Decomposition of leaf and root litter of Chihuahuan desert shrubs: effects of three years of summer drought

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One of the more uncertain aspects of nutrient cycling in desert ecosystems is the extent to which decomposition is controlled by water availability. Some of this uncertainty may be partly related to the duration of the studies and/or differences in the chemical composition of the decaying litter. We conducted a 3-year field study of rainfall to determine the impact of summer (June – September) drought on decomposition of leaf and root litter of two shrub species (*Larrea tridentata* and *Prosopis glandulosa*) in the northern Chihuahuan Desert (New Mexico, U.S.A.). In both species, leaf litter decayed at a faster rate and was less effected by drought than root litter. Drought had no influence on the rates of decomposition of leaves of either species during the first 18 months, but caused decay rates to decline by about 25% during the latter half of the study. Drought decreased decay of root litter in both species by about 25% throughout the 3 years. There was a general increase in percent nitrogen (%N) of decomposing leaf litter in both species. Root litter %N declined slightly in *Larrea* but remained relatively constant in *Prosopis*. Using a modified version of the CENTURY model, we were able to predict most aspects of observed leaf and root litter mass loss and nitrogen dynamics. Overall, the results of this study suggest that relatively large changes in precipitation produce comparatively small changes in rates of decay of both leaf and root litter.

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Introduction

The availability of nutrients, particularly nitrogen, has a major role in controlling the primary productivity of desert ecosystems (Charley, 1972; Romney *et al.*, 1978; Parker *et al.*, 1984a; Fisher *et al.*, 1988). Desert soils are generally poorly developed and low

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in organic matter and nutrients relative to other ecosystems. However, litter and nutrient inputs may sporadically be high relative to the pool sizes (Crawford & Gosz, 1982), resulting in temporal and spatial heterogeneity in litter and nutrient pools (Charley, 1972; Noy-Meir, 1973; Schlesinger *et al.*, 1996). Predicting the distribution, cycling, and availability of nutrients in desert ecosystems depends to a large extent on an understanding of decomposition. Considerable uncertainty and controversy exists regarding decomposition processes and their control by biotic and abiotic factors (Whitford *et al.*, 1981; Schaefer *et al.*, 1985). For example, some studies suggest that arthropod detritivores may control mass loss of litter either directly via transporting material below ground (Whitford *et al.* 1982, 1988; Silva *et al.*, 1985) or indirectly via predation on decomposer organisms or more complicated trophic interactions (Santos & Whitford, 1981; Parker *et al.*, 1984*a*). Others (e.g. Comanor & Staffeldt, 1978; Moorhead & Reynolds, 1989*b*) suggest that abiotic processes (physical, chemical, and UV degradation of exposed materials) play a significant role in the decomposition of surface litter. Moorhead & Reynolds (1989*a*) also suggest that surface decomposition in deserts is qualitatively different from below-ground decomposition, which is controlled by microbial decomposers as in more mesic ecosystems.

Among the uncertain aspects of decomposition and nutrient cycling in arid ecosystems is the role that moisture plays as a controlling factor (Santos *et al.*, 1984; Whitford *et al.*, 1986; Strojan *et al.*, 1987; Moorhead & Reynolds, 1989*b*). A number of studies have examined the effects of moisture on decomposition under arid conditions by employing moisture augmentation (e.g. Whitford *et al.*, 1986, 1988; MacKay *et al.*, 1987*a*). However, Whitford *et al.* (1995) suggest that conclusions regarding the effects of moisture on decomposition in arid systems may depend on whether water is added or removed. In addition, the North American deserts are characterized by high moisture variability, and especially by month-to-season long droughts (MacMahon, 1979; Conley *et al.*, 1992). Thus, further studies of the impact of drought on decomposition are needed.

The objectives of the present study were: (1) to elucidate the specific effects of drought on decomposition and nutrient cycling associated with litter of the two co-dominant shrubs in the northern Chihuahuan Desert, *Larrea tridentata* (evergreen) and *Prosopis glandulosa* (winter deciduous); (2) to examine differences in effects of drought on surface processes and below-ground processes (see Moorhead & Reynolds, 1989*a*); and (3) to determine the extent to which decomposition under arid conditions is predictable using the CENTURY model (Parton *et al.*, 1987), which has been used successfully in other ecosystems to predict litter and soil organic matter decay and associated carbon (C) and nitrogen (N) dynamics. To accomplish these objectives, mesh bags containing root and leaf litter of these species were buried or placed on the surface under select shrubs as part of a larger manipulative study of the impact of drought on the growth and physiology of *Larrea* and *Prosopis* (Reynolds *et al.*, 1999). From January 1992 to June 1995 we followed the mass, C, and N of the litter and used these data as the basis for parameterizing the CENTURY model.

Methods

Study site

This experiment was part of a manipulative study of the impact of summer drought on the growth and physiology of *Larrea* and *Prosopis*, and the associated dynamics of soil resources (nutrients, water). See Reynolds *et al.* (1999) for a detailed description of that study and of the study site in south-central New Mexico, *ca.* 30 km N of Las Cruces in the northern Chihuahuan Desert. This area is part of the Jornada LTER located at the southern end of the Jornada del Muerto Basin of south-central New

Mexico, U.S.A. (Doña Ana County). The decomposition of *Larrea* litter was studied on a gently sloping, eroded terrace composed of shallow, coarse-textured soils (*ca.* 80% sand, 10% silt, 10% clay) and dominated by a sparse cover of *Larrea* (<30%) with scattered subshrubs and forbs (hereafter referred to as the *Larrea* site). The decomposition of *Prosopis* litter was studied in a dune area located about 20 km NW of the *Larrea* site in a broad, flat subsidiary basin characterized by aeolian soils (*ca.* 86% sand, 6% silt, 8% clay) and dominated by a sparse cover of *Prosopis* (<20%), with a few other scattered forbs and grasses.

Climate and drought treatment

Details regarding the climate of the Jornada Basin are provided in Conley *et al.*(1992). The mean annual temperature is 16°C. The mean monthly maximum temperature is highest in June (36°C) and lowest in January (13°C). Night-time freezing temperatures occur on average from late October through early April (165 days). Conley *et al.* (1992) characterized the semi-arid climate of the Jornada as having three distinct seasons: hot, dry springs (April–June); hot, moist summers (July–October); and cold, moderately dry winters (November–March). Total annual precipitation is about 230 mm, of which nearly 65% falls during the summer period as localized showers associated with thunderstorms; about 25% falls in winter as rain and snow associated with frontal storms over the region; and about 10% occurs in the spring.

  Given that Reynolds *et al.* (1999) found that winter soil moisture recharge could begin as early as October, and because rainfall-initiated summer growth can occasionally begin mid-to late June, we designate the period from June to September as *summer* for the purposes of applying the drought treatment. The rest of the year (October 1–May 30) is referred to as *winter/spring*. Summer drought treatment (exclusion of June–September rainfall) was accomplished using small rain-excluding shelters designed to cover a specific shrub and an area about 5 × the size of its canopy. The rain shelters were constructed of metal frames, which were open on the sides and covered with thin polyethylene film roofs (6 mil, 0.15 mm thick). The polyethylene roof was only on the shelter during the summer drought treatment period, during which time there were also microclimate effects associated with polyethylene film (and to a lesser extent, the shelter framework). Trasmissivity of the polyethylene averaged 85% for visible radiation (400–700 nm) and 82% for ultraviolet (340–400 nm). Total solar radiation was reduced by 15–35% depending upon cloud cover and time of year. Midday air temperatures under shelters differed only slightly from ambient (±1°C), but temperatures under the shrub canopies at the soil surface and at 10 cm depth differed by as much as 6°C and 2°C, respectively (descriptions and photos of shelters provided in Reynolds *et al.*, 1999).

Litterbag sampling

In December of 1991 we collected leaves and excavated roots (1–8 mm dia.) from the two species at the two sites. This material was air-dried and 5g was apportioned into a $12 \times 12 \, cm^2$ fiberglass screen (1.5 mm mesh) litterbag. A total of 400 litterbags, 100 of each litter type of each species, were initially numbered and weighed and separated into two groups: those to be placed under shrubs that received natural rainfall (control) and those that were under shrubs subjected to summer rainfall exclusion in each year (treatment). Litterbags containing leaf litter were placed on the soil surface under the respective shrub canopy, and litterbags containing root litter were buried 10 cm beneath the surface of the shrubs. Six to eight litterbags were randomly collected once or twice a year during the 41-month duration of the study (January 1992–June 1995). At each sampling, litterbags were oven-dried to constant weight at

Table 1. *Measured and estimated chemical composition of initial litter (values are expressed as % of total dry mass)*

Fraction	Larrea		Prosopis	
	Leaf	Root	Leaf	Root
Carbon	52＋0·4*	50＋0·4*	47＋0·2*	50＋0·9*
Nitrogen	2·2＋0·1*	2·4＋0·2*	2·5＋0·1*	2·1＋0·4*
Soluble	25[†]	25[†]	24[‡]	24[‡]
Lignin	10[§]	22[‖]	8[¶]	16[¶]

*Measured in this study (＋1 s.d.).

[†]Comanor & Staffeldt (1978) reported that late season, senescent leaves consisted of 17–25·5% soluble extractives, while Moorhead & Reynolds (1989*a*, *b*) measured 25% solubles in a mixture of leaf and stem litter, and Cepeda-Pizarro & Whitford (1990) estimated a 'labile' fraction ranging from 25% to 33% for leaf litter. We have assumed 25% solubles for both leaf and root litter. Litter structural fraction is assumed to be 1− solubles.

[‡]Cepeda-Pizarro & Whitford (1990) estimated 24% 'labile' fraction from decay rates of *Prosopis* leaf litter, and we have assumed a similar value for both leaves and roots.

[§]Elkins & Whitford (1982), Schaefer *et al.* (1985) and Cepeda-Pizarro & Whitford (1990) all reported similar lignin contents of leaf litter (9·5–10·6%).

[¶]Cepeda-Pizarro & Whitford (1990) measured 7.9% lignin for *Prosopis* leaf litter, and we have assumed a similar value for leaves and 2 × that for roots.

[‖]We have no lignin measurements for root litter. Moorhead & Reynolds (1993) reported a lignin content of 22% for combined leaf and stem litter of *Larrea*. We have used this value for roots, as well.

60°C and weighed to determine the litter mass remaining, and samples were digested to determine total Kjeldahl N, total C, and ash. Except for the above determinations, we did not measure chemical composition of the litter. However, for some of the data analyses and for the purposes of modeling litter decomposition, it was necessary to be able to partition the litter into several chemical fractions—e.g. soluble (metabolic), recalcitrant (structural), and lignin fractions. These values were estimated from other studies and are reported in Table 1 along with initial litter chemistry measured in this study.

Data analyses

Data for litter mass and N content were each subjected to a multiple analysis of variance (AOV) to identify effects of four different factors—species differences, litter differences (leaf *vs.* root), drought treatment, and time (an independent factor since at any one sampling time a completely independent sample was collected)—on the amount of litter mass remaining and its N content. Because the principal focus of this study was on the effect of drought on decomposition, we also isolated that treatment effect by carrying out single-factor AOVs to determine specific effects of drought on the decomposition of individual litter types of each of the species. In order to compare decomposition rates through time between species, litter types, and especially between control and drought treatment, we also fit data for litter mass through time to a double exponential model, chosen to estimate the decay constants for the labile (metabolic) and structural fractions of litter (Cepeda-Pizarro & Whitford, 1990; Urquiaga *et al.*, 1998). Instead of allowing four fitting parameters, however, we assumed a fixed metabolic fraction for the litter of the two species (25% and 24% for *Larrea* and *Prosopis*, respectively). This was done to specifically partition the variation in litter mass decay between the decay rate constants associated with metabolic and structural fractions, and not into differences in metabolic fractions, which, in fact, were identical among the material split among control and drought treatments, and very similar

among all the litter used in this experiment. Also, we omitted the last data set sampled from this analysis since some of those samples had a gain rather than loss of mass. All statistical analyses were performed using Data Desk (Velleman, 1995).

Model simulations

To predict C and N dynamics of litter decomposition, we used the CENTURY model (Parton *et al.*, 1987) because of its relative simplicity. CENTURY is similar to a number of other models that have been developed to predict decay of various C and N pools representing different chemical fractions of litter and soil organic matter (SOM) (see Parnas, 1976; Anderson, 1979; van Veen & Paul, 1981; Pastor & Post, 1986; Parton *et al.*, 1987; Moorhead & Reynolds, 1991). Only the decomposition component of the CENTURY model was used for this study. CENTURY simulates decay from two constituent fractions of litter (metabolic and structural) and three fractions of soil organic matter (active, slow, and passive). Flows of C from the various fraction pools are governed by intrinsic decomposition rates (k), microbial efficiencies, and soil texture (for partitioning flow of carbon from active SOM into slow or passive SOM). All rates of C flow are affected in the same way by functions of monthly soil temperature and moisture (ratio of monthly rainfall to potential evapo-transpiration). Nitrogen dynamics are closely coupled to C flows, with movement of N determined as the product of C flow times the N/C ratio of recipient pool. The N/C ratio of initial litter is fixed at 1/150 for the structural pool, but variable for the metabolic pool (depending on the N content of incoming litter). Nitrogen mineralization occurs at the rate of C mineralization times the N/C ratio of specific pool, whereas N immobilization (from soil inorganic N) into an organic matter pool occurs if additional N is required to maintain the specified N/C ratio of pool.

Initial trials to use CENTURY with parameter values as presented in Parton *et al.* (1987) resulted in overestimates of mass loss and poor predictions of the impacts of drought. Thus, we incorporated several changes into CENTURY to make it more applicable to arid ecosystems in general. The overestimation of litter decay rates appeared to be partly related to the partitioning of litter into metabolic and structural fractions (Eqn (2) in Parton *et al.*, 1987), which yielded a metabolic fraction that was too great for both species—a problem that has been encountered with other applications of CENTURY (Moorhead *et al.*, 1999). Thus, we partitioned litter into the two fractions based on literature values for *Larrea* and *Prosopis* (see Table 1). We changed the time step of the model from monthly to daily to accommodate the high within-month variation in moisture of the soil and litter pools. Others (Parton *et al.*, 1996) have incorporated this change into CENTURY in order to predict ecosystem processes that operate at scales of less than a month. Changing to a daily time step necessitated changing the monthly averaged temperature and moisture scalars for decay.

To account for the effect of temperature on decomposition, we used the same functional relationships employed by Parton *et al.* (1987), but used daily average soil temperatures at 1 cm (for leaf litter) and 10 cm (for root litter). Different methods were used for scaling the effect of moisture on leaf litter decomposition and root litter decomposition. For leaf litter decomposition, we used the functional relationship in Parton *et al.*, in which the decomposition rate is scaled by a monthly moisture index, M_d, calculated as the ratio of precipitation (PPT) to potential evapo-transpiration (PET). However, we calculated a daily value for PPT/PET based on a 30-day running sum of PPT and a 30-day running sum of PET. PET was calculated using Eqn (12) of Kemp *et al.* (1997). For root litter decomposition, however, this simple moisture scalar resulted in overestimates of mass loss for both species and did not reproduce the effect of drought on root litter decay. We thus presumed that root litter decay was more

Table 2. *Decay constants, N/C ratios, and conversion efficiencies for various litter and soil organic matter fractions used in CENTURY (this study)*

Fraction	k value (day^{-1})	N/C ratio	Conversion	Efficiency
Metabolic (soluble)	0·05	1/10 + (variable)	Metabolic → active OM	0·45
Structural	0·013*	1/150	Structural → active OM	0·45
			Structural → slow OM	0·70
Active OM	0·016[†]	1/8	Active OM → slow OM[‡]	($\simeq$0·40)[§]
Slow OM	0·00054	1/11	Slow OM → active OM[‡]	0·45
Passive OM	0·000019	1/11	Passive OM → active OM	0·55

*k is modified by lignin fraction (L_s): $k' = k\,e\,(-3·0L_s)$, 0·013 is the maximum value (with 20% lignin, $k' \approx 0·007$).

[†]k is modified by the fraction of silt+clay in the soil (T): $k' = k\,(1 - 0·75\,T)$.

[‡]Conversions of Active OM to Slow OM and vice versa are assumed to incure small fractions that become stablilized as Passive OM (these fractions are 0.004 and 0.03, respectively, and have the same efficiency as the primary conversions).

[§]Efficiency is a function of the fraction of silt+clay in the soil (T): $E = 1 - (0·85 - 0·68\,T)$.

strongly related to actual soil moisture content. Because we only had soil water measurements at 30 and 60 cm, we estimated soil water content at 10 cm using a soil water model (SWB) developed for the Jornada Basin (Kemp *et al.*, 1997). The model was calibrated and tested for both the *Larrea* and *Prosopis* sites using water content data collected at 30 and 60cm depths. We then calculated a moisture scalar (M_{d-root}), varying from 0 to 1, which was a function of soil water content:

$$M_{d-root} = (\text{SWC}_{10} - \text{SWC}_{min})/(\text{SWC}_{max} - \text{SWC}_{min})$$

where SWC_{10} is the volumetric soil water content (in this case, the 5–15 cm soil layer), SWC_{max} equals maximum volumetric water content of the soil (approximately field capacity), and SWC_{min} equals a minimum volumetric water content where decomposition rate is assumed to be zero. We determined that the best fit to data for non-droughted *Larrea* root decomposition was with SWC_{max} equal to the value at $-0·02$ MPa and SWC_{min} equal to the value at $-1·5$ MPa. We then used this single set of parameters for all simulations of root decay for control and treatment for both species.

With all of these changes in place, estimated rates of root litter decay were still somewhat too great, so, as a last resort, we decreased the intrinsic decay constants for the root litter pools by 20%, making them equivalent to those for surface litter pools. Our justifications for this are that (i) arid ecosystems are dominated by fungi that probably have lower maximum decay rates than the bacteria-dominated agricultural soil upon which the decay constants of CENTURY were based (Whitford & Parker, 1989); and (ii) our data provided no support for the assumption of Parton *et al.* (1987) that decay rates of surface litter are fundamentally lower than those of below-ground litter — in fact, our data suggest the opposite. Evaluation and comparison of model predictions were carried out using linear regression between observed mean values and predicted values corresponding to the times at which observed values were obtained (Table 2).

Results

Rainfall and water availability

The study period (January 1992–June 1995) was characterized by above-average winter/spring rainfall during 1992, 1993, and 1995 and below-average rainfall in two
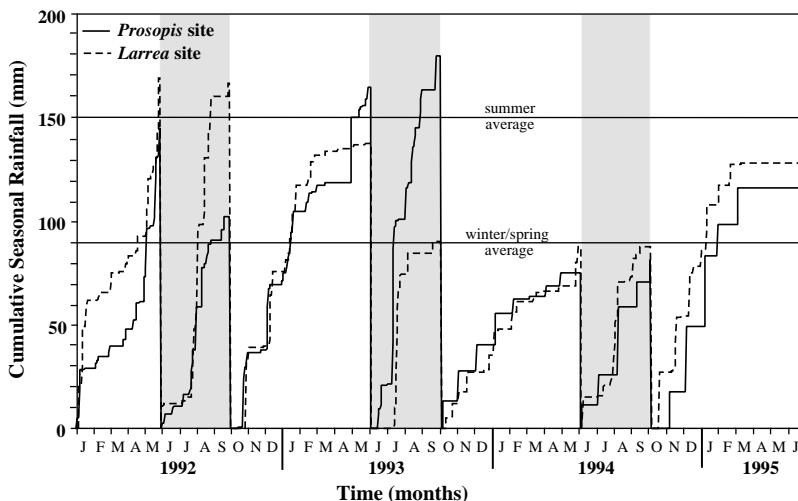
Figure 1. Observed cumulative seasonal rainfall at the *Larrea* and *Prosopis* study sites in the Jornada Basin, New Mexico. The summer period is defined in this study as the period from June to September (indicated by shaded regions; average rainfall *ca.* 150 mm); winter/spring is the period from October to May (average rainfall *ca.* 90 mm).

of the three summers (Fig. 1). Winter/spring precipitation in the first year was much above normal at both sites. Note that only January–May precipitation is shown for the first year (1992) in Fig. 1, but that both sites received about 125 mm of rainfall during three months prior to the start of the study, with about 60 mm falling on December 23. In fact, soils were saturated to 60 cm when litter was placed into the sites *ca.* January 1. The first winter/spring was followed by nearly average summer rainfall (1992) at the *Larrea* site (166 mm from 21 separate events), but only about 2/3 average at the *Prosopis* site (103 mm from 15 separate events). The second winter/spring season (October 1992–May 1993) had about 1·5 × average rainfall. Summer rainfall in the second year (1993) was slightly above normal at the *Prosopis* site (182 mm over 19 events), but was only about 60% of average at the *Larrea* site (90 mm over eight events). The third winter/spring season (October 1993–May 1994) had nearly average rainfall, followed by much below normal (*ca.* 50%) summer rainfall at both sites. Rainfall during the fourth winter/spring period (October 1994–May 1995) was about 1·5 × average at both sites.

Simulated soil water content in the 5–15 cm layer of the soil is shown in Fig. 2. Soil water content was similar between the sites except during the second summer (months 18–21) when the *Prosopis* site, which received about twice the rainfall of the *Larrea* site, had much greater soil moisture. Interestingly, the similarly greater rainfall at the *Larrea* site during the first summer produced almost no difference in soil water storage between the sites. The effect of summer drought on soil water is shown as a percentage difference from the control water contents (Fig. 2). Drought had a similar effect on water content at both sites during the first and third summers, but had a comparatively greater effect on soil water at the *Prosopis* site during the second summer.

Litter analyses

The multiple AOV for all data reveals a significant mass loss through time, which differs between species, litter type (leaf *vs.* root), and drought treatment, with the
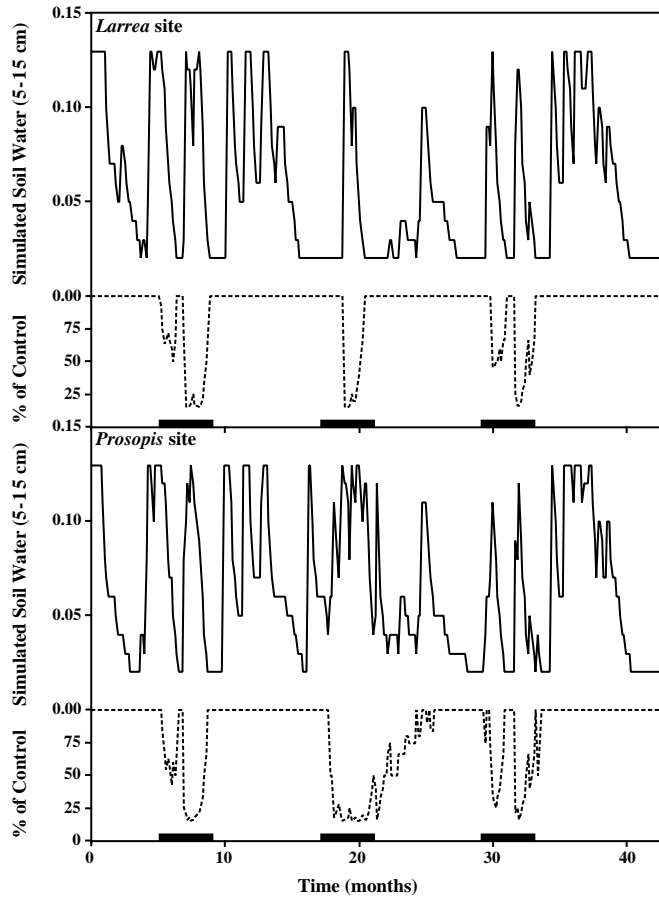
Figure 2. Simulated soil water content for the 5–15 cm depth (solid lines) predicted from natural rainfall inputs at each site (root litter was buried at *ca.* 10 cm). The predicted effect of the drought treatment on soil water content is shown as a percentage departure (dashed lines) from the undroughted control values. Black bars along the abscissa indicate the period of the drought treatment.

greatest effect being due to litter type ($F_{litter} = 1061$; $F_{species} = 144$; $F_{drought} = 52$; see Table A1 for complete results of AOV). There are also small, but significant interactions between litter type and time, and among species, litter type, and time, which indicates a difference in mass loss of leaf *vs.* root litter through time (which differs for each species). Leaf surface litter decayed faster than buried root litter in both species (Fig. 3), about twice that of root litter over the study period. The pattern of litter mass loss was similar in both species during the first 2 years, with a 40–50% reduction in leaf litter and a 20–25% reduction in root litter during the first year, followed by smaller losses the second year. In the third year, *Larrea* leaves and roots continued to lose mass, in contrast to *Prosopis* leaves and roots. Over the 41 months of the study, total mass loss of *Larrea* leaf and root litter receiving natural rainfall was 74% and 36%, respectively. Total mass loss of *Prosopis* leaf and root litter receiving natural rainfall was 60% and 35%, respectively. The effect of drought on litter decay varied between litter types and species (Table A2). Drought had little impact on mass loss of leaf litter of either species during the first 18 months of decomposition (Fig. 3a,b). Patterns of decay of leaf litter over the remaining 23 months of the study
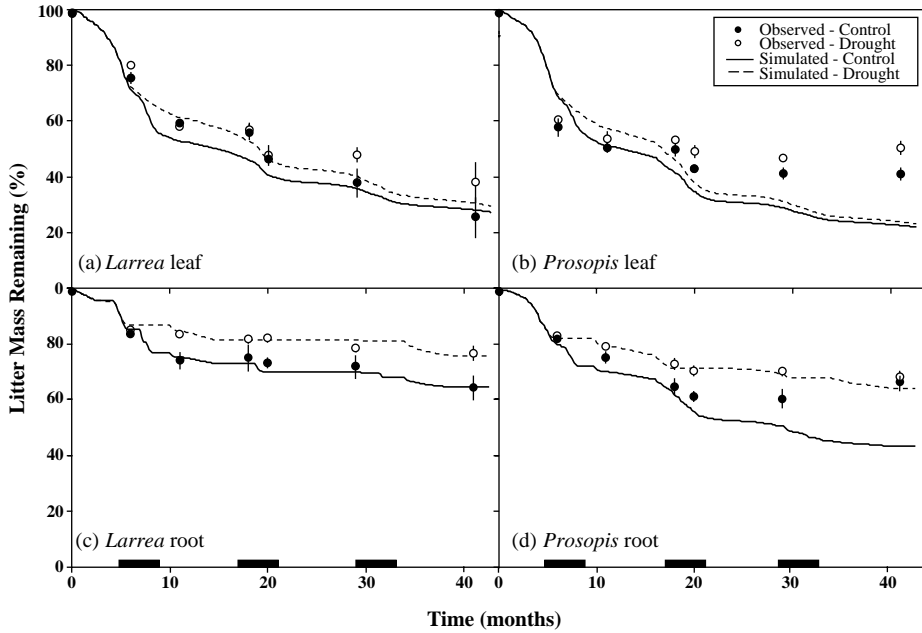
Figure 3. Observed mass loss for leaf litter (placed on the soil surface) and root litter (buried at 10 cm) compared with predicted mass loss (lines) using the CENTURY model. Observed data are for *Larrea* and *Prosopis* litter, which received natural rainfall (solid symbols) or subjected to summer drought (open symbols). Points are means of 6–8 litterbags sampled at each date with vertical bars showing ± 1 S.E.

Table 3. *Decay coefficients for metabolic (k_1) and structural (k_2) litter fractions determined from best fit of litter mass data to a double exponential equation (based on fixed starting metabolic and structural fractions for each species; see Table 1 and Methods)*

Species	Litter types	Treatment	k_1 (month^{-1})	k_2 (month^{-1})	MSE
Larrea	Leaf	Control	−0·169	−0·0227	2617
		Droughted	−0·176	−0·0175	1472
	Root	Control	−0·190	−0·00088	1652
		Droughted	−0·091	−0·0	551
Prosopis	Leaf	Control	−3·00	−0·0268	2133
		Droughted	−3·62	−0·0209	1712
	Root	Control	−0·143	−0·0095	1595
		Droughted	−0·156	−0·0033	808

show reduced decay rates in drought-treated litter, but this effect is only marginally significant for *Larrea* leaf litter ($p = 0.075$). Drought had a greater impact on decay of root litter than of leaf litter (Fig. 3; Table A2), with droughted litter of both species having significantly less mass loss than litter receiving natural rainfall.

Further insight into the nature of variation in decomposition among species, litter type, and drought is provided by examining the decay rates for metabolic (k_1) and structural (k_2) fractions of litter, as calculated from double exponential regression
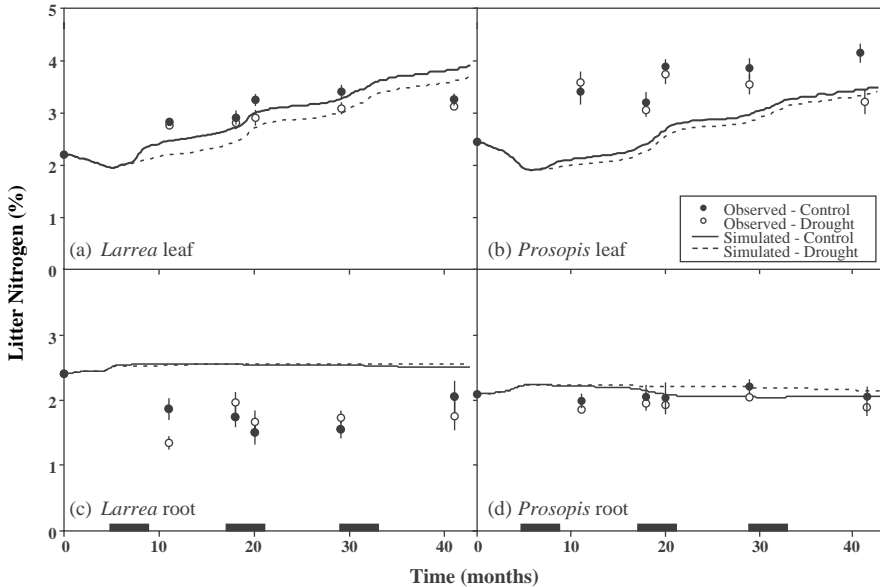
Figure 4. Observed nitrogen content of leaf litter (placed on the soil surface) and root litter (buried at 10 cm) compared with predicted values (lines) using the CENTURY model. Observed data are for *Larrea* and *Prosopis* litter, which received natural rainfall (solid symbols) or subjected to summer drought (open symbols). Points are means of 6–8 litterbags sampled at each date with vertical bars showing ± 1 S.E.

(Table 3). The rate of decay of the metabolic fraction was typically an order of magnitude or more greater than that of the structural fraction for all litter. Both k_1 and k_2 decay rates differed between the species and/or litter type, and to a lesser extent, as a result of drought. There are two major differences among k_1 values with regard to species or litter type. The k_1 value for decay of leaf litter is about 20-fold greater for *Prosopis* (*ca.* 3·3 month^{-1}) than *Larrea* (*ca.* 0·17 month^{-1}), and the k_1 value for *Prosopis* leaf litter is more than 20-fold greater than for *Prosopis* root litter (*ca.* 0·15 month^{-1}). The only effect of the drought treatment on the k_1 values was with respect to *Larrea* root litter, for which drought reduced k_1 by about half (0·091 for droughted *vs.* 0·190 for control). The k_2 values for decay of leaf litter structural materials were similar for the two species (0·023 − 0·027), and were similarly reduced by drought in both species (*ca.* 22%). The k_2 values for root litter varied between the species (being about 10 × greater for *Prosopis* than *Larrea*), and are reduced greatly by drought in both species (> 60%).

The ANOVA of N content (%N) for all litter reveals significant differences through time due to species, litter type, and drought, with the greatest effect due to litter type ($F_{\text{litter}} = 1142$; $F_{\text{species}} = 108$; $F_{\text{drought}} = 20$; Table A3). Litter of both leaves and roots of both species had similar initial N contents (2·1–2·5%). However, %N of leaf litter increased significantly during the study ($p < 0.001$), whereas %N of root litter either decreased (*Larrea*) or was similar (*Prosopis*) throughout the study (Fig. 4). Drought had a small, but significant, effect on %N of leaf litter in both species (Table A4). This effect is largely the result of differences that occurred after the first 18 months of decomposition, at which time %N of control leaf litter became greater than that of droughted litter. Drought did not significantly affect the %N of root litter in *Larrea*, but slightly reduced %N of root litter in *Prosopis* (Table A4).

Table 4. *Regression of predicted values against measured mean values of litter mass and nitrogen content*

Model predictions	r^2	
	Mass remaining	% Nitrogen
Larrea		
Leaf		
Control	0·94	0·50
Droughted	0.91	0·47
Root		
Control	0·93	n.s.
Droughted	0·82	n.s.
Prosopis		
Leaf		
Control	0·56(a)	n.s.
Droughted	n.s.	n.s.
Root		
Control	0·61	n.s.
Droughted	0·92	n.s.

Note: Predicted values were obtained from CENTURY model simulations for times corresponding to data measurement times. All regression values were significant ($p < 0.05$) with intercepts not significantly different from 0, and slopes not significantly different from 1·0, except for (a), in which slope and intercept were significantly different from 1·0 and 0.

Model predictions

CENTURY predicts leaf decomposition in *Larrea* quite well, with predictions within $\pm 10\%$ of most of the observed values (Fig. 3(a); Table 4). The maximum prediction error is 21% for drought-treated leaf litter mass at the end of the study period. Predictions of root litter mass loss using the modified moisture scalar are also quite good for *Larrea* (Fig. 3(c)), with all predictions within $\pm 5\%$ of the observations for the duration of the study. CENTURY predicts leaf decay in *Prosopis* to within 20% of observed values during the first 20 months of the study, but overestimates rates by as much as 50% during the second 21 months of the study (Fig. 3(b); Table 4). Predictions of *Prosopis* root litter mass loss are quite accurate in the case of the drought-treated litter, but the model overestimates mass loss of control litter by as much as 35% during the latter half of the study (Fig. 3(d)). Much of the apparent lack of fit of the model with observed mass of *Prosopis* leaf and root litter during the last half of the study is probably related to problems with the data rather than the model, since there was almost no mass loss in the litterbags during this period (and some even gained mass), which suggests contamination by soil.

Predictions of litter N content through time by the model are generally less accurate than predictions of litter mass (Fig. 4 *vs*. Fig. 3). Regression analysis indicates that only predictions of N content of *Larrea* leaf litter are significantly correlated with observations (Table 4). However, the model predictions are perhaps better than indicated by these regression analyses. CENTURY correctly predicts qualitative differences in trends of %N between leaf and root litter and predicts an overall increase in leaf litter %N through time (following an initial decrease), which matches the relative increases observed in both species (Fig. 4(a, b)). The model predicts *Prosopis* root litter %N within *ca*. 5% (Fig. 4(d)), but because predicted %N is essentially constant, it is not significantly correlated with the small variations in the

observed values. Model predictions overestimate %N in *Larrea* by 25% or more (Fig. 4(c)), but this lack of model success may be related to both the high variability in observed data (there is no clear trend in the litter N content through time) and an initial %N estimate that is too high.

Discussion

Our results show that the effect of drought on decomposition depends on whether it is leaf or root litter and the particular chemical fraction that is decaying. In the case of decomposition of leaf litter on the soil surface, we found no significant impact of drought on litter mass loss of either species during the first 18 months of the study (January 1992–July 1993), the period when most of the readily decomposable material (metabolic fraction) was lost. We also found no significant impact of drought on the calculated decay constants for the metabolic fraction (k_1) in either species. This conclusion should not, however, be interpreted as meaning complete insensitivity to moisture. For example, the relatively large losses of leaf litter (*ca*. 40% in *Prosopis* and 22% in *Larrea*; Fig. 3) during the first 5 months of the study may have been partly related to the much greater than normal winter/spring rainfall during the period. The best evidence for no effect of drought *per se* on decay of the labile fraction of the leaf litter is provided at the next sampling date, November 1992. Over the period from June through September, all summer moisture (100 mm at the *Prosopis* site and 165 mm at the *Larrea* site) was withheld in the drought treatment and yet there was no difference in mass loss between the control and drought treatments. There was very little litter mass loss over the next winter–spring period, such that by the third sampling date at 18 months there was still no effect of drought treatment. That there is no impact of drought on decomposition of leaf litter during the first half of this study is consistent with previous studies that report little or no effect of rainfall on decomposition of *Larrea* litter (Whitford *et al.*, 1982, 1986; Santos *et al.*, 1984; Schaefer *et al.*, 1985).

Several investigators (e.g. Whitford *et al.*, 1982; Silva *et al.*, 1985) suggest that the moisture insensitivity of decay of surface litter in the Jornada Basin is due to termites or other microarthropods transporting the material into the soil pool. When microarthropods and/or termites were removed, rates of mass loss from bags of leaf litter were reduced substantially (Santos & Whitford, 1981; Parker *et al.*, 1984*b*), and the resulting mass loss was much more strongly related to levels of soil moisture (Whitford & Parker, 1989). However, we saw no obvious evidence of termite activity in the litter samples, and furthermore, the increase in the N content of the remaining litter, that we observed in both control and treatment litter during the first half of the study (Fig. 4) is not consistent with the removal of litter mass by termites (Schaefer *et al.*, 1985). Thus, it is doubtful that termite activity was a significant factor in surface litter mass loss in this study. Fowler & Whitford (1980) and MacKay *et al.* (1987*b*) also reported no effect of termites (or microarthropods) on loss of *Larrea* leaf litter at nearby sites. Studies of mass loss of surface litter in these systems suggest that 20–35% of the mass loss is due to physical processes (Comanor & Staffeldt, 1978; Moorhead & Reynolds, 1989*b*; MacKay *et al.*, 1994), and while some processes such as photochemical breakdown of litter are relatively insensitive to moisture, one principal physical agent, leaching, is sensitive to moisture (Comanor & Staffeldt, 1978; Moorhead & Reynolds, 1989*b*). Also, if physical agents completely dominated the control of decay during the first half of the study, we would not expect to see an increase in N content of the remaining litter (Montaña *et al.*, 1988; Moorhead & Reynolds, 1989*b*). Thus, it seems that much of the surface mass loss must be a result of saprophyte-mediated decay. Insensitivity to drought is perhaps best explained by

the fact that the decomposers are relatively more limited by nutrients (N) and/or carbon than moisture (MacKay *et al.*, 1987*a*; Moorhead & Reynolds, 1991), and that the intervening periods of moisture are sufficient to compensate for relatively long drought periods. Our findings may be somewhat exceptional, however, since the periods between drought were characterized by mostly above-normal rainfall.

The conclusion that surface decay is relatively insensitive to drought applies primarily to the readily decomposable (metabolic) materials, since mass loss of the structural material during the later half of the study was significantly affected by drought. The calculated k_2 values for leaf litter (Table 3) indicate that drought reduced the decomposition rates of the structural components by about 22%, a result that is also reflected in differences between the control and droughted litter masses at the sample dates following the first 18 months of the study. These findings are consistent with other studies that have concluded that rates of surface litter decay are related to moisture availability (Comanor & Staffeldt, 1978; Strojan *et al.*, 1987; Moorhead & Reynolds, 1989*b*). Significantly, we suggest that the apparent contra-dictions regarding the effect of moisture on decay of surface litter in deserts may be related in part to the duration of the studies and/or differences in the chemical composition of the decaying litter.

In contrast to leaf litter, buried root litter of both species decomposed slower and was more strongly affected by drought, especially during the first 18 months of the study (Fig. 3). *Larrea* root litter decomposed only about half as fast as leaf litter, largely due to decreased decomposition rates of the structural fraction. Drought significantly reduced mass loss of both metabolic and structural fractions of *Larrea* root litter (Table 3). *Prosopis* root litter also decomposed slower than its leaf counterpart, but only the decay of the structural fraction was significantly reduced by drought (Table 3). This contrasts with others studies of these species that found more rapid decay of buried as compared to surface litter (Santos & Whitford, 1981; Elkins & Whitford, 1982), and with conclusions regarding decay in general (Parton *et al.*, 1987). This difference in rates of surface *vs.* below-ground decay may be affected by a number of factors, such as climate (Whitford *et al.*, 1982, 1986, 1995; Santos *et al.*, 1984; Schaefer *et al.*, 1985), seasonal variability (Comanor & Staffeldt, 1978; Moorhead & Reynolds, 1989*b*), microbial colonization of litter (MacKay *et al.*, 1987*a*; Moorhead & Reynolds, 1991), and soil texture and moisture (Parton *et al.*, 1987). For example, Comanor & Staffeldt (1978) found that root decay tended to exceed below-ground decay during winter–spring periods when soils were wetter and warmer than the surface, whereas decay of surface leaf litter tended to exceed that of roots in late spring through summer. We believe that an important factor influencing this relationship is the size and degree of lignification of the root litter (see also Fahey *et al.*, 1988). In our study, we included a broad range of root material (1–8 mm dia.) in the litterbags to represent a broad spectrum of root litter that would be available to decomposers. Our rationale for this was the previous finding (Reynolds *et al.*, 1999) of relatively low turnover of fine roots in these species, implying that longer-lived roots are larger and more lignified when death finally occurs. This material would be expected to decompose more slowly than litter consisting solely of unlignified fine root litter (Fahey *et al.*, 1988).

The dynamics of root litter N content also contrasts with the general increase in N of decomposing leaf litter of both species. Root litter %N either declined slightly (*Larrea*) or remained relatively constant (*Prosopis*), in contrast with Moorhead & Reynolds (1991) who found that buried litter of *Larrea* tended to immobilize N during decay, apparently because of nutrient limitations of the decaying microbes. Mun & Whitford (1998) also found an increase in N of decaying root litter of five different species. The differences between those studies and ours may be due to the considerably higher initial N concentration of the root litter in this study, almost $2 \times$ that of *Larrea* litter in Moorhead & Reynolds (1991) and $3 \times$ that of the average

N of litter in Mun & Whitford (1998). This was apparently sufficient to eliminate N immobilization by decomposers.

Reynolds *et al.* (1999) found that extractable N (NO_3^- and NH_4^+) of soils increased by 30–300% during the drought treatment used in the present study, but that this increase was not accompanied by an increase in total soil N. Furthermore, the extractable soil N was relatively transient, returning to levels comparable to non-droughted treatments during the following season. Based on this, Reynolds *et al.* concluded that the increased soil N during drought periods was possibly a result of released labile N from dead microbial biomass, which was not compensated for by microbial or plant uptake. The present study supports these conclusions since neither the impacts of drought on litter mass loss (which are on the order of 10–25%) nor the even smaller impacts of drought on the N content of litter (on the order of 5–15%) can explain the large, relatively transient differences in extractable soil N.

Model predictions

To use CENTURY in this arid system, we modified the model from the Parton *et al.* (1987) version in four ways: (i) a daily time step was implemented; (ii) litter was partitioned into metabolic and structural fractions based on literature values for *Larrea* and *Prosopis*; (iii) decay constants for root litter were reduced by 20% (making them equivalent to leaf litter); and (iv) a moisture scalar—calculated as a function of soil water content rather than the PPT/PET ratio—was used to control decay of root litter. The daily time step was necessary to account for the large variability in soil moisture in the Jornada Basin and to be able to account for droughts of varying duration. However, while this modification is necessary to predict root litter decay, we found that the best predictions of leaf decomposition is accomplished using a scheme very similar to the Parton *et al.* (1987) version. For control of leaf litter decay we calculated a daily equivalent of the monthly temperature and moisture scalars used in CENTURY by using a 30-day running average of daily surface temperature and a 30-day running sum of daily PPT/ET. Although we tried several other methods for calculating daily scalars or a moisture scalar that was more directly related to actual surface moisture availability (e.g. water content of the 0–5 cm soil surface layer), we found that all limited decay rates too strongly, resulting in underestimates of mass loss for both control and droughted surface litter. While this supports our conclusion that surface mass loss is not strongly related to surface moisture, the exact nature of this insensitivity and its specific relation to drought insensitivity remains unclear. It is possible that surface decomposition is uncoupled from short-term ambient moisture availability because of a greater moisture-holding capacity of litter than of the soil (see Schaefer *et al.*, 1985; Montaña *et al.*, 1988), but this explanation certainly would not apply to season-long drought. In any case, the use of the simple, long-term PPT/PET index of CENTURY appears adequate for predicting decay of surface litter in the Jornada Basin and presumably in other arid ecosystems. The actual functional form of the relationship (with M_d varying from 0·24 to 1·00 as PPT/PET varies from 0 to 1·25) is also consistent with the assumption that 25% of surface decay results from physical processes not controlled by moisture availability (Comanor & Staffeldt, 1978; Moorhead & Reynolds, 1989*b*).

Attempts to predict decay of buried root litter by using a moisture index similar to that used for surface litter resulted in large overestimates of mass loss under all circumstances, implying that mass loss of root litter is more strongly limited by moisture than is leaf litter. Modifying the moisture scalar for decay of root litter to directly reflect daily soil water availability at 5–15 cm results in improved predictions of root litter mass loss. With this modification, CENTURY predicted mass loss of both control and drought-treated *Larrea* root litter and drought-treated *Prosopis* litter

exceptionally well. The model predicts decay rates for *prosopis* control root litter, that are too great during the latter half of the study, similar to the prediction errors associated with prosopis leaf litter. However, as noted earlier, these discrepancies are probably due to contamination of litter bags by soil, rather than to shortcomings of the model.

CENTURY did not predict the N content of decaying litter as well as mass loss. However, these predictions are qualitatively correct in terms of predicting N immobilization in leaf litter (after the first year) and do predict relatively constant N of root litter after the first year (Fig. 4). Consequently, CENTURY appears to be relatively robust in terms of predicting N dynamics of litter in this arid system, particularly following the initial microbial colonization and equilibration period. It appears that predictions of N content of leaf litter could be improved if the model had predicted immobilization of N during the first year of the study, instead of a net N loss from litter. The predicted decline in litter N content in the first year results from the high decay rate of the relatively N-rich metabolic fraction of the leaf litter. Although litterbags were not sampled for N content of litter until 11 months into the study, that first analysis reveals that N contents in leaf litter had already increased substantially, suggesting that most of the N from decaying litter had been immobilized by the microbial decomposers. Some studies in arid and semi-arid ecosystems have found substantial immobilization of N during decomposition of surface litter (Comanor & Staffeldt, 1978; Fisher *et al.*, 1990; Moorhead & Reynolds, 1991; Seastedt *et al.*, 1992), whereas others have found little or no immobilization (Schaefer *et al.*, 1985; Montaña *et al.*, 1988). Montaña *et al.* (1988) suggest that immobilization decreases with increasing aridity, presumably because of a decrease in microbial activity. Our data reveal a decrease in immobilization with drought, but the difference is relatively small (5–10%), and even the complete withholding of all summer rainfall does not produce a qualitative change in N immobilization. Alternatively, MacKay *et al.* (1987*a*) argue that the amount of N immobilization is more limited by C availability than aridity *per se*. This suggests that the initial N immobilization we found could be partly due to the large amounts of C concentrated in litterbags, and that model predictions may be appropriate for more continuous, low-level C inputs of natural litter. While the N contents of leaf litter revealed a similar pattern of immobilization in both species, N content of root litter differed between the species, with *Prosopis* litter having relatively constant N, whereas *Larrea* root litter had a decline in N during the first year. Sampling frequency was not sufficient to identify the specific pattern of *Larrea* root litter N during the first year, and we have no explanation for the difference between the species. Since the model predicts N content of *Prosopis* root litter to within 5% for the entire study, we have no grounds for suggesting changes to the way in which the model treats root litter N dynamics.

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Appendix A

Results of ANOVA are given in Tables A1–A4.

Table A1. *Results of MANOVA for significant effects of Species, Litter type (leaf vs. root), Treatment (natural rain vs. drought), and Time on mass loss of litter*

Source	F	p
Constant	589,590	<0·001
Species	144	<0·001
Litter type	1061	<0·001
Treatment	52·4	<0·001
Time	96·3	<0·001
Species * Litter type	1·59	0·21
Species * Treatment	3·05	0·08
Species * Time	1·37	0·24
Litter type * Treatment	0·86	0·36
Litter type * Time	14·2	<0·001
Treatment * Time	2·56	0·039
Species * Litter type * Treatment	0·34	0.56
Species * Litter type * Time	11·0	<0.001
Species * Treatment * Time	0·63	0·64
Litter type * Treatment * Time	0·71	0·58
Species * Litter type * Treament * Time	0·45	0·77

Table A2. *Results of ANOVA for significant effects of drought and interaction of drought with time on mass loss of litter*

Species	Litter type	Drought		Drought × time	
		F	*p*	*F*	*p*
Larrea	Leaf	3·26	0·075	0·55	0·73
	Root	28·92	<0·001	1·88	0·11
Prosopis	Leaf	25·14	<0·001	1·98	0·10
	Root	46·01	<0·001	4·33	0·0037

Table A3. *Results of MANOVA for significant effects of Species, Litter type (leaf vs. root), Treatment (natural rain vs. drought), and Time on % N content of litter*

Source	F	p
Constant	15,273	<0.001
Species	108	<0.001
Litter type	1142	<0.001
Treatment	20.5	<0.001
Time	6.27	<0.001
Species * Litter type	5.55	0.019
Species * Treatment	3.63	0.058
Species * Time	2.24	0.07
Litter type * Treatment	2.95	0.09
Litter type * Time	6.59	<0.001
Treatment * Time	0.65	0.63
Species * Litter type * Treatment	0.02	0.89
Species * Litter type * Time	1.03	0.39
Species * Treatment * Time	1.16	0.33
Litter type * Treatment * Time	1.85	0.12
Species * Litter type * Treatment * Time	2.08	0.08

Table A4. *Results of ANOVA for significant effects of drought and interaction of drought with time on %N of litter*

Species	Litter Type	Drought		Drought $\times$ time	
		F	p	F	p
Larrea	Leaf	15.37	<0.001	0.71	0.59
	Root	0.62	0.43	2.19	0.081
Prosopis	Leaf	9.05	0.0038	1.74	0.15
	Root	4.65	0.051	0.41	0.80