were constructed from 20 × 20 mesh (~0.9 mm openings) fiberglass window screen (Phifer Wire Products, Tuscaloosa, Alabama, USA) and filled with either 4 g mesquite leaflets or 3.5 g of Lehmann lovegrass material. The initial concentration of litter in litterbags (400 g/m<sup>2</sup>) was equivalent to several years of accumulated litter inputs (average subcanopy leaf-litter inputs of 130 g·m<sup>-2</sup>·yr<sup>-1</sup>; H. L. Throop and S. R. Archer, *unpublished data*). For every 10 litterbags filled, a subsample of litter was dried at 60°C and reweighed in order to establish a wet-to-dry mass relationship.

#### *Land-management treatments*

Litterbags were deployed in plots mimicking seven different land covers that occur in the context of woody-plant encroachment and subsequent brush management (hereafter denoted as “placements” for expediency). *Mesquite* placements were centered around mature mesquite trees. Selected trees had a minimum basal diameter of 30 cm (combined diameter if more than one stem) and did not overlap with neighboring tree canopies or shelter sub-canopy woody plants. *Girdle* placements consisted of mesquite trees (same selection criteria as the mesquite placements) on which all main stems were girdled (minimum 1-cm cut depth) with a chainsaw near ground level on 22 January 2004. All but one girdled tree had some branches that leafed out in spring 2004. Hence, stems with live branches were regirdled to ~3-cm cut depth on 27 May 2004 and the cuts painted with diesel fuel. Subsequent resprouts were removed periodically as needed. *New-stump* placements were centered around large mesquite trees felled on 22 January 2004. Leaves, stems, and branches from felled trees were removed from the site to minimize litter inputs. Stumps were painted with diesel fuel on 27 May 2004 to discourage sprouting. Resprouts were removed periodically as needed.

To explore potential legacy effects of brush management, we deployed litter bags in areas that had undergone brush management decades earlier. *Skeleton* placements were centered around standing skeletons of large trees killed by a 1960 aerial application of 2,4,5-trichlorophenoxyacetic acid (Martin and Ward 1966). *Old-stump* placements were centered around stumps remaining from mesquite trees felled by cutting near ground level in a 1935 study (Santa Rita Experimental Range Archives, University of Arizona, Tucson, Arizona, USA).

Decomposition rates on shrub-influenced soils were compared to those on soils not currently or historically impacted by shrubs. *Grass* placements were established in inter-tree areas at least 2 m from mesquite canopy edges. *Bare-ground* placements were located on naturally occurring patches of bare ground in areas at least 2 m from mesquite canopy edges. Seedlings emerging in the

vicinity of litterbags in bare-ground placements were removed manually as needed during the course of the study.

There were five replicate plots for each placement setting, yielding a total of 35 plots. Fences consisting of barbed wire and buried poultry mesh were erected around all placement plots to exclude cattle and minimize rodent disturbance. Soil organic C (SOC) measurements at the site suggest that SOC (mean ± SE) is elevated under mesquite canopies relative to inter-canopy spaces (16.02 ± 0.91, 7.04 ± 0.37, and 5.72 ± 0.74 g C/cm<sup>3</sup> to 5 cm for mesquite canopy, grass canopy, and bare ground, respectively), and is intermediate under brush-management treatments (9.60 ± 1.18 and 5.38 ± 0.11 g C cm<sup>-3</sup> for skeletons and old stumps, respectively) (M. P. McClaran and D. A. Martens, *unpublished data*).

#### *Litterbag deployment*

Litterbags were deployed 9–11 February 2004 and were secured to the soil surface with sod staples. Litterbags were placed no farther than 1 m from the target tree bole (where applicable) and at least 10 cm from adjacent litter bags. One litterbag of each litter type was collected from each placement plot immediately after deployment. One additional litterbag from each litter type × placement plot replicate was collected 1, 3, 6, and 12 months after the initial deployment. In total, 350 litterbags were deployed and collected (2 litter species × 7 placement types × 5 replicates/plot × 5 collection dates).

#### *Sample analyses*

Litterbags were dried at 60°C immediately after field collection, sieved to remove mineral soil, and weighed to determine mass change. Litterbag contents were ground to pass through a number-60 mesh screen on a Wiley Mill (Thomas Scientific, Swedesboro, New Jersey, USA). Subsamples of ground material from each litterbag were ashed at 500°C for four hours; all data were analyzed on an ash-free basis to exclude mass gain from mineral soil that entered the bags. Percentage of ash remaining was used as an index of soil infiltration into litterbags; this was a highly conservative estimate because some soil was removed by sieving. Subsamples from each litterbag were analyzed for C and N content on an elemental analyzer (ECS 4010; Costech Analytical Technologies, Valencia, California, USA).

Litter decomposition was assumed to be the proportional difference in ash-free dry mass between the initial (0 month) and subsequent litterbag collections. The decay constant,  $k$ , was determined for each litter type by placement combination using a single exponential decay model (Olson 1963):

$$M_t = M_0 e^{-kt} \quad (1)$$

where  $M_t$  is the litter mass at time  $t$  and  $M_0$  is the initial litter mass.

### *Light interception and soil-surface temperature*

Photosynthetically active radiation (PAR, 400–700 nm) reaching the soil surface was quantified on a seasonal basis to determine interception of solar radiation by mesquite canopies. A line quantum sensor (LI-191, LI-COR, Lincoln, Nebraska, USA) was used to take PAR measurements at 0.5-m intervals along bole-to-canopy dripline transects oriented in the four cardinal directions in each of four mature mesquite trees (basal diameter  $\geq 25$  cm). Paired measurements in inter-canopy zones served to quantify incoming PAR. Measurements were taken on cloudless days at 08:00, 11:00, and 14:00 hours (MST) in January, April, July, and October. Canopy interception for a given date was calculated as the mean of the ratio of under-canopy to inter-canopy readings.

Soil-surface temperatures were monitored hourly beginning 19 February 2004 using temperature dataloggers (iButton models DS1921L-F50 and DS1921G-F5, Dallas Semiconductor Corporation, Dallas, Texas, USA) sealed within empty litterbags and secured to the soil surface with sod staples. Due to technical difficulties, no data are available for 2 August through 27 October. Each replicate placement plot had at least one temperature logger; mesquite canopy and girdled plots had two loggers. The positions of loggers were random relative to tree boles and were re-randomized each time loggers were downloaded and redeployed (approximately every 85 days).

### *Statistical analyses*

Changes in litterbag mass, C content, and N content throughout the study were analyzed using a four-way, split-plot model ANOVA. Litter type (SP), placement (PL), and time ( $T$ ) were considered main effects. Plot replicate was nested within placement and was considered a random factor. Decay constants were analyzed with a three-way, split-plot model ANOVA in which SP and PL were main effects. Plot replicate was nested within placement and was considered a random factor.

Patterns of soil-surface temperature and soil infiltration into litterbags, two potential decomposition drivers, were analyzed for placement effects. Hourly temperature data were condensed into daily means for each placement. Seasonal differences in daily means were factored out of the data by obtaining the residuals from a one-way ANOVA with date as the main effect. These residuals were then used to assess placement effects using a one-way ANOVA with placement as the main effect. Placement differences for soil infiltration were also analyzed with a one-way ANOVA. The relationship between  $k$  and the two decomposition drivers was assessed with linear regression. These tests were performed separately from the main analyses due to correlation between the variables.

All analyses were performed using JMP 5.0 (SAS Institute 2003). Where needed, data were natural-log or

arcsine transformed prior to analyses to improve normality.

## RESULTS

### *Litter mass loss*

Litterbag mass for all placement and litter types decreased with time, with greatest mass loss rates occurring in the first six months of the experiment (Fig. 2). A single exponential decay model (Eq. 1) fit the data well ( $R^2$  values ranging from 0.86 to 0.96); a double exponential-decay model did not substantively improve the fit. Mesquite litter decomposed more rapidly than lovegrass litter (Table 1;  $F_{1,28} = 176.45$ ,  $P < 0.001$ ). After 12 months, mesquite litterbags had significantly less mass remaining than did lovegrass litterbags regardless of placement (pooled across placements: mesquite =  $52.8\% \pm 0.8\%$  [mean  $\pm$  SE], Lehmann lovegrass =  $67.9 \pm 1.3\%$ ;  $F_{1,28} = 55.21$ ,  $P < 0.001$ ).

Litter in bare, grass, old-stump, and skeleton placements decayed more rapidly than litter in new-stump, recently girdled, or intact-canopy placements (Table 1, Fig. 2). Separation into these two groups occurred gradually while mass loss changed with time ( $F_{24,28} = 4.26$ ,  $P < 0.001$ , for  $T \times PL$ ). Decomposition of Lehmann lovegrass litter followed similar patterns, although placements did not fall out as tightly into two distinct groups.

### *Litter carbon dynamics*

Initial mean C concentrations ([C]) in mesquite litter ( $53.2\% \pm 0.1\%$ ) were significantly higher than those in Lehmann lovegrass litter ( $48.4\% \pm 0.1\%$  C;  $P < 0.001$ ,  $F_{1,68} = 755.5$ ). For both species, C losses closely tracked mass loss patterns, leading to a strong linear relationship between mass remaining and C remaining, with no significant placement effects (overall relationship for all treatments:  $y = 13.70 + 0.87x$ ,  $R^2 = 0.98$  for mesquite and  $y = 12.29 + 0.88x$ ,  $R^2 = 0.98$  for Lehmann, where  $y = C$  remaining [as a percentage] and  $x =$  mass remaining [as a percentage]). The initial 1:1 relationship between percentage mass remaining and C remaining steadily diverged as the mass remaining decreased. The slight decrease in C loss relative to total mass loss led to increases in litter [C] over time for both species (data not shown).

### *Litter nitrogen dynamics*

The initial nitrogen concentration ([N]) was significantly greater for mesquite than lovegrass ( $3.4\% \pm 0.02\%$  vs.  $1.1\% \pm 0.03\%$  N [mean  $\pm$  SE;  $P < 0.001$ ,  $F_{1,68} = 1474$ ). There was a net loss of the total N mass through time for all litter and placement combinations. Mesquite litter lost proportionally less N than total mass, yielding a slope of 0.68 for this relationship ( $R^2 = 0.82$ ), which did not differ among placements (Fig. 3A). In contrast, the relationship between total mass loss and N loss for lovegrass litter was much weaker ( $R^2 = 0.14$ ; Fig. 3B). Despite the net loss of total N from litterbags,

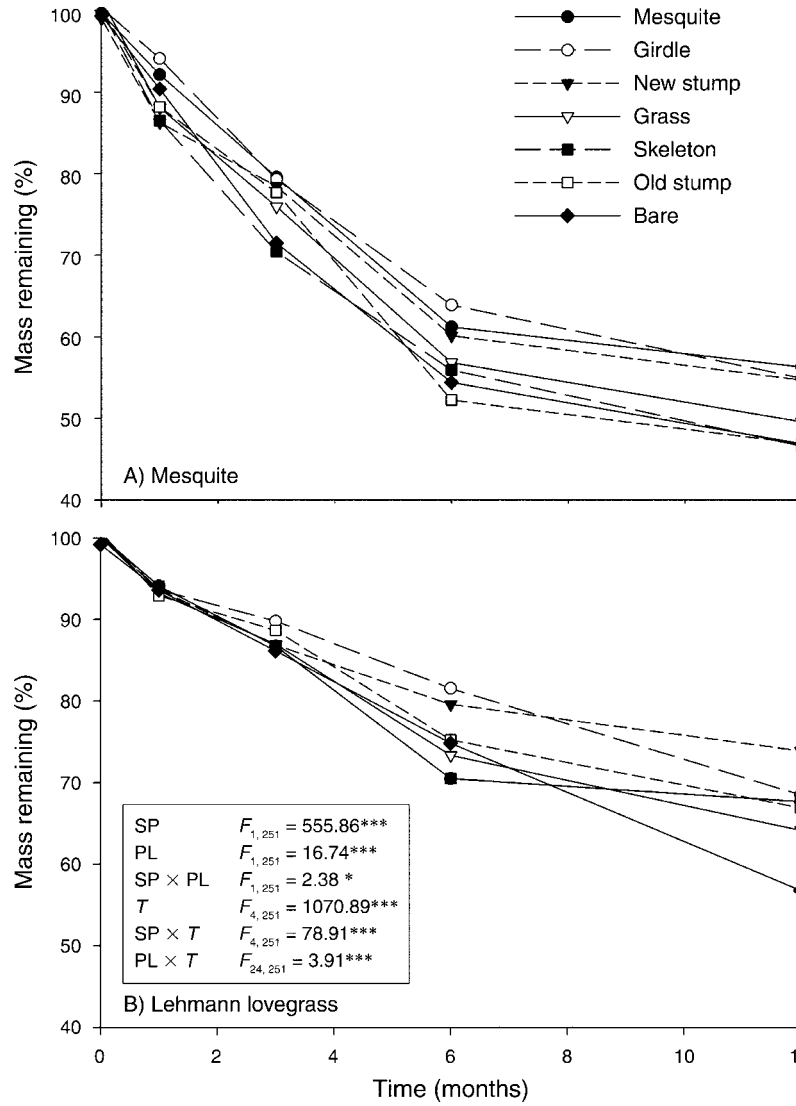


FIG. 2. Mean mass remaining through time for (A) mesquite and (B) Lehmann lovegrass litter in different placements. Standard errors (bars omitted for clarity) averaged across all times and placements were 1.4 for mesquite and 0.9 for Lehmann lovegrass. ANOVA tables show  $F$  and  $df$  values from significant terms in a four-way ANOVA where SP is litter type, PL is placement, and  $T$  is time. \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

TABLE 1. Decay constants ( $k$ ; Eq. 1) and  $R^2$  values for mesquite and Lehmann lovegrass leaf litter under seven different land-cover placements.

Land-cover placement	Mesquite			Lehmann lovegrass		
	$k$ ( $yr^{-1}$ )			$k$ ( $yr^{-1}$ )		
	Mean	SE	$R^2$	Mean	SE	$R^2$
Mesquite	0.553 <sup>c</sup>	0.0247	0.87	0.350 <sup>de</sup>	0.0269	0.92
Girdle	0.573 <sup>bc</sup>	0.0169	0.91	0.350 <sup>de</sup>	0.0207	0.96
New stump	0.549 <sup>c</sup>	0.0300	0.88	0.279 <sup>c</sup>	0.0118	0.88
Grass	0.664 <sup>ab</sup>	0.0252	0.86	0.427 <sup>d</sup>	0.0437	0.88
Skeleton	0.696 <sup>a</sup>	0.0332	0.87	0.389 <sup>d</sup>	0.0406	0.81
Old stump	0.729 <sup>a</sup>	0.0403	0.87	0.389 <sup>d</sup>	0.0326	0.93
Bare	0.713 <sup>a</sup>	0.0350	0.89	0.546 <sup>c</sup>	0.1041	0.96

Note: Means with the same lowercase superscript letter do not differ significantly from each other ( $P > 0.05$ );  $n = 5$  decay constants.

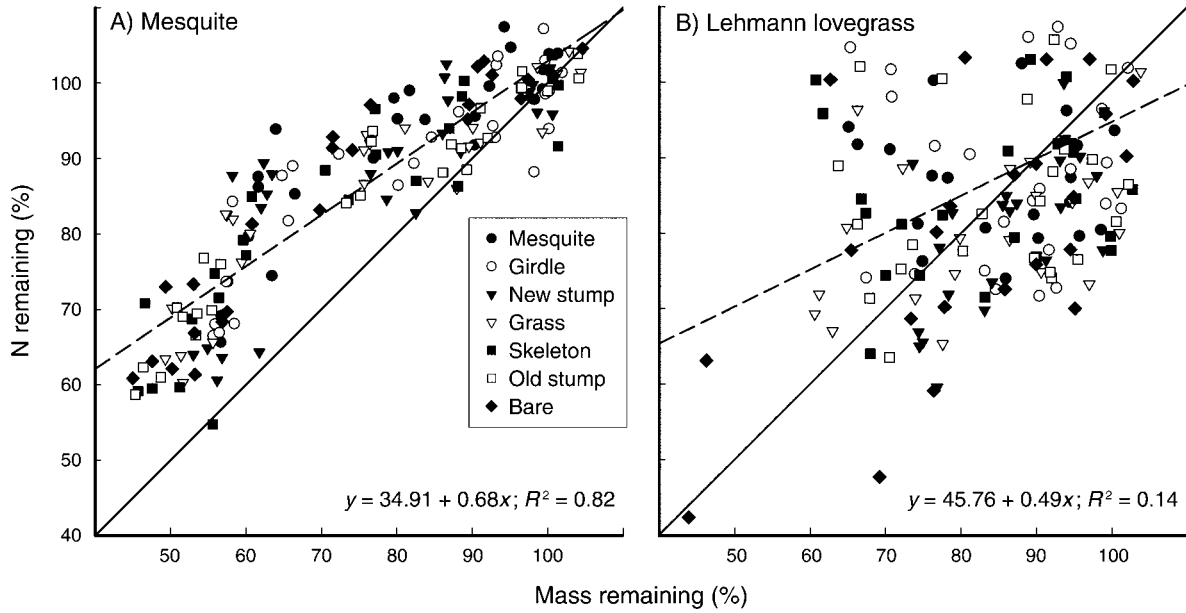


FIG. 3. Relationship between mass remaining and N remaining for (A) mesquite and (B) lovegrass litter. The solid line depicts the 1:1 relationship; the dashed line depicts linear regression.  $P < 0.001$  for regressions of both species.

there was an increase in [N] through time for both litter types (Fig. 4), with the exception of the new-stump placement for lovegrass. Patterns of [N] through time differed between species, with mesquite litter [N] generally peaking at six months and then declining for most placements; trends in lovegrass [N] were more variable, but generally increased with successive collection dates. Across placements, [N] increased significantly for both species from the initial and final litter

collections ( $3.4\% \pm 0.02\%$  to  $4.2\% \pm 0.06\%$  [mean  $\pm$  SE] for mesquite and  $1.1\% \pm 0.03\%$  to  $1.3\% \pm 0.04\%$  for Lehmann lovegrass).

Initial C:N ratios were significantly lower for mesquite than lovegrass litter ( $15.7 \pm 0.1$  vs.  $45.0 \pm 1.3$  [mean  $\pm$  SE];  $P < 0.001$ ,  $F_{1,68} = 534.2$ ). Mesquite litter C:N declined significantly between 0- and 6-month collections ( $16.7 \pm 0.1$  to  $13.0 \pm 0.2$ ), did not change significantly between 6- and 12-month collections, and

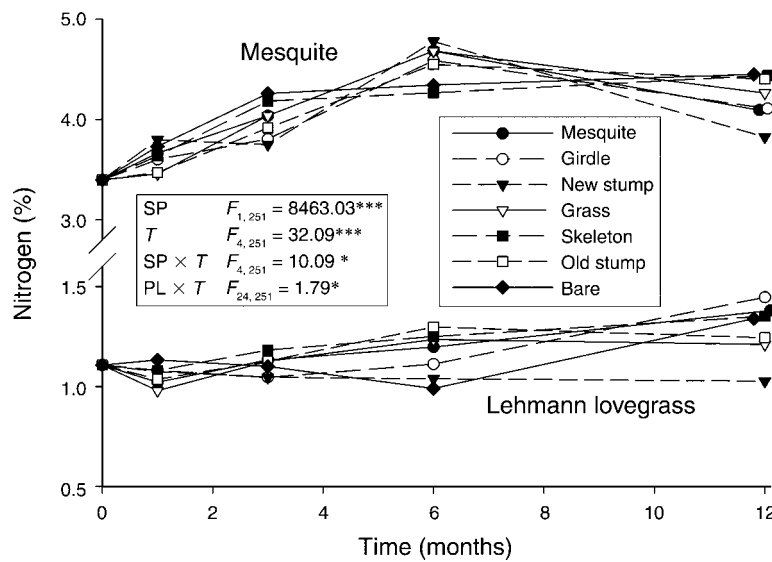


FIG. 4. Mean N concentration through time for mesquite and Lehmann lovegrass litter in different placements. Standard error bars are omitted for clarity; average SE for %N across all times and placements was 0.04 for mesquite and 0.02 for Lehmann lovegrass. The ANOVA table shows  $F$  and  $df$  values from significant terms in a four-way ANOVA where SP is litter type, PL is placement, and  $T$  is time.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

TABLE 2. Photosynthetically active radiation (PAR, 400–700 nm) intercepted by mature mesquite canopies on four dates over an annual cycle.

Date	Under-canopy PAR ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	Light interception (%)	<i>n</i>
July 2004	846 $\pm$ 26	47.9 $\pm$ 1.4	304
October 2004	584 $\pm$ 23	51.2 $\pm$ 1.7	292
January 2005	457 $\pm$ 20	45.8 $\pm$ 1.6	275
April 2005	824 $\pm$ 22	42.5 $\pm$ 1.3	289

Notes: Values are means ( $\pm$ SE) of morning, noon, and afternoon measurements on cloudless days from under four different trees; *n* is the number of paired (under-canopy and inter-canopy) measurements. Light interception decreased only slightly during winter and spring (January and April) at this subtropical site due to lack of synchronous leaf drop.

exhibited no significant placement effects (data not shown). Lovegrass litter C:N ratios were much more erratic with respect to placement and time, showing no significant directional trends or consistent patterns among placements (data not shown).

#### Light interception and soil-surface temperature

Mesquite canopies intercepted 42.5–51.2% of incoming photosynthetically active radiation over an annual cycle (Table 2). Accordingly, mean daily soil-surface temperatures differed significantly among placements ( $P < 0.0001$ ,  $F_{6,1890} = 183.5$ ) (Table 3). Mean temperatures were highest in bare and grass placements, intermediate in historical brush-management and new-stump placements, and lowest in girdle and mesquite placements. The range of mean monthly temperatures observed across placements increased from  $\sim 1^\circ\text{C}$  in January to  $\sim 4^\circ\text{C}$  in July. Plot-level annual means of daily temperature residuals had minimal predictive power for *k* ( $y = 0.005x + 0.364$ ,  $R^2 = 0.004$ ,  $P = 0.12$  for Lehmann lovegrass;  $y = 0.041x + 0.639$ ,  $R^2 = 0.18$ ,  $P < 0.05$  for mesquite).

#### Soil infiltration

Litterbag ash content, a conservative indicator of soil accumulation as used in this study, differed significantly among placements at the 12-month collection ( $F_{6,63} =$

12.02,  $P < 0.0001$ ). Ash content was greatest in the bare and historical brush-management placements, intermediate in the grass placement, and lowest in the mesquite and contemporary brush-management placements (Table 4). The decay constant varied 2.6-fold across species and placements (Table 1), but not in relation to the radiant-energy environment. Instead, there was a strong negative relationship across collection dates between ash content and mass remaining (Fig. 5). There was a positive relationship between the natural logs of ash content ( $x$ , %) and *k* at the 12-month collection ( $y = 0.005x + 0.300$ ,  $R^2 = 0.40$ ,  $P < 0.001$  for Lehmann lovegrass;  $y = 0.004x + 0.513$ ,  $R^2 = 0.62$ ,  $P < 0.001$  for mesquite).

#### DISCUSSION

The decay constants observed in this study ( $k = 0.28$  to  $0.72 \text{ yr}^{-1}$ ) and percentage mass loss after one year are similar to those reported from decomposition studies in deserts around the world (Whitford 2002). Despite these similarities, drylands and disturbed areas have proven challenging to predictive modeling of decomposition dynamics (Whitford et al. 1981, Moorhead et al. 1999). At regional scales, empirical models based on actual evapotranspiration (AET) strongly predict decomposition rates (Meentemeyer 1978, Couteaux et al. 1995, Aerts 1997). At local scales in arid systems, however, decomposition rates are typically underestimated with the AET model (Whitford et al. 1981). Local-scale mechanistic models usually predict decomposition rates based on substrate quality, particularly lignin concentrations and C:N ratios; but these models typically overestimate decomposition losses in desert and tundra systems (Moorhead et al. 1999). Our leaf-litterbag experiments generated some novel insights into how decomposition processes might be altered when positive or negative and direct or indirect effects of vegetation are simultaneously considered in a land management or plant community-dynamics context—insights that could improve the predictive ability of decomposition rates. In particular, the serendipitous finding that soil infiltration had a strong positive impact on litter decomposition rates suggests that incorporating parameters describing

TABLE 3. Daily temperature residual values and monthly temperatures in surface litterbags in contrasting placements for a representative winter (January) and summer month (July).

Placement of litter bags	Monthly temperature ( $^\circ\text{C}$ )					
	Daily residual temperature ( $^\circ\text{C}$ ) <sup>†</sup>		January		July	
	Mean	SE	Mean	SE	Mean	SE
Mesquite	-1.1 <sup>c</sup>	0.08	10.8	0.5	29.7	0.5
Girdle	-1.1 <sup>c</sup>	0.09	10.7	0.5	29.8	0.4
New stump	0.0 <sup>d</sup>	0.04	9.9	0.5	33.1	0.6
Grass	0.6 <sup>b</sup>	0.05	10.0	0.4	33.3	0.6
Skeleton	0.2 <sup>d</sup>	0.03	10.1	0.5	32.6	0.6
Old stump	0.4 <sup>c</sup>	0.05	10.3	0.5	33.7	0.6
Bare	1.0 <sup>a</sup>	0.05	10.8	0.4	33.7	0.6

<sup>†</sup> Residual values were obtained from a one-way ANOVA of mean daily temperature with date as the main effect. Values with the same lowercase superscript letter do not differ significantly from each other ( $P > 0.05$ ).



soil movement into dryland decomposition models may improve their predictive capability.

#### *Direct influences of woody encroachment*

The hypothesis presented in our initial conceptual model (Fig. 1) that mesquite plants establishing in grasslands have a direct, positive effect on decomposition rates relative to grasses via enhanced litter quality was supported. Although litter quality, particularly C:N, is typically a key regulator of decomposer activity and hence a good indicator of decomposability in mesic systems (Hobbie 1992, Aerts 1997), it has been suggested that litter quality is relatively unimportant in dryland systems where biological processes may play a limited role in decomposition (Steinberger and Whitford 1988, Whitford 2002). More rapid decomposition of low C:N mesquite litter (initial C:N =  $15.7 \pm 0.1$  [mean  $\pm$  SE]) compared to high C:N lovegrass litter (initial C:N =  $45.0 \pm 1.3$  [mean  $\pm$  SE]), however, suggests that litter quality is an important driver in this system, at least in the early stages of decomposition. Although our only litter-quality metrics were C and N content and C:N ratios, lower decomposition rates of grass leaves may also reflect their higher concentrations of silica and cellulose (Vicari and Bazely 1993, Mtambanengwe and Kirchmann 1995). Moreover, the more rapid decomposition of mesquite leaves suggests that tannins and other secondary compounds that are typically higher in leaves of unpalatable shrubs than in grasses (Horner et al. 1988, Sharma et al. 1995, Kraus et al. 2003) may be of little consequence. Both mesquite and lovegrass litters used for this study may have had slightly higher [N] than would occur for litter naturally entering the litter pool as material could have been removed before resorption was complete or before additional decomposition as standing dead occurred. For mesquite, higher C:N would also be expected for entire *leaves* relative to the *leaflets* used for this study (mean C:N = 19.3 for naturally abscising leaf litter, November–February; H. L. Throop and S. R. Archer, *unpublished data*). Increased [N] of experimental litter could have elevated decomposition rates relative to naturally senescing litter.

Without specifically quantifying decomposer activities, we cannot be sure of the extent to which relationships between litter quality and decomposition were driven by biological vs. physical processes. Changes in [C] and [N] in the litterbags over time suggest observed mass losses were not due solely to physical fragmentation of the litter. A 1:1 relationship between C or N remaining and mass remaining would occur for physical fragmentation alone, but both species diverged from this relationship over time (Fig. 3 for N). There was no evidence, however, for an initial N-immobilization phase, a typical indicator of microbial activity in litterbag studies (Hobbie 2000, Aerts et al. 2006), as N mass remaining for both litter types and all placements decreased with time. Although total N decreased, [N] increased significantly with time for both

TABLE 4. Percentage of ash in 12-month litterbags from the different land-cover placements.

Land-cover placement	% Ash <sup>†</sup>			
	Lehmann lovegrass		Mesquite	
	Mean	SE	Mean	SE
Mesquite	5.5 <sup>a</sup>	0.4	15.5 <sup>a</sup>	2.7
Girdle	5.0 <sup>a</sup>	0.4	11.1 <sup>a</sup>	0.3
New stump	4.3 <sup>a</sup>	0.4	11.2 <sup>a</sup>	0.8
Grass	13.9 <sup>b</sup>	2.1	28.0 <sup>b</sup>	4.1
Skeleton	23.4 <sup>c</sup>	4.4	45.0 <sup>c</sup>	5.2
Old stump	24.6 <sup>c</sup>	4.6	45.2 <sup>c</sup>	3.9
Bare	17.4 <sup>c</sup>	2.3	40.2 <sup>c</sup>	6.6

<sup>†</sup> Within each species, values with the same lowercase superscript letters do not differ significantly from each other. Averages for soil-free leaves are  $8.73\% \pm 0.05\%$  ash and  $4.15\% \pm 0.08\%$  ash (mean  $\pm$  SE) for mesquite and lovegrass, respectively.

species. It is unclear, however, whether this increase was due to an influx of N from decomposers, or to preferential biological metabolism or physical breakdown of non-N compounds.

#### *Indirect influences of woody encroachment*

Direct, positive effects of mesquite litter on decomposition rates were offset by indirect influences of mesquite canopies, although not all patterns fit the predictions of our initial conceptual model (Fig. 1). For both litter types, decay constants were lower in mesquite-canopy placements than in grass or bare placements, supporting our hypothesis that decomposition rates are decelerated by mesquite via indirect influences of canopies. Physical effects of canopies were consistent with the observed decomposition dynamics. Mesquite canopies at our site obstruct solar radiation to the soil surface (Table 2), thereby potentially decreasing decomposition from photodegradation (Cybulski et al. 2000, Pancotto et al. 2005, Austin and Vivanco 2006). Physical fragmentation of litter from rainfall should also be reduced under canopies due to lower under-canopy precipitation and raindrop velocity (Breshears et al. 1997, Whitford 2002). Although canopy-induced changes in surface temperatures have been attributed to changes in decomposition rates in other studies (Piene and van Cleve 1978), the weak relationship between decay constants and soil-surface temperatures observed in our study suggests that canopy attenuation of temperature did not strongly influence decomposition. Soil-surface temperatures in our experiment (Table 3), even beneath mesquite canopies, often exceeded the  $\sim 25$ – $35^\circ\text{C}$  temperatures optimal for microbial activity (Kirschbaum 1995, Moorhead et al. 1996), potentially limiting the timeframe in which canopy temperature attenuation would affect decomposition processes. The observed decomposition patterns, however, were inconsistent with what would be expected if canopies were inducing changes in biological activity of decomposers (Fig. 1). If decomposition was limited by microbial

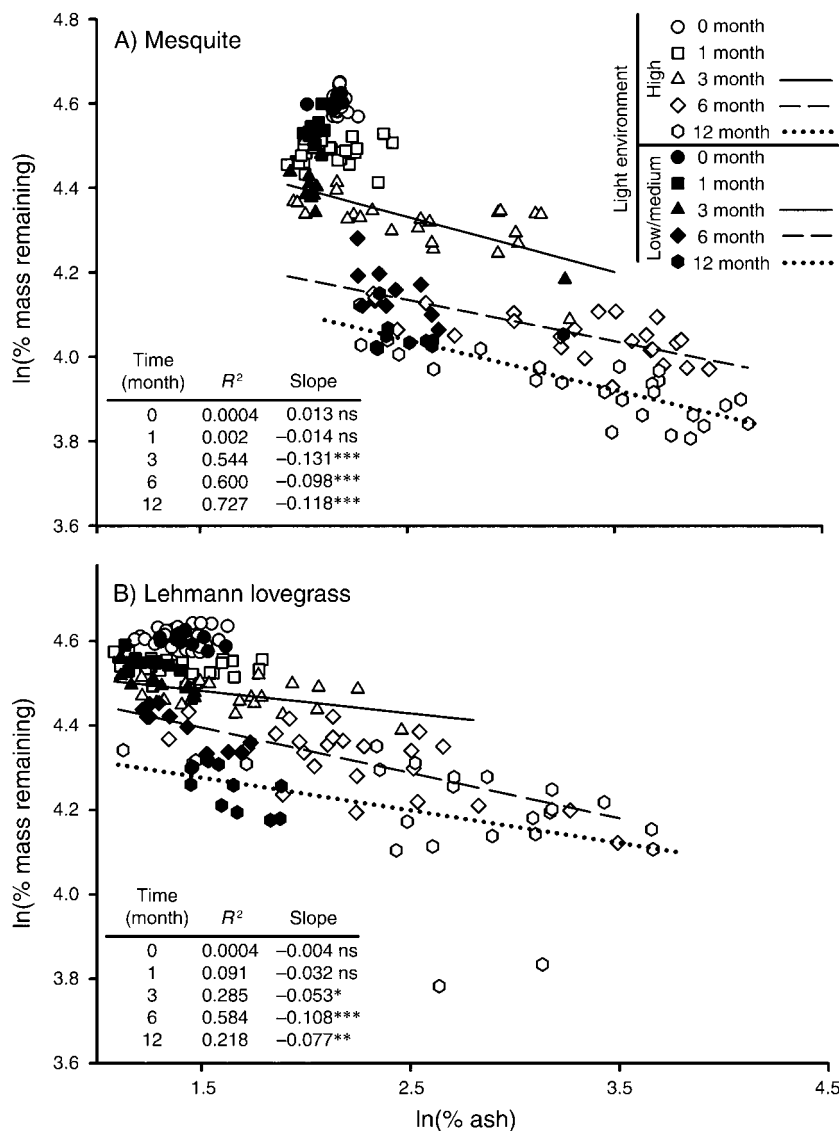


FIG. 5. Relationship between percentage ash in litterbags (an index of soil infiltration) and the percentage of ash-free dry mass remaining at each of the five collection dates. Note that data on both axes are natural-log transformed. The light environment in which bags were placed is indicated as high (bare, grass, old-stump, and new-stump placements) or low/medium (mesquite and girdled placements). Linear regressions were calculated for each collection date (including data for both light environments); regression parameters are presented in the inset tables; ns = not significant; \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ . Within individual collection dates, there was no relationship between ash content and mass remaining for the 0- and 1-month collections, but significant negative relationships were observed for 3-, 6-, and 12-month collections. Mass remaining did not correspond to light environment. Lines for significant regressions are displayed.

populations, decomposition rates should have been greater under canopies and in contemporary management placements where organic matter and microbial activity are likely to be concentrated (Charley and West 1977, Smith et al. 1994, Schlesinger et al. 1996).

The historical and contemporary management placements allowed us to explore the mechanisms by which woody canopies influence litter decomposition, as well as assess some of the biogeochemical implications of brush management or nonanthropogenic shrub mortality. The similarity in decay constants among the

mesquite placements and the contemporary shrub-removal placements (girdle and new stump) was surprising, and did not support the hypothesis in our initial conceptual model that mesquite-canopy removal would have immediate, positive influences on decomposition rates (Fig. 1). Results from the contemporary shrub-removal placements suggest that physical effects of canopies cannot explain slower decomposition in mesquite placements compared to that in bare and grass placements. While a partial woody skeleton remained for girdled trees, no physical canopy effects could have

occurred for the new-stump placements where shrubs were felled and removed. At the initiation of the study, the mesquite and contemporary shrub-removal placements are presumed to have had similar soil, litter, and microbial pools. These pools would likely be greater than those in bare placements (Smith et al. 1994, McCulley et al. 2004). If the observed decomposition patterns were driven by soil fertility or microbial biomass we would have expected *higher* rates of decomposition at sites with intact or recently removed canopies. Instead, decomposition rates were *lower* under intact and recently removed canopies.

How might the lack of physical effects of shrub canopies on litter decomposition be explained? The strong relationship between decay rates and percentage ash of retrieved litter suggests that soil infiltration into litterbags was a major driver of decomposition (Table 4). Studies in the Chihuahuan Desert suggest that relatively rapid decomposition of buried litter is primarily driven by biological processes, in contrast to the slower, physically driven decomposition of surface litter (Santos et al. 1981, Elkins and Whitford 1982). Possible mechanisms for soil-infiltration enhancement of decomposition include biological (e.g., increased microbial colonization) and physical (e.g., soil causing fragmentation or abrasion) processes.

We propose that among-placement differences in soil influx into litterbags are driven by grass cover. Grass cover in dryland systems can strongly decrease aeolian and fluvial soil movement (Weltz et al. 1998, Okin and Gillette 2001). Soil influx was greatest on the bare and the historical brush-removal placements, which had little ground cover, and was minimal in mesquite and contemporary brush-removal placements, which had high grass cover. Average grass cover at our desert grassland site is greater under shrub canopies than in intercanopy areas (Tiedemann and Klemmedson 1977), a pattern that persists for up to several decades after mesquite removal (Cable 1971, McClaran 2003, Tiedemann and Klemmedson 2004). We suggest this as the mechanism for minimal influx of soil into litterbags in the contemporary brush-management placements. An accounting of this influx of soil and the extent to which it blocks solar radiation to decomposing material may also govern the extent of photodegradation (e.g., Austin and Vivanco 2006) in decomposition. A more detailed, explicit quantification of soil movement and infiltration patterns would be an instructive next step. In addition to affecting soil transport, the elevated grass cover associated with woody canopies may have further retarded decomposition through altering microclimate and intercepting solar radiation.

If we had not manipulated canopy cover, then physical effects of canopies would be a logical explanation for slow decomposition under mesquite trees. Slow decomposition under contemporary shrub-removal placements, however, suggest that that canopy physical effects are not the relevant mechanism. Given recently

reported positive relationships between UV and decomposition rates in a semiarid system (Austin and Vivanco 2006), photodegradation would seem a plausible mechanism. However, we observed 2.6-fold differences in decay rates across placements in open, high-radiant-energy environments (Table 1, Fig. 5) where UV levels would likely have been uniformly relatively high. We propose that photodegradation effects may be nullified once soil accumulation on litter progresses to a certain point. Differences in the experimental design of our study and that of Austin and Vivanco (2006) make it difficult to assess the relative importance of photodegradation and soil accumulation. Potential UV impact was likely reduced in our study due to obstruction of solar radiation by the litterbag mesh and as we used considerably more leaf mass per unit area than Austin and Vivanco (2006). Litterbags and leaf mass per area used in our study could potentially either enhance or depress soil-litter mixing relative to typical conditions. On the other hand, use of boxes rather than litterbags by Austin and Vivanco (2006) would have minimized soil-litter mixing, and overestimated the importance of UV degradation in driving decomposition if soil cover of litter minimizes UV effects. Future studies in arid systems teasing these two mechanisms apart would be enlightening.

*Woody encroachment, brush management,  
and decomposition*

Our results suggest a revised conceptual model for litter decomposition in dryland systems subject to woody encroachment and brush management in which the dominant processes controlling the initial stages of decomposition shift with time, land cover, and management history (Fig. 6). In the revised model, initial stages of litter decomposition are relatively rapid in dryland grasslands because fallen litter, initially subject to strong physical forces, is readily buried by aeolian and alluvial processes. As woody plants establish, the net effect of positive direct influences and negative indirect influences of woody plants on litter decomposition are contingent upon microsite and soil transport dynamics. Initially, young shrubs with relatively open canopies will cause increased decomposition rates primarily due to an influx of highly decomposable litter. Low grass cover under small trees will permit soil and litter mixing, enhancing decomposition rates. As shrub canopies develop and if under-canopy grass cover or biomass increases, litter will accumulate in sub-canopy locales due to both leaf fall and enhanced capture of litter laterally transported by aeolian and alluvial processes (Schlesinger and Pilmanis 1998, Okin and Gillette 2001). Initial decomposition rates of this litter will be slow because of elevated inputs of low-quality grass litter and because increased grass cover will limit soil movement, causing litter to remain on the surface where it is subject to weak biological and physical decomposition drivers.

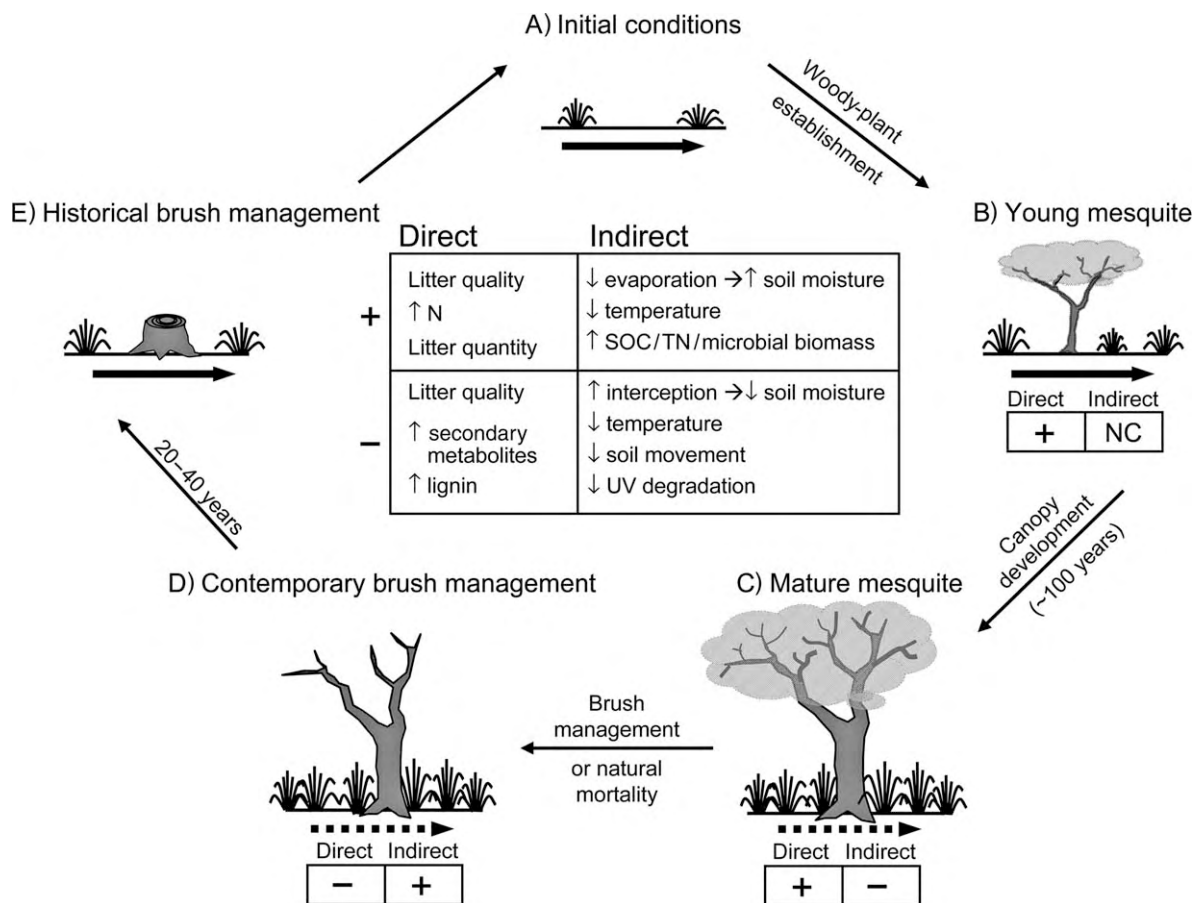


FIG. 6. Revised conceptual model for litter decomposition based on the results of this study. The center matrix provides an overview of possible direct and indirect effects of mesquite encroachment on decomposition; perimeter matrices show net outcome (+, -, or NC [no change]) of direct and indirect effects of mesquite in different settings. Arrows beneath diagrams depict relatively high (solid) or low (dashed) soil movement. Woody-plant establishment (B) in the grassy matrix (A) leads to an initial acceleration of decomposition due to direct influences of enhanced litter quality and quantity with no change in indirect influences. As mesquite plants mature (C), direct positive influences and indirect negative influences both increase, with a net effect of decreasing decomposition. This deceleration is driven primarily by decreased soil movement and mixing with the litter, apparently the result of enhanced sub-canopy grass biomass. After brush management or natural mortality, decomposition initially remains slow while high grass cover persists (D). Field data for this site suggest that by 20–40 years after woody-plant mortality (E), grass cover will decline, at which time soil-movement rates will increase and decomposition will return to pre-encroachment rates (A). In systems where grass production is adversely affected by woody-plant establishment, soil stability and hence decomposition rates would be expected to differ from what is shown here. Abbreviations: SOC, soil organic carbon; TN, total nitrogen; UV, ultraviolet.

In the revised model, it is important to account for whether woody plants have a positive, neutral, or negative effect on herbaceous production (Scholes and Archer 1997, Hughes et al. 2006). Our desert grassland system exhibits a positive relationship between woody and herbaceous cover (Tiedemann and Klemmedson 2004), so the conceptual model in Fig. 6 would need to be adapted in systems where tree–grass interactions are otherwise. Furthermore, livestock herbivory is commonly associated with woody-plant encroachment; the intensity and seasonality of grazing would also be expected to influence shrub–grass interactions, grass cover, biomass and composition, soil stability, and, hence, decomposition.

Shrub removal changes both the physical and biological drivers of decomposition in our model, but at different temporal scales. Following brush management or natural mortality, litter decomposition remains slow for a number of years due to the persistence of high grass biomass. At our study site, altered grass biomass may persist for up to 20 years following shrub removal (Tiedemann and Klemmedson 2004), suggesting a long-term legacy of low decomposition rates. As grass biomass declines in the decades following shrub removal, soil mixing is predicted to gradually increase, causing litter decay rates to accelerate. While the contemporary shrub-removal litterbag placements indicate that biogeochemical influences of woody plants

persist after their removal, the historical management placements suggest this legacy effect had disappeared by 45 years after shrub removal. Future studies with a time scale intermediate to our contemporary and 45-year management placements are needed to clarify the temporal scale of canopy legacy effects on initial stages of decomposition.

The proliferation of woody plants on rangelands prompted the development and widespread implementation of a variety of brush-management techniques beginning in the mid-1900s (Scifres 1980, Valentine 1989, Peterson 1995, Bovey 2001, Hamilton et al. 2004), and these have left a legacy of aboveground and belowground biogeochemical impacts (e.g., Teague et al. 1999, Asner et al. 2003). Specific brush-management techniques will differ in their impact on litter decomposition, depending on the type of disturbance, treatment efficacy, and the extent to which they co-occur with other land-use practices such as livestock grazing. Brush-management treatments that minimally disturb below-canopy soil (e.g., herbicide applications and prescribed burning) should allow low decomposition rates on shrub-influenced patches to persist after brush management; these treatments may be most advisable for managers wishing to minimize short-term C losses after brush management. In contrast, brush-management techniques that cause extensive disturbance to the soil surface, such as chaining, root plowing and grubbing, may increase decomposition rates due to surface-soil disturbances. These practices likely superimpose a variety of new short- and long-term direct and indirect effects on decomposition processes via their dramatic alteration of surface roughness, water infiltration and runoff, vegetation cover, and aboveground net primary productivity; and by initiating large, synchronous inputs of leaf, stem, and coarse woody debris onto the soil surface with widely varying degrees of contact and incorporation into the soil. Such treatments ostensibly increase exposure to direct sunlight and UV radiation and may promote soil movement via wind and water, particularly during the immediate post-treatment period when vegetation is reestablishing.

To date, there has not been sufficient research to permit robust generalizations on brush-management effects on decomposition. The efficacy of brush-management treatments varies widely, depending upon the species involved, their seed bank, the extent to which vegetative regeneration is possible, post-treatment climatic conditions and the nature of subsequent management (e.g., seeding of grasses, livestock grazing, or the type of follow-up brush management). Vegetation responses to brush management have been widely described in the range-management literature, with a historic emphasis on enhancing livestock-forage production, stream flow, and groundwater recharge. More recently, brush management has emerged as a tool for manipulating wildlife habitat (e.g., Scifres et al. 1988, Ben-Shaher 1992) and managing invasive species (e.g.,

Paynter and Flanagan 2004). By comparison, very little is known of brush-management effects on nutrient cycling. There have been few attempts to model brush-management effects on ecosystems (but see Carlson and Thurow 1996, Grant et al. 1999); and the future development of such models would likely benefit from field studies elucidating how various brush-management practices might impact the C and N cycling via decomposition to complement the traditional emphasis on water-cycle impacts (e.g., Newman et al. 2006). Lessons learned from studies of temperate forest clear-cutting and tropical deforestation would be instructive starting points; but it is likely that the geographically extensive shrublands, savannas, and woodlands of drylands would have novel behaviors. For example, predicting brush-management effects on litter decomposition in desert grasslands will require information on shrub-grass interactions and herbaceous biomass influences on soil movement at a decadal timescale.

#### *Implications for predicting decomposition rates*

Results from our study suggest that models emphasizing AET, litter quality, and photodegradation miss other salient parameters in arid systems. In arid systems, models must take microsite variability into account because of extreme heterogeneity in abiotic conditions among canopy and intercanopy settings. For mechanistic models, biologically driven decomposition dynamics must be based on a broader suite of variables than litter quality. Moorehead and Reynolds (1991) improved the predictive power of a mechanistic model by incorporating a time lag for microbial colonization. Results from our study suggest that this time lag may be represented as a function of rates of soil movement that facilitate decomposer colonization and biological activity. Refinement of our understanding of the rates and dynamics of soil movement and soil-litter mixing in dryland systems will ultimately aid in predicting rates of litter burial and subsequent decomposition. These relationships may be a critical component to increasing our understanding of the biogeochemical consequences of woody encroachment and brush management.

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#### LITERATURE CITED

- Aerts, R. 1997. Climate, leaf litter chemistry, and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* 79:439–449.
- Aerts, R., R. van Logtestijn, and P. Karlsson. 2006. Nitrogen supply differentially affects litter decomposition rates and

- nitrogen dynamics of sub-arctic bog species. *Oecologia* 146: 652–658.
- Archer, S. 1995. Tree–grass dynamics in a *Prosopis*–thornscrub savanna parkland: Reconstructing the past and predicting the future. *Ecoscience* 2:83–99.
- Archer, S., D. S. Schimel, and E. A. Holland. 1995. Mechanisms of shrubland expansion: land use, climate, or CO<sub>2</sub>? *Climatic Change* 29:91–99.
- Asner, G., S. Archer, R. Hughes, R. Ansley, and C. Wessman. 2003. Net changes in regional woody vegetation cover and carbon storage in Texas drylands, 1937–1999. *Global Biogeochemical Cycles* 9:1–20.
- Austin, A. T., and L. Vivanco. 2006. Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature* 442:555–558.
- Barnes, P. W., J. R. Shinkle, S. D. Flint, and R. J. Ryel. 2005. UV-B radiation, photomorphogenesis and plant-plant interactions. Pages 313–340 in K. Esser, U. Lüttge, W. Beyschlag, and J. Murata, editors. *Progress in Botany*. Volume 66. Springer-Verlag, Berlin, Germany.
- Ben-Shaher, R. 1992. The effects of bush clearance on African ungulates in a semi-arid nature reserve. *Ecological Applications* 2:95–101.
- Binkley, D. 1984. Does forest removal increase rates of decomposition and nitrogen release? *Forest Ecology and Management* 8:229–233.
- Bovey, R. W. 2001. *Woody plants and woody plant management: ecology, safety, and environmental impact*. Marcel Dekker, New York, New York, USA.
- Breshears, D. D., P. M. Rich, F. J. Barnes, and K. Campbell. 1997. Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. *Ecological Applications* 7:1201–1215.
- Cable, D. R. 1971. Lehmann lovegrass on the Santa Rita Experimental Range, 1937–1968. *Journal of Range Management* 24:17–21.
- Carlson, D. H., and T. L. Thurow. 1996. Comprehensive evaluation of the improved SPUR model (SPUR-91). *Ecological Modelling* 85:229–240.
- Cepeda-Pizarro, J. G., and W. G. Whitford. 1990. Decomposition patterns of surface leaf litter of six plant species along a Chihuahuan desert watershed. *American Midland Naturalist* 123:319–330.
- Charley, J. L., and N. E. West. 1977. Micro-patterns of nitrogen mineralization activity in soils of some shrub-dominated semi-desert ecosystems of Utah. *Soil Biology and Biochemistry* 9:357–365.
- Couteaux, M. M., P. Bottner, and B. Berg. 1995. Litter decomposition, climate and litter quality. *Trends in Ecology and Evolution* 10:63–66.
- Cybulski, W. J., W. T. Peterjohn, and J. H. Sullivan. 2000. The influence of elevated ultraviolet-B radiation (UV-B) on tissue quality and decomposition of loblolly pine (*Pinus taeda* L.) needles. *Environmental and Experimental Botany* 44:231–241.
- Edmonds, R. L. 1979. Decomposition and nutrient release in Douglas-fir needle litter in relation to stand development. *Canadian Journal of Forest Research* 9:132–140.
- Elkins, N. Z., and W. G. Whitford. 1982. The role of microarthropods and nematodes in decomposition in a semi-arid ecosystem. *Oecologia* 55:303–310.
- Grant, W. E., W. T. Hamilton, and E. Quintanilla. 1999. Sustainability of agroecosystems in semi-arid grasslands: simulated management of woody vegetation in the Rio Grande Plains of southern Texas and northeastern Mexico. *Ecological Modelling* 124:29–42.
- Hamilton, W. T., A. McGinty, D. N. Ueckert, C. W. Hanselka, and M. R. Lee. 2004. *Brush management: past, present, future*. Texas A&M University Press, College Station, Texas, USA.
- Hester, J. W., T. L. Thurow, and C. A. J. Taylor. 1997. Hydrologic characteristics of vegetation types as affected by prescribed burning. *Journal of Range Management* 50:199–204.
- Hobbie, S. E. 1992. Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution* 7:336–339.
- Hobbie, S. E. 2000. Interactions between litter lignin and soil nitrogen availability during leaf litter decomposition in a Hawaiian montane forest. *Ecosystems* 3:484–494.
- Hope, G. D., C. E. Prescott, and L. L. Blevins. 2003. Responses of available soil nitrogen and litter decomposition to openings of different sizes in dry interior Douglas-fir forests in British Columbia. *Forest Ecology and Management* 186: 33–46.
- Horner, J. D., J. R. Gosz, and R. G. Cates. 1988. The role of carbon-based plant secondary metabolites in decomposition in terrestrial ecosystems. *American Naturalist* 132:869–883.
- Houghton, R. A. 2003. Why are estimates of the terrestrial carbon balance so different? *Global Change Biology* 9:500–509.
- Hughes, R. F., S. R. Archer, G. P. Asner, C. A. Wessman, C. McMurtry, J. Nelson, and R. J. Ansley. 2006. Changes in aboveground primary production and carbon and nitrogen pools accompanying woody plant encroachment in a temperate savanna. *Global Change Biology* 12:1733–1747.
- Kirschbaum, M. U. F. 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. *Soil Biology & Biochemistry* 27:753–760.
- Kraus, T. E. C., R. A. Dahlgren, and R. J. Zasoski. 2003. Tannins in nutrient dynamics of forest ecosystems—a review. *Plant and Soil* 256:41–66.
- Mack, M. C., and C. M. D’Antonio. 2003. The effects of exotic grasses on litter decomposition in a Hawaiian woodland: the importance of indirect effects. *Ecosystems* 6:723–738.
- Martin, C. S., and D. E. Ward, Jr. 1966. Using aerial applications—two annual sprays control mesquite. *Progressive Agriculture in Arizona* 18:20–21.
- McClaran, M. P. 2003. A century of vegetation change on the Santa Rita Experimental Range. Pages 16–33 in M. P. McClaran, P. F. Ffolliott, and C. B. Edminster, editors. *Santa Rita Experimental Range: 100 years (1903–2003) of accomplishments and contributions*. Proceedings of 30 October–1 November 2003 conference, Tucson, Arizona, USA. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA.
- McClaran, M. P., and M. E. Anable. 1992. Spread of introduced Lehmann lovegrass along a grazing intensity gradient. *Journal of Applied Ecology* 29:92–98.
- McClaran, M. P., P. Ffolliott, and C. Edminster, editors. 2003. *Santa Rita Experimental Range: 100 years (1903–2003) of accomplishments and contributions*. Proceedings RMRS-P-30, USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA.
- McCulley, R. L., S. R. Archer, T. W. Boutton, F. M. Hons, and D. A. Zuberer. 2004. Soil respiration and nutrient cycling in wooded communities developing in grassland. *Ecology* 85: 2804–2817.
- Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology* 59:465–472.
- Melillo, J. M., J. D. Aber, and J. F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63:621–626.
- Moorhead, D. L., W. S. Currie, E. B. Rastetter, W. J. Parton, and M. E. Harmon. 1999. Climate and litter quality controls on decomposition: an analysis of modeling approaches. *Global Biogeochemical Cycles* 13:575–589.
- Moorhead, D. L., and J. F. Reynolds. 1991. A general model of litter decomposition in the northern Chihuahuan Desert. *Ecological Modeling* 56:197–219.

- Moorhead, D. L., R. L. Sinsabaugh, A. E. Linkins, and J. F. Reynolds. 1996. Decomposition processes: modelling approaches and applications. *Science of the Total Environment* 183:137–149.
- Mtambanengwe, F., and H. Kirchmann. 1995. Litter from a tropical savanna woodland (miombo): chemical composition and C and N mineralization. *Soil Biology and Biochemistry* 27:1639–1651.
- Newman, B. D., B. P. Wilcox, S. R. Archer, D. D. Breshears, C. N. Dahm, C. J. Duffy, N. G. McDowell, F. M. Phillips, B. R. Scanlon, and E. R. Vivoni. 2006. The ecohydrology of arid and semiarid environments: a scientific vision. *Water Resources Research* 42:W06302 [doi:10.1029/2005WR004141].
- Okin, G. S., and D. A. Gillette. 2001. Distribution of vegetation in wind-dominated landscapes: implications for wind erosion modeling and landscape processes. *Journal of Geophysical Research* 106(D9):9673–9684.
- Olson, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44:322–331.
- Pancotto, V. A., O. E. Sala, T. M. Robson, M. M. Caldwell, and A. L. Scopel. 2005. Direct and indirect effects of solar ultraviolet-B radiation on long-term decomposition. *Global Change Biology* 11:1982–1989.
- Paynter, Q., and G. J. Flanagan. 2004. Integrating herbicide and mechanical control treatments with fire and biological control to manage an invasive wetland shrub, *Mimosa pigra*. *Journal of Applied Ecology* 41:615–629.
- Peterson, J. G. 1995. Ecological implications of sagebrush manipulation—a literature review. Montana Fish, Wildlife and Parks, Wildlife Management Division, Helena, Montana, USA.
- Piene, H., and K. van Cleve. 1978. Weight loss of litter and cellulose bags in a thinned white spruce forest in interior Alaska. *Canadian Journal of Forest Research* 8:42–46.
- Salimon, C. I., E. A. Davidson, R. L. Victoria, and A. W. F. Melo. 2004. CO<sub>2</sub> flux from soil in pastures and forests in southwestern Amazonia. *Global Change Biology* 10:833–843.
- Santos, P. F., J. Phillips, and W. G. Whitford. 1981. The role of mites and nematodes in early stages of buried litter decomposition in a desert. *Ecology* 62:664–669.
- SAS Institute. 2003. JMP 5.0. SAS Institute, Cary, North Carolina, USA.
- Schlesinger, W. H., and A. Pilmanis. 1998. Plant–soil interactions in deserts. *Biogeochemistry* 42:169–187.
- Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. F. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77:364–374.
- Scholes, R. J., and S. R. Archer. 1997. Tree–grass interactions in savannas. *Annual Review of Ecology and Systematics* 28:517–544.
- Schussman, H., E. Geiger, T. Mau-Crimmins, and J. Ward. 2006. Spread and current potential distribution of an alien grass, *Eragrostis lehmanniana* Nees, in the southwestern USA: comparing historical data and ecological niche models. *Diversity and Distributions* 12:582–592.
- Scifres, C. J. 1980. Brush management: principles and practices for Texas and the Southwest. Texas A & M University Press, College Station, Texas, USA.
- Scifres, C. J., W. T. Hamilton, B. H. Koerth, R. C. Flinn, and R. A. Crane. 1988. Bionomics of patterned herbicide application for wildlife habitat enhancement. *Journal of Range Management* 41:317–321.
- Sharma, G. D., R. R. Mishra, and S. Kshattriya. 1995. Fungi and litter decomposition in the tropics. Pages 39–57 in M. V. Reddy, editor. *Soil organisms and litter decomposition in the Tropics*. Westview Press, Boulder, Colorado, USA.
- Smith, J. L., J. J. Halvorson, and J. H. Bolton. 1994. Spatial relationships of soil microbial biomass and C and N mineralization in a semi-arid shrub-steppe ecosystem. *Soil Biology and Biochemistry* 26:1151–1159.
- Steinberger, Y., and W. G. Whitford. 1988. Decomposition processes in Negev ecosystems. *Oecologia* 75:61–66.
- Teague, W., J. Foy, B. Cross, and S. Dowhower. 1999. Soil carbon and nitrogen changes following root-plowing of rangeland. *Journal of Range Management* 52:666–670.
- Tiedemann, A. R., and J. Klemmedson. 1977. Effect of mesquite trees on vegetation and soils in the desert grassland. *Journal of Range Management* 30:361–367.
- Tiedemann, A. R., and J. Klemmedson. 1986. Long-term effects of mesquite removal on soil characteristics. I. Nutrients and bulk density. *Soil Science Society of America Journal* 50:472–475.
- Tiedemann, A. R., and J. O. Klemmedson. 2004. Responses of desert grassland vegetation to mesquite removal and regrowth. *Journal of Range Management* 57:455–465.
- Valentine, J. F. 1989. Range development and improvements. Third edition. Academic Press, San Diego, California, USA.
- van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics* 31:197–215.
- Vicari, M., and D. R. Bazely. 1993. Do grasses fight back? The case for antiherbivore defenses. *Trends in Ecology and Evolution* 8:137–141.
- Wardle, D. A., K. I. Bonner, G. M. Barker, G. W. Yeates, K. S. Nicholson, R. D. Bardgett, R. N. Watson, and A. Ghani. 1999. Plant removals in perennial grassland: vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. *Ecological Monographs* 69:535–568.
- Wardle, D. A., M.-C. Nilsson, C. Gallet, and O. Zackrisson. 1998. An ecosystem-level perspective of allelopathy. *Biological Reviews* 73:305–319.
- Wertz, M. A., M. R. Kidwell, and H. D. Fox. 1998. Influence of abiotic and biotic factors in measuring and modeling soil erosion on rangelands: state of knowledge. *Journal of Range Management* 51:482–495.
- Wessman, C., S. Archer, L. Johnson, and G. Asner. 2004. Woodland expansion in US grasslands: assessing land-cover change and biogeochemical impacts. Pages 185–208 in G. Gutman, A. C. Janetos, C. O. Justice, E. F. Moran, J. F. Mustard, R. R. Rindfuss, D. Skole, B. L. Turner II, and M. A. Cochrane, editors. *Land change science: observing, monitoring and understanding trajectories of change on the earth's surface*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Whitford, W. G. 2002. Decomposition and nutrient cycling. Pages 235–274 in W. Whitford, *Ecology of desert systems*. Academic Press, San Diego, California, USA.
- Whitford, W. G., V. Meentemeyer, T. R. Seastedt, K. Cromack, D. A. Crossley, P. Santos, R. L. Todd, and J. B. Waide. 1981. Exceptions to the AET model: deserts and clear-cut forest. *Ecology* 62:275–277.
- Zhang, Q. H., and J. C. Zak. 1995. Effects of gap size on litter decomposition and microbial activity in a subtropical forest. *Ecology* 76:2196–2204.
- Zou, C., P. W. Barnes, S. R. Archer, and C. R. McMurtry. 2005. Soil moisture redistribution as a mechanism of facilitation in savanna tree–shrub clusters. *Oecologia* 145:32–40.