Mechanisms of surface litter mass loss in the northern Chihuahuan desert: a reinterpretation

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A re-examination of surface litter decomposition studies in the northern Chihuahuan desert (New Mexico, U.S.A.) suggests mass loss patterns may be more closely regulated by abiotic processes than originally thought. Although biological mechanisms have been proposed to explain the high rate of surface litter disappearance in this ecosystem, non-biological processes, such as the leaching of solubles and photochemical degradation of lignins, may account for much of the total loss. Results of some recent studies may be better explained when the probable contributions of abiotic factors are considered.

Introduction

Decomposition rates of surface litter in the northern Chihuahuan desert are much higher than estimates based on actual evapotranspiration, lignin content, and carbon:nitrogen ratios (Elkins, Steinberger *et al.*, 1982; Whitford, Meentemeyer *et al.*, 1981; Schaefer, Steinberger *et al.*, 1985), all of which are good predictors of decomposition in more mesic environments (Meentemeyer, 1978; Schaefer, Steinberger *et al.*, 1985). As an explanation of this apparent anomaly, Whitford, Freckman *et al.* (1983) have proposed that the rapid disappearance of surface litter is primarily due to its transport into the soil by microfauna acting relatively independent of environmental constraints. This has led to a hypothesis that surface litter decomposition is under more direct biotic control in the northern Chihuahuan desert than in most other ecosystems (e.g. Whitford, Meentemeyer *et al.*, 1981; Whitford, Repass *et al.*, 1982; Whitford, 1986). Support for this view was provided by Santos, Elkins *et al.* (1984), who reported significantly higher correlations between long-term rainfall and observed decomposition patterns than with actual precipitation during the period of study.

However, other findings are inconsistent with various aspects of this hypothesis. For example, in previous studies in the northern Chihuahuan desert, Santos & Whitford (1981) and Whitford, Repass *et al.* (1982) reported decomposition rates to be greatest during the summer when temperature and precipitation inputs are highest, suggesting decomposition is not independent of environmental conditions. Strojan, Randall *et al.* (1987) demonstrated that the conclusions of Santos, Elkins *et al.* (1984) were based on results derived from a severely restrictive statistical model; following a re-analysis of the Santos, Elkins *et al.* data, they concluded that litter mass losses were better correlated to actual rainfall than with long-term precipitation patterns. In Colorado shortgrass steppe, Vossbrinck, Coleman *et al.* (1979) found significant mass loss (7·2% in 7 months) in surface litter treated with general biocides ($HgCl_2$ and $CuSO_4$) to restrict all biological

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activity. Similarly treated surface litter has been observed to lose about 15% of its original mass (June–September) in the northern Chihuahuan desert (Loring, pers. comm.).

The above studies suggest that abiotic processes may be more important contributors to decomposition than initially thought. The purpose of this paper is to present a re-interpretation of the results of earlier decomposition studies conducted in the northern Chihuahuan desert. Our hypotheses are: (1) abiotic processes contribute more to surface litter mass losses than previously thought, and (2) long-term decomposition patterns can be better described when the highly variable, short-term dynamics of abiotic processes are considered.

Analyses of abiotic decomposition factors

Precipitation effects

Whitford, Steinberger *et al.* (1986) added supplemental water (irrigation sprinklers) to a creosotebush (*Larrea tridentata*)-dominated community and followed patterns of mass loss of *Larrea* litter over a 1-year period. Results for the control (natural rainfall) and two treatments, 6·35 mm water added weekly and 25 mm water added monthly, are shown in Fig. 1. In the controls, creosotebush litter lost 12–14% of its original mass from December–July. During this same period, watered litter lost significantly more mass: from December–March, about 20% of the original biomass, followed by a period (to July) of little additional loss (Fig. 1).

Whitford, Steinberger *et al.* (1986) suggested that initial leaching of soluble compounds from the watered litter (December–March) may have resulted in decreased microbial activity, subsequently lowering mass losses from March–July. However, this hypothesis seems unlikely since: (1) they found no difference in protozoan populations and microbial biomass between the watered and unwatered sites; (2) winter temperatures and con-sistently low populations of decomposer organisms suggest low levels of biological activity during most of the December–July period; and (3) water augmentation did not reduce subsequent mass losses of the irrigated litter during the summer (July–October).
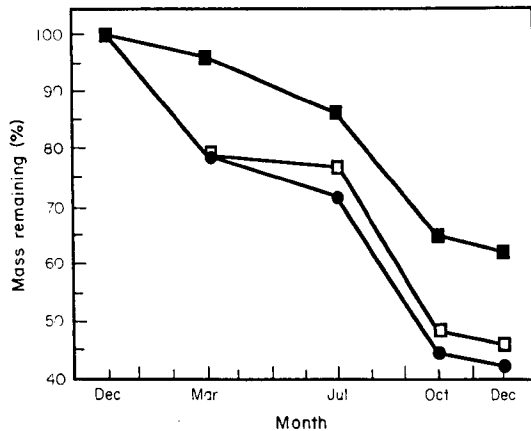
Figure 1. Surface litter mass remaining through time. No significant differences ($p < 0.05$) between the two irrigated treatment sample means at any time. Significant differences existed between controls and both treatment sample means in March, October and final December, and between controls and +6·35 mm/week sample means in July (Whitford, Steinberger *et al.*, 1986). ■, natural rain; ●, +6·35 mm/week; □, +25 mm/month.

A close examination of initial patterns of litter disappearance observed by Whitford, Steinberger *et al.* (1986) suggests a high correlation to patterns of water input. Unwatered litter lost 12–14% of its original biomass during a period when about 40 mm precipitation was received (December–July). This amounts to about 0·325% mass loss per mm rain. In comparison, the watered litter lost 20% of its initial mass during a period receiving about 72 mm water (December–March), yielding about 0·278% mass loss per mm. In fact, this latter value is a minimum estimate since sampling frequency was too low to determine if this 20% mass loss plateau was achieved earlier than the March date. In any case, these values are remarkably similar, given the limitations in data interpretation, and suggest an important direct effect of water input on initial rates of surface litter mass loss.

A similar effect of moisture availability on litter decomposition was also reported by Comanor & Staffeldt (1978) for *Artemisia tridentata* leaf litter in the Great Basin desert, Nevada. Initial mass loss rates were higher in cool, wet periods than in warm, dry periods, and correlated well with short-term precipitation input. They also found that initial rates of creosotebush litter mass loss in the northern Chihuahuan desert were related to soil moisture content (and precipitation pattern). In addition, they reported that up to 25·5% of *Larrea* leaf litter mass could be removed by leaching in laboratory experiments. When leaching and CO_2 evolution (10% of the original mass) were combined, the result (35·5%) was similar to the observed total mass loss in the field (39·1%; May–August).

Others have also found that rainfall patterns are directly correlated to litter losses. Santos & Whitford (1983) reported that precipitation accounted for 37–78% of the variability in surface litter mass losses in the White Sands National Monument gypsum dune ecosystem (northern Chihuahuan desert) and Strojan, Randall *et al.* (1987) found that rainfall pattern was highly correlated to the decomposition of various litter types in the Mojave desert. In the latter study, creosotebush leaves lost about 43% of their original mass in one year and the quantities of mass lost between sampling dates were highly correlated to the total precipitation received in the interims ($r^2 = 0·75$). Strojan, Randall *et al.* (1987) also found that actual rainfall was highly correlated to observed decomposition in the Chihuahuan desert (discussed above).

Sunlight and heat effects

In addition to water, other abiotic factors may directly affect litter mass losses. Pauli (1964) was among the first to note the degradation of complex organic molecules in litter (such as lignins) is enhanced by high radiation intensity, high temperatures, and frequent wetting–drying cycles characteristic of the northern Chihuahuan desert. Surface soil temperatures in the summer may exceed 60–65°C (Whitford & Ettershank, 1975) and convection storms are frequent from July through October. These conditions might contribute to the deterioration of exposed creosotebush litter, which is approximately 9·5–10·63% lignin by dry weight (Elkins, Steinberger *et al.*, 1982; Schaefer, Steinberger *et al.*, 1985).

Although photodegradation of recalcitrant organic compounds has not received much attention in the ecological literature, there are at least two other fields in which this phenomenon has been examined: (1) photodegradation of dissolved humic substances in aquatic systems, and (2) photoreactivity of lignins leading to degradation of paper products. In the former, Zafiriou, Joussot-Dubien *et al.* (1984) showed that photo-chemical reactions contribute to the degradation of dissolved humic substances and Frimmel & Bauer (1987) found that ultraviolet radiation produced significant bleaching of humic compounds coupled with a loss of organic carbon. Zepp, Baughman *et al.* (1981) further report on the photochemical properties of other humic substances. In the field of paper quality analysis, discoloration of paper products when exposed to ultraviolet light is a result of photochemically induced degradation of lignins (Lewis & Fronmuller, 1945). Subsequent studies have identified photochemically reactive sites on lignin and related

compounds and elucidated the mechanisms of this degradation (Leary, 1968; Lin & Kringstad, 1970; Gierer & Lin, 1972; Castellan, Vanucci et al., 1987).

As previously discussed, Whitford, Steinberger et al. (1986) found that watered litter lost about 20% of its original mass from December–March with no further losses from March–July. This indicates the additional 30% loss of watered litter observed from July through October was probably not due to leaching. However, photochemical degradation of reactive compounds could account for a substantial portion of this total since lignins comprise about 10% of the original litter mass (Elkins, Steinberger et al., 1982; Schaefer, Steinberger et al., 1985). Loring's (pers. comm.) observations of about 15% mass loss of biocide-treated litter (July–September) is about half that observed by Whitford, Steinberger et al., (1986) (July–October). The litter used in Loring's study was initially treated by soaking in aqueous solution so much of its soluble content was probably removed before being placed in the field. This strongly suggests that abiotic processes other than leaching could significantly contribute to the observed mass losses in both studies.

It is clear from the above that photochemically induced degradation of recalcitrant compounds may be an additional mechanism driving decomposition of exposed litter in extreme environments such as the northern Chihuahuan desert. Although direct observations supporting this hypothesis are limited, Schaefer, Steinberger et al. (1985) found that surface litter loss rates in this system were *inversely* proportional to lignin content, further suggesting the importance of lignin degradation to observed patterns of mass loss.

Interactions of abiotic effects

It is likely that abiotic mechanisms also interact to further affect decomposition. Fowler & Whitford (1980) noted slower mass loss rates in fresh creosotebush litter than in senescent litter when rainfall was low; there were no differences when rainfall increased. They suggested younger litter contained soluble compounds that required a relatively large amount of water to dissolve, while older material readily lost mass with little precipitation, due to the cumulative effects of previous photochemical deterioration or changes in chemical structure resulting from prior losses of soluble compounds. In essence, weathered litter is probably more structurally fragile, easily fragmented by the physical action of rain. On the other hand, fresh litter has more structural integrity and loses mass primarily as the result of leaching or fragmentation resulting from the more vigorous action of heavier rainfall.

Conclusions

Biological activity has been hypothesized as the major factor driving mass losses of surface litter in the northern Chihuahuan desert (Whitford, 1986) and is clearly a principal component of decomposition processes elsewhere (Swift, Heal et al., 1979; Seastedt, 1984). However, abiotic mechanisms may also be important: leaching may remove 25% of the initial mass of creosotebush leaf litter (Comanor & Staffeldt, 1978) and photochemical degradation of lignins could account for another 10% (Schaefer, Steinberger et al., 1985). Therefore, estimates of the importance of biological activity in decomposition should be adjusted for possible abiotic contributions. For example, Whitford, Steinberger et al. (1986) showed that total litter losses from December to October (35–50%) exceeded the maximum combined content of solubles (25%) and lignin (10%) by 0–15%. Similarly, Loring (pers. comm.) found that mass loss from untreated litter (30%) was about twice that of biocide-treated litter (15%) and Whitford, Repass et al. (1982) reported that insecticides reduced monthly litter mass losses by about 5–15% (May–October). These studies suggest that biological activity was responsible for the loss of as much as 15% of untreated litter mass.

It is difficult to quantify the relative importances of various factors to patterns of decomposition in past studies in the northern Chihuahuan desert. For example, estimates of microarthropod contributions to surface litter losses are inconsistent. Silva, MacKay *et al.* (1985) and Whitford, Bryant *et al.* (1980) found that microarthropod activity had no effect on the loss of surface litter while Whitford, Repass *et al.* (1982) and Santos & Whitford (1983) reported significantly reduced losses with insecticide treatment. The presence of termite activity further complicates interpreting study results, for although creosotebush litter is not a preferred food, Santos & Whitford (1981) reported termites remove other plant materials from litter bags; amounting to about a third of the observed losses. Unfortunately, most studies do not mention whether termite activity was present or provide an estimate of its importance (e.g. Santos, Elkins *et al.*, 1984).

In this desert, surface creosotebush litter loses about 32–65% of its mass annually (Schaefer, Steinberger *et al.*, 1985; Whitford, Steinberger *et al.*, 1986), with most of that loss in the middle to late summer when temperature, rainfall and sunlight intensity are high (Fowler & Whitford, 1980; Comanor & Staffeldt, 1978). These climatic conditions are optimal for abiotic decomposition processes and we propose abiotic mechanisms may explain as much as 25–35% of the original mass, about 50–75% of the total annual loss. This is substantially more than the 25–40% of the total litter mass loss in a semi-arid grassland which Vossbrinck, Coleman *et al.* (1979) attributed to abiotic mechanisms. However, the desert system has the more severe climate, and creosotebush leaves are likely to be qualitatively different from the blue grama grass (*Bouteloua gracilis*) used by Vossbrinck, Coleman *et al.* (1979).

It appears that the loss of surface litter in the northern Chihuahuan desert is more closely regulated by abiotic environmental variables than previously thought. Although substrate leaching is a phenomenon common to more mesic systems, the rapid photodegradation of reactive constituents (including lignins) is not. Therefore, litter mass losses are much higher than predicted based on models such as Meentemeyer (1978). In addition, the rapid loss of lignins would help to explain the extremely low organic carbon content of many soils in the northern Chihuahuan desert (Pauli, 1964). We feel that these considerations may be generally representative of warm deserts.

Addendum

In a recent study of surface grass litter decomposition in the Bolson de Mapimi (Chihuahuan Desert, northern Mexico), Montana, Ezcurra *et al.* (1988) concluded that abiotic factors were largely responsible for mass losses. In particular, the loss rate of *Sporobolus airoides* (Torr.) was constant over time, independent of temperature or moisture regimes. For both *S. airoides* and *Hilaria mutica* (Buckl.), litter C:N ratios remained constant throughout the study period (29 months) although 80 and 40% of the original masses were lost, respectively. The constant C:N ratios suggest little biological activity in spite of the significant disappearance of litter. These data and conclusions are consistent with our interpretation of factors driving mass losses of surface litter in the northern Chihuahuan desert.

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