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# THE EFFECTS OF LITTER QUALITY AND CLIMATE ON DECOMPOSITION ALONG AN ELEVATIONAL GRADIENT

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*Abstract.* The process of decomposition is controlled by both biotic and abiotic factors. While it has been widely hypothesized that litter quality and climatic conditions regulate decomposition, the relative importance of these factors appears to vary across biomes. This study examines the decomposition of native plant litter along an elevational gradient in northern Arizona to determine the influence of litter quality and climate on the rate of decomposition in semiarid communities. A litter-bag experiment was performed using needle/leaf litter from *Pinus ponderosa, Pinus edulis, Juniperus monosperma, Gutierrezia sarothrae,* and *Bouteloua gracilis.* The five litter types are representative of the dominant local vegetation and offer a range of litter qualities. The bags were placed along a gradient, running from Great Basin Desert scrub (1960 m) through a pinyon–juniper woodland (2100 m) and up into a ponderosa pine forest (2280 m). Samples were collected and analyzed over a period of 2 yr. Decomposition was closely correlated with the relative proportion of easily decomposed carbon fractions to recalcitrant fractions for the first year. Litter from *G. sarothrae* and *B. gracilis* contained relatively low levels of lignin and high levels of cellulose and carbohydrates, and these litter types exhibited significantly faster rates of decay than the highly lignified pine and juniper litter. The order of the relative rates of decomposition was *G. sarothrae* $\gg$ *B. gracilis* $>$ *J. monosperma* $>$ *P. ponderosa* $=$ *P. edulis.* There was no correlation between initial litter nitrogen content and the rate of decomposition, suggesting that decomposition is limited by carbon substrates rather than by nutrient content. Decomposition rates were significantly greater at the upper elevation sites, which were colder and wetter. Evidence strongly suggests that decomposition is limited by moisture in these ecosystems. Warmer temperatures resulting from climate change may not increase the rate of decomposition in the Southwest unless accompanied by increases in available moisture.

*Key words:* Bouteloua gracilis; *carbon;* Gutierrezia sarothrae; Juniperus monosperma; *lignin; mass loss; nitrogen;* Pinus edulis; Pinus ponderosa.

## INTRODUCTION

Current general circulation models project that the temperature of the earth's atmosphere will increase by 1°C in the next 35 yr (Mitchell et al. 1990, Houghton et al. 1992, IPCC 1996), altering global climate patterns and hence impacting many ecosystem processes. These large-scale changes in climate will have a significant impact on the carbon cycle. As a key component of the carbon cycle, decomposition rates will undoubtedly be altered, with the magnitude of these changes being closely related to the degree of climate change and the specific soil and vegetative factors (Berg et al. 1990, Anderson 1991, Klopatek et al. 1992).

Litter decomposition rates are closely correlated with environmental factors and litter quality. Litter quality defines how beneficial the litter is to the microbial community as an energy or nutrient source. Although litter quality invariably refers to the chemical constituents, it has been described in several ways. Litter nutrient concentration (Millar et al. 1948, Merrill and Cowling 1966, Berg and Staaf 1980, Schlesinger and Hasey 1981, Gallardo and Merino 1993, Berg et al. 1996) and the concentration of carbon fractions (e.g., lignin) (Fogel and Cromack 1977, Meentemeyer 1978, Stohlgren 1988) have been identified as indicators of litter quality due to their influence on microbial activity and litter decay rates. The ratio between carbon (or carbon fractions) and nutrients is another measure of litter quality (Melillo et al 1982). Since high nutrient concentration in relation to stored energy (low carbon : nutrient ratio) promotes a faster rate of decomposition (Berg et al. 1982*b*), carbon : nitrogen and lignin : nitrogen ratios are widely used as litter quality variables (Melillo et al. 1982, Blair 1988, Taylor et al. 1989, Harmon et al. 1990, Parton et al. 1994).

Many decomposition studies have identified the lignin concentration and the lignin : nitrogen ratio as the most reliable predictors of decomposition rates. A number of widely used terrestrial ecosystem simulation models have been developed that use the lignin : nitro-

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gen ratio as a key parameter governing litter decomposition rates, for example BIOME-BGC (Running and Hunt 1993) and CENTURY (Parton et al. 1994). Yet there is still no universally accepted litter-quality variable. For example, in arid regions these traditional litter-quality variables appear to be inapplicable. Schaefer et al. (1985) and Cepeda-Pizarro and Whitford (1989) found that percentage of lignin, lignin : nitrogen ratio, and carbon : nitrogen ratio failed to correlate with mass loss rates for native litter.

The failure of litter-quality variables to predict decay rates in extreme environments exemplifies the importance of environmental factors. Aerts (1997) depicts the factors controlling litter decomposition as a triangular relationship with leaf litter chemistry and climate. Theoretically, litter quality controls the potential rate of decomposition only as long as climatic and edaphic factors are held constant (Swift et al. 1979). As temperature and moisture availability regulate many ecosystem functions, including microbial activity and nutrient storage, they are considered the most critical driving forces in ecosystems, and to have the greatest control over decomposition (Swift et al. 1979, Waring and Schlesinger 1985). In fact, when predicting large-scale decomposition patterns, litter quality may explain only a small fraction of the decomposition rate, with much of the variation explained by climate (Ryan et al. 1990, Berg et al. 1993*a*).

The effect of temperature and moisture on decomposition varies throughout different biomes according to the litter quality of the native species and the severity of the climate (Berg et al. 1990, 1993*b*). Few decomposition studies have been performed in situ with the purpose of determining the effect of differences or changes in climate. The most relevant studies have analyzed differences in decomposition rates of native litter types along climatic gradients. Studies by Berg and others analyzing differences in decomposition rates along climatic gradients in the coniferous forests of eastern Europe confirmed that increasing both temperature and moisture increased decomposition rates (Berg et al. 1990, 1993*a*, *b*). deCatanzaro and Kimmins (1985) placed native conifer and broadleaf litters along a moisture gradient in a North American mixed conifer forest, but found no differences in decomposition rates at any of the climatically different sites. Similarly, in desert ecosystems, Cepeda-Pizarro and Whitford (1989) and Steinberger et al. (1990) found no significant correlations between moisture and mass loss rates at their sites along moisture gradients in the United States and Israel, respectively. Conversely, in an arid to semiarid system, Amundson et al. (1989) found differences in microbial activity and litter decomposition along a moisture gradient in Nevada. They found that microbial activity (measured as $CO_2$ evolution) was greatest at the upper, more mesic sites and that litter mass loss was correlated with precipitation events. It is apparent from these papers that the climatic factors that are most limiting to decomposition are not uniform and that there is some doubt as to the effect that directional climate change will have on decomposition in many regions of the world.

It is apparent that in arid and semiarid lands the pattern of decomposition is complicated by the lack of moisture and often by extreme soil temperatures. Meentemeyer's (1978) regional-scale decomposition model, using percentage of lignin as a litter-quality variable as well as actual evapotranspiration, worked well for most of North America but seriously underestimated decomposition rates in the southwestern United States. In these arid lands, abiotic or physical weathering of litter is important, and the structure of the decomposer community is different than in mesic ecosystems (Whitford et al. 1981). The weathering of litter by precipitation (or runoff), high temperatures, radiation, and wind cause more noticeable fragmentation and loss of litter than in mesic systems (Schaefer et al. 1985, Whitford et al. 1986). Additionally, the role of microarthropods is apparently enhanced, and decomposition by fungi and bacteria is isolated to periods of high moisture (Santos and Whitford 1981, Parker et al. 1984). Microarthropods graze on microbes and fungi, fragment litter, and move it below ground. These abiotic and biotic factors combine to increase decomposition rates beyond predicted values based on controlling factors typical of more mesic ecosystems. The explicit differences in the decomposition process between arid and mesic regions make the prediction of decomposition rates over a broad scale difficult. Thus, we wanted to determine the factors that control decomposition in these semiarid systems while establishing possible linkages between arid and mesic systems.

In this study we examined how litter quality and climate influenced the decomposition of plant litter across a major climatic gradient in northern Arizona. Our first objective was to determine which litter-quality variables correlate with mass loss rates to predict decomposition rates of the dominant regional species. Our second objective was to determine which climatic conditions most significantly affect decomposition in this region. A climate-change scenario was mimicked by moving litter samples among sites along an elevational/climatic gradient. Differences in decomposition rates among sites should be directly attributable to differences in climatic regimes.

## MATERIALS AND METHODS

### *Study area*

We established a litter decomposition experiment along an elevational gradient in the Deadman's Wash study area of northern Arizona. Deadman's Wash is located in the Coconino National Forest, due north of Flagstaff, Arizona, on the leeward side of the San Francisco Mountains. We identified five sites covering a 7-km transition zone from Great Basin Desert scrub

TABLE 1. A general description of the five study sites and the vegetation changes across the elevational gradient.

Site 1—Great Basin Desert scrub (DS)
Elevation 1960 m (6430 feet); slope 2.3%
Dominant vegetation: *Eurotia lanata* (winter-fat), *Bouteloua gracilis* (blue grama)
Site 2—Transition zone between Great Basin Desert scrub and pinyon–juniper woodland (DS-PJ)
Elevation 2018 m (6620 feet); slope 2.0%
Dominant vegetation: *Juniperus monosperma* (one-seeded juniper), *Gutierrezia sarothrae* (snakeweed), *Bouteloua gracilis*
Site 3—Pinyon–juniper woodland (PJ)
Elevation 2094 m (6870 feet); slope 4.2%
Dominant vegetation: *Pinus edulis* (pinyon pine), *Juniperus monosperma, Bouteloua gracilis*
Site 4—Transition zone between pinyon–juniper woodland and ponderosa pine forest (PJ-PP)
Elevation 2222 m (7290 feet); slope 4.3%
Dominant vegetation: *Pinus edulis, Juniperus monosperma, Pinus ponderosa* (ponderosa pine), *Poa fendleriana* (mutton grass), *Bouteloua gracilis*
Site 5—Ponderosa pine forest (PP)
Elevation 2277 m (7470 feet); slope 5.3%
Dominant vegetation: *Pinus ponderosa, Poa fendleriana, Muhlenbergia montanus* (mountain muhly)

through pinyon–juniper woodlands and into ponderosa pine forest (Table 1). Study sites were situated in each of these three communities and in the transition zones (ecotones) between the Great Basin Desert shrubsteppe and the pinyon–juniper woodland and between the pinyon–juniper woodland and the ponderosa pine forest. Each site consisted of a randomly selected 1-ha plot within the preselected community type, which was subdivided into four quadrants. The five sites were all located within one nearly 10 000-ha grazing allotment and were fenced in order to prevent disturbance from livestock grazing. All sites were located so that geologic, topographic, and edaphic differences were minimized. The sites ranged in aspect from 20 to 130°, with slopes from 2 to 5%. The soils at all sites were derived from volcanic material and are classified as Typic Argiborolls at the upper elevations and grading through Aridic Argiustolls and into Haplustolls at the lower elevations. The soils are all silty clay loams and are slightly basic to slightly acidic.

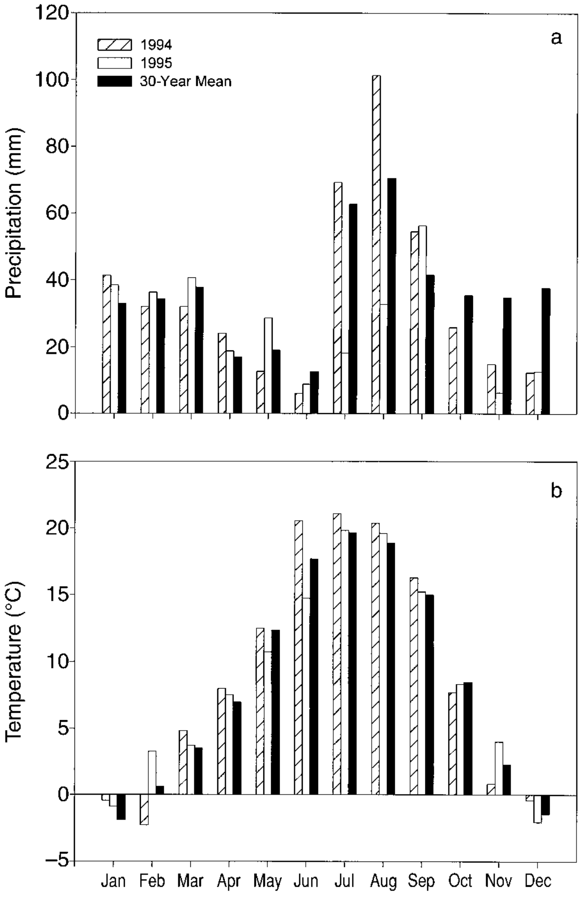

FIG. 1. Monthly averages of (a) precipitation and (b) temperature over the study period (1994, 1995) and 30-yr averages. Both precipitation and temperature measurements were taken at Sunset Crater National Monument, ~15 km from the study area.

Ecosystem processes in this semiarid region are strongly influenced by a bimodal pattern of precipitation, and by cold winters and hot summers (Fig. 1). Data from a nearby climatological station (Fig. 1) were used to generate the respective temperature and precipitation regimes for the individual sites (Fig. 2). The lower and upper sites differ with mean annual temperatures of 8.5 and 5.5°C and mean annual precipitation of 320 to 530 mm, respectively, with a uniform gradation across the sites between them. Thus, our study differed from others examining altitudinal effects on decomposition (e.g., Schinner 1982, deCatanzaro and Kimmins 1985, Amundson et al. 1989) in that it examined decomposition in communities going from dry and hot to wet and cold and the ecotones between them.

### *Experimental design*

We designed a litter-bag experiment using the litter of the dominant species from each zone. Abscising leaf litter was collected from *Pinus ponderosa* Lawson. (ponderosa pine), *Pinus edulis* Engelm. (pinyon pine), *Juniperus monosperma* (Engelm.) Sarg. (one-seeded juniper), and *Bouteloua gracilis* (H.B.K.) Lag. (blue grama grass) (Kearney and Peebles 1960). Dead leaves and stems were collected from *Gutierrezia sarothrae*

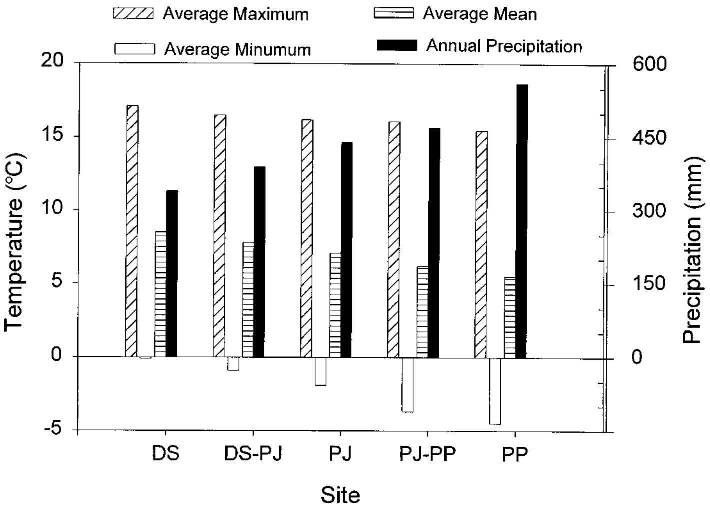

FIG. 2. Thirty-year average annual mean, maximum, and minimum temperatures and precipitation data for the five field sites as predicted with a microclimate model (data from Klopatek et al. 1998). DS = desert scrub, DS-PJ = desert scrub/pinyon–juniper woodland transition zone, PJ = pinyon–juniper woodland, PJ-PP = pinyon–juniper woodland/ponderosa pine transition zone, PP = ponderosa pine forest.

(Pursh) Britt. & Rusby. (snakeweed) (Kearney and Peebles 1960) in the fall, when growth had ceased. Each litter type was separated from any foreign material and thoroughly mixed to ensure the purity and homogeneity of the samples. We constructed 20 × 20 cm litter bags using 55-μm mesh cloth on the bottom and 1-mm mesh cloth on the top (LIDET 1995). The different mesh sizes allow access by invertebrate decomposers through the larger mesh on top without losing any part of the sample from the bottom. Ten grams of air-dried litter was added to each bag and the resulting mass was recorded. The bags were sealed with stainless steel staples and labeled with aluminum tags.

We placed 36 litter bags of each species at their resident sites and the adjacent sites. Bags containing litter from *Pinus edulis* (PIED), *Juniperus monosperma* (JUMO), and *Bouteloua gracilis* (BOGR) were placed at all five sites. *Gutierrezia sarothrae* (GUSA) litter was placed at the lower three sites (DS, DS-PJ, PJ) and *Pinus ponderosa* (PIPO) litter was placed at the upper three sites (PJ, PJ-PP, PP). We placed the bags in a randomly selected noncanopy areas (interspaces) in each quadrant at each site in order to minimize intrasite differences. The bags were anchored to the soil with wire and covered with 2.5-cm mesh nylon netting to prevent movement. Four replicates of each litter type from each site were collected nine times over a 24-mo period. Thus, a total of 864 litter bags were placed in the study area for this experiment. At the time of collection, bags were transported in separate plastic bags in order to minimize loss. The bags were kept in a ice chest to minimize decomposition during transport, and were oven-dried immediately upon return.

### *Laboratory analysis*

The litter bags were placed in a drying oven at 65°C for a minimum of 12 h or until thoroughly dried, removed from the oven, and left at room temperature for 24 h to allow them to equilibrate. We then weighed the samples to determine mass loss. Samples were ground through a 20-mesh sieve in a Wiley mill and analyzed for ash content, carbon, and nitrogen.

We determined the ash content of the litter samples using dry ignition. Moisture content was determined from a 0.5-g sample dried for 24 h at 95°C. The sample was then placed in a muffle furnace for 4 h at 500°C (Allen 1989). We used the ash content as a correction factor for litter contaminated by mineral soil (Blair 1988). Carbon and nitrogen values were determined using a Perkin-Elmer CHNS-O analyzer (Norwalk, Connecticut). We verified carbon values by calculating 48% of the ash-free values (Schlesinger 1977). Phosphorus values were determined with a tri-acid wet digestion technique (W. Stock, *unpublished manuscript*).

In addition, subsamples of the initial litter samples for lignin, cellulose, and carbohydrates were analyzed by the USDA Forest Products Laboratory (Madison, Wisconsin). Klaison lignin was determined gravimetrically after digestion with 72% $H_2SO_4$ for 1 h at 30°C, followed by hydrolysis with 4% $H_2SO_4$ for 1 h at 121°C (Effland 1977). Carbohydrate content was determined by anion exchange high-performance chromatography using pulsed amperometric detection.

### *Statistical analysis*

The annual decomposition constant $k$ was calculated according to the formula proposed by Olson (1963):

$$\ln(x_0/x_t) = kt$$

where $x_0$ is the original mass of the litter, $x_t$ is the mass remaining at time $t$, and $t$ is the time in years. The $k$ values were calculated for both the first and second years for the individual species at each site. Linear regressions of the $k$ values vs. yearly precipitation were performed, and $t$ tests were used to determine the statistical differences among the slopes of the regression lines.

Mass loss data were analyzed using analysis of vari-

TABLE 2. The initial litter chemistry of *Bouteloua gracilis, Juniperus monosperma, Pinus edulis, Pinus ponderosa,* and *Gutierrezia sarothrae,* expressed as potential litter-quality variables.

| | Litter-quality variables | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | % N | % P | C:N | C:P | N:P | % lignin | Lignin : N | Lignin : carb. | % cellulose |
| *Bouteloua gracilis* | 0.539 | 0.041 | 72.02 | 948.8 | 13.2 | 20.2 | 37.5 | 0.36 | 31.6 |
| *Juniperus monosperma* | 0.915 | 0.078 | 54.93 | 647.4 | 11.8 | 41.4 | 45.2 | 1.40 | 16.8 |
| *Pinus edulis* | 0.590 | 0.172 | 84.39 | 288.7 | 3.4 | 45.5 | 77.1 | 1.44 | 16.6 |
| *Pinus ponderosa* | 0.715 | 0.064 | 69.41 | 777.4 | 11.2 | 43.7 | 61.2 | 1.24 | 19.5 |
| *Gutierrezia sarothrae* | 0.603 | 0.029 | 78.31 | 1615.4 | 20.6 | 30.5 | 50.6 | 0.69 | 25.4 |

ance procedures and Tukey's studentized range test ($\alpha = 0.05$) with a SAS statistical program (SAS Institute 1989). Stepwise regressions were performed to determine correlations between mass loss and litter quality and/or climatic factors. Models of mass loss were constructed using a SAS multiple linear regression program. Both simple linear regression and power models (Melillo et al. 1982) were tested.

## RESULTS

### *Initial litter chemistry*

Results of the chemical analyses of the initial litter samples are shown in Table 2. The three woody species, *P. ponderosa*, *P. edulis,* and *J. monosperma,* had high levels of lignin in their needles (scales). Typical of grass species, *B. gracilis* had the lowest lignin and the highest cellulose contents. Nitrogen concentration was the only tested variable for which some clear distinctions could be made among the *P. ponderosa, P. edulis,* and *J. monosperma* litters.

The values for initial litter chemistry were tested for their usefulness as litter-quality variables. When sorting the species from high to low litter quality, each of the potential litter-quality variables classified the litter types differently. *P. edulis* was an exception, having the poorest litter quality according to all of the variables except percentage of cellulose. Values for *G. sarothrae* were generally intermediate among the litter types. The other litter types displayed more variation in relation to one other. *B. gracilis* had the lowest nitrogen concentration (low litter quality) but the most favorable litter quality relative to several other variables (e.g., percentage lignin, lignin : nitrogen ratio). *J. monosperma* had the highest litter quality according to nitrogen concentration and carbon : nitrogen ratio. However, when evaluating the other variables, the litter quality of one-seeded juniper diminishes compared to the other litter types. Since each of the litter-quality variables classifies the litter types differently in relation to each other, there exists a range of possibilities for utilizing litter quality as a predictor of mass loss.

### *Mass loss*

Leaf litter decomposition appears to follow an exponential decay pattern for *B. gracilis* and a linear pattern for the other species (Fig. 3). However, these patterns are complex due to the bimodal pattern of precipitation, which resulted in distinct seasonal pulses. The greatest rate of decay occurred during the summer months (approximately from day 200 to 300), when temperatures were high and ample moisture was provided by the summer monsoonal precipitation (Fig. 1). There was also a high rate of decay during the autumn, with frequent periods of wetting and drying (Amato et al. 1983). Little or no decomposition occurred during late spring/early summer, when there was typically little available moisture. Decomposition continued during the winter months despite mean air temperatures below 0°C. This can be attributed to high levels of soil moisture, to insulation with snow cover (Waring and Schlesinger 1985), and to daytime temperatures that are often above freezing.

*Gutierrezia sarothrae* and *B. gracilis* litter decomposed significantly faster ($\alpha = 0.05$) than litter from the three woody species (Fig. 4, Table 3). Additionally, *G. sarothrae* decomposed significantly more rapidly than *B. gracilis.* There were no significant differences among the decomposition rates of *J. monosperma, P. ponderosa, and P. edulis.* The order of decomposition rates after 12 mo was *G. sarothrae* $\gg$ *B. gracilis* $>$ *J. monosperma* $>$ *P. ponderosa* $>$ *P. edulis*; this relationship was apparent at each of the earlier collection dates and held for the pooled data as well as the mass loss results at each individual site. Although none of the differences in cumulative mass loss was statistically significant early in the study, the trends were clear (Fig. 3). The decomposition constants over the final 12 mo of the study (Table 3) were not significantly different among *B. gracilis, P. ponderosa*, *P. edulis,* and *J. monosperma.* Although the cumulative mass loss of *B. gracilis* was significantly greater than that of the three tree species, the four species all decomposed at the same rate during the second year of the study.

### *Litter quality*

We examined relationships between the initial litter-quality variables and mass loss. Regression analysis using a single variable generally explained only a small portion of the variance, with none of the litter-quality variables accounting for more than 38% of the variation. The lack of a substantial relationship was assumed to be due to the climatic differences among sites.

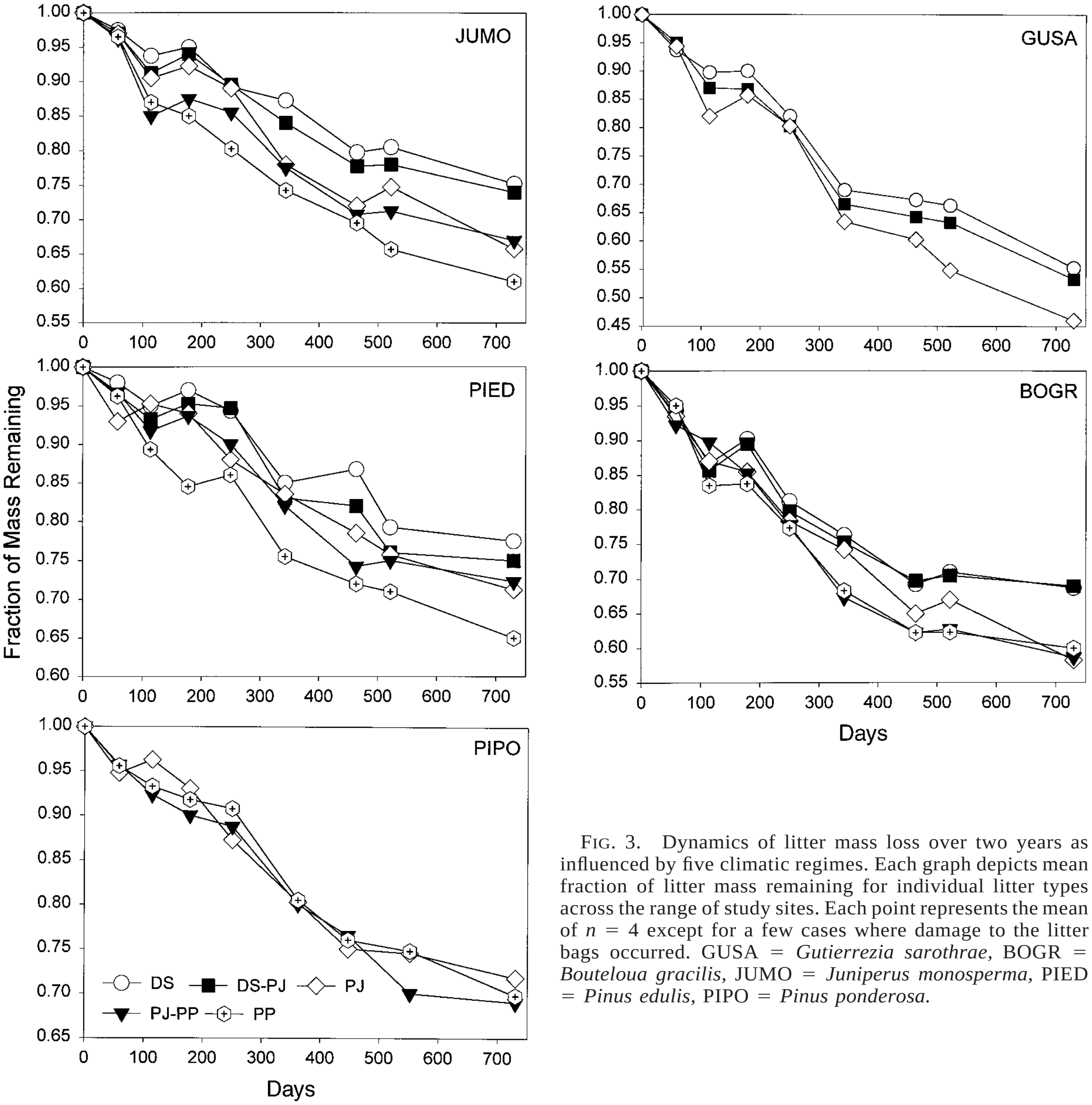

FIG. 3. Dynamics of litter mass loss over two years as influenced by five climatic regimes. Each graph depicts mean fraction of litter mass remaining for individual litter types across the range of study sites. Each point represents the mean of $n = 4$ except for a few cases where damage to the litter bags occurred. GUSA = *Gutierrezia sarothrae,* BOGR = *Bouteloua gracilis,* JUMO = *Juniperus monosperma,* PIED = *Pinus edulis,* PIPO = *Pinus ponderosa.*

We then performed a regression analysis for mass loss of species at each site to eliminate climatic differences among sites (Table 4). There was a slight improvement in the $r^2$ values, but there was no consistently best predictive variable across sites. The lignin : cellulose ratio explained the most variation at the lower three sites (DS, DS-PJ, PJ), but the lignin : carbohydrates ratio was the best overall predictor of mass loss across the climatic gradient. Only at the upper, more mesic site (PP) did nitrogen concentration exhibit any statistical correlation with of mass loss ($r^2 = 0.462$, $P < 0.01$). Although percentage of phosphorus, carbon : phosphorus ratio, and nitrogen : phosphorus ratio exhibited high $r^2$ values for the lower three sites, the relationships were negative, with greater mass loss occurring for litter types containing low levels of phosphorus. At these concentrations, we are unaware of any negative effects that phosphorus would have on the decomposition process.

The results also revealed that nitrogen does not play a large role in controlling decomposition in these systems, contrary to the findings of others (e.g., Melillo et al. 1982, Harmon et al. 1990). Nitrogen concentration produced consistently low $r^2$ values, none of which were significant. Only the lignin : nitrogen ratio was significant, but it greatly reduced the $r^2$ value of the lignin component alone.

### *Climatic influences*

Field data and model output substantiated that the temperature decreased from top to bottom and that the

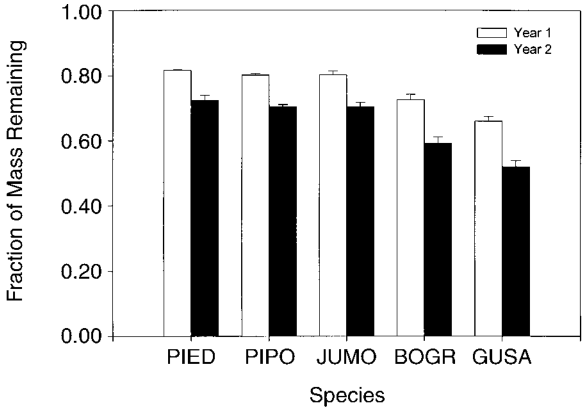

FIG. 4. Mean fraction of litter mass remaining for litter of *Pinus edulis,* (PIED), *Juniperus monosperma* (JUMO), *Pinus ponderosa* (PIPO), *Bouteloua gracilis* (BOGR), and *Gutierrezia sarothrae* (GUSA) averaged across the study sites. Error bars show +1 SE.

gradient was rather uniform across the sites (Fig. 2) (Klopatek et al. 1998). Precipitation followed a reverse gradient, increasing as altitude increased. The climatic influences were not only in evidence on a seasonal basis at each site, but had a pronounced annual effect across all sites. Annual mass loss increased with each successive site moving up the elevational gradient (Fig. 5). Decomposition rates were significantly slower at the lowest site (DS) compared to the highest site (PP). The rates for the different litter types at the middle three sites (DS-PJ, PJ, and PJ-PP) were not significantly different from the rates at either end of the gradient. Decomposition rates of all the litter types were more rapid at the mesic sites, despite the cooler temperatures.

Fig. 6 shows the combined effects of climate and litter quality on the decomposition constants (*k* values) for the five species along the gradient. Statistical analysis of slopes of the *k* values proved to be similar for *B. gracilis, J. monosperma,* and *P. edulis,* but were significantly different as compared to those for *G. sarothrae* and *P. ponderosa,* which were also different. These data support those of Hart et al. (1992), who found that *P. ponderosa* needles had exceedingly slow decomposition rates, and show that *P. edulis* exhibits even slower decomposition. Contrasting the two years of data show that the all the *k* values decreased during the second year.

### *Decomposition relationships*

In order to determine the amount of variation explained by the combination of climate and carbon quality, stepwise regression was performed on the pooled data. We pooled only the mass loss results for *P. edulis, J. monosperma,* and *B. gracilis* because all of these litter types were placed at all five locations along the gradient. We added the model estimates of temperature and moisture to account for differences among sites. Percentage of lignin explained the most variance among litter-quality variables. Precipitation was the climate variable most closely associated with differences in decay rates among sites. We used these variables to produce the following regression model:

$$\begin{aligned}&\text{Percentage mass loss (after 12 mo)}\\&\quad = -0.8208 - 0.0045(\text{lignin})\\&\qquad + 0.1977(\log[\text{precipitation}])\end{aligned}$$

($r^2 = 0.922$, $P < 0.0001$), where lignin is expressed as a percentage of total carbon and precipitation is measured in millimeters per year.

We also examined the combined mass lost after 2 yr and arrived at the following regression equation:

$$\begin{aligned}&\text{Percentage mass loss (after 24 mo)}\\&\quad = 0.2344 - 0.0045(\text{lignin}) + 0.0006(\text{precipitation})\end{aligned}$$

($r^2 = 0.681$, $P < 0.001$).

In order to determine whether litter decomposition occurs in a two-stage process, we evaluated the mass loss only during the second year. There were no significant relationships among any of the proposed litter-quality and climate variables and mass loss during the second year. The variables together accounted for no more than 15% of the variability. We also tested the power model proposed by Melillo et al. (1982), but this failed to increase the correlation coefficient for either period.

## DISCUSSION

Our findings support the idea that decomposition is controlled to some degree by initial litter chemistry, as proposed in the model of Currie and Aber (1997). We determined lignin content to be the best predictor of the overall decomposition rate. Litter containing high lignin concentrations decomposed significantly more slowly than did litter low in lignin. Litter high in lignin not only contains a large amount of decay-resistant carbon material, but also has a relatively small proportion of the easily decomposed substrates (i.e., cellulose, carbohydrates). *Bouteloua gracilis* and *G. sarothrae* decompose more rapidly than the three woody species due to more favorable proportions of all their carbon constituents.

Litter types with favorable initial chemical constit-

TABLE 3. Rates of decay (*k* values) for five litter types over the first and the second year.

| Species | *k* value<br>First year | <br>Second year |
|---|---|---|
| *Gutierrezia sarothrae* | $-0.4159^{a}$ | $-0.2508^{a}$ |
| *Bouteloua gracilis* | $-0.3365^{b}$ | $-0.1283^{b}$ |
| *Juniperus monosperma* | $-0.2237^{c}$ | $-0.1456^{b}$ |
| *Pinus edulis* | $-0.1982^{c}$ | $-0.1509^{b}$ |
| *Pinus ponderosa* | $-0.2205^{c}$ | $-0.1339^{b}$ |

*Note*: Different superscript letters within columns indicate significant differences resulting from Tukey's test.

TABLE 4. Coefficient of variation determined through regression analysis between the proposed litter-quality variables and mass loss for the species present at each of the five sites.

| | Site | | | | |
|---|---|---|---|---|---|
| Predictor | DS | DS-PJ | PJ | PJ-PP | PP |
| % lignin | 0.316* | 0.811** | 0.445** | 0.472** | 0.062 |
| % cellulose | 0.306* | 0.817*** | 0.356** | 0.404* | 0.022* |
| % carbohydrates | 0.267* | 0.788*** | 0.317* | 0.374* | 0.032 |
| % nitrogen | 0.122 | 0.310 | 0.097 | 0.034 | 0.462 |
| % phosphorus | 0.522** | 0.607*** | 0.348** | 0.245 | 0.124 |
| Lignin : carbohydrates | 0.393*** | 0.860*** | 0.433** | 0.415* | 0.024 |
| Lignin : cellulose | 0.420** | 0.865*** | 0.456 | 0.437* | 0.014 |
| Carbon : nitrogen | 0.040 | 0.030 | 0.011 | 0.025 | 0.326 |
| Carbon : phosphorus | 0.849*** | 0.591* | 0.648* | 0.294* | 0.083 |
| Lignin : nitrogen | 0.135 | 0.362* | 0.258* | 0.377* | 0.000 |
| Nitrogen : phosphorus | 0.738*** | 0.509** | 0.578** | 0.241 | 0.110 |

* $P < 0.05$, **$P < 0.01$, ***$P < 0.001$; all other values are nonsignificant.

uents decomposed rapidly in the early stages of the study. When these chemical constituents were exhausted, we expected the decomposition rate to slow considerably (McClaugherty et al. 1985, Harmon et al. 1990). Alternatively, recalcitrant litter types will decompose at a more constant rate. At a later stage of decay, the recalcitrant litter types will exhibit decay rates similar to more favorable litter types, even though the rapidly decomposing litter will have greater cumulative mass loss (Berg et al. 1982*a*). After 24 mo, cumulative mass loss was greatest for *B. gracilis* and *G. sarothrae,* which are composed of a large percentage of readily decomposed carbon compounds. However, the decomposition rate of *B. gracilis,* with the highest quality litter, slowed substantially over the last 12 mo and was not significantly different than the rate for the three woody species.

Along with the changes in decay dynamics, we observed a switching of factors controlling the rate of decomposition. After 24 mo, our model explained less of the variation in decomposition than it did after 12 mo (as suggested by Harmon et al. 1990). In addition, we found little evidence to correlate with mass loss that occurred from 12 to 24 mo based on the tested independent variables. This is most likely due to a switching of the control of the decay dynamics from a

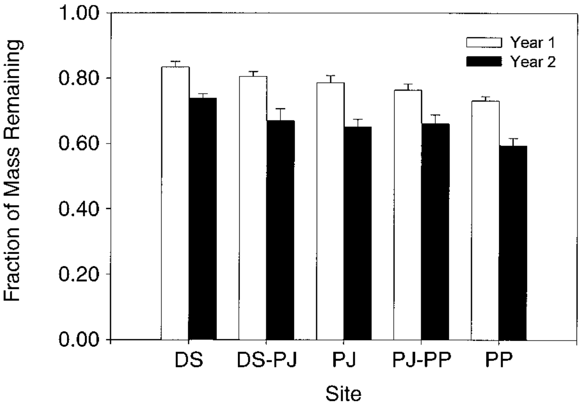

FIG. 5. Mean fraction of litter mass remaining at the five study sites. Sites are shown in order of elevation from the lowest elevation site (DS) to the highest elevation site (PP). Averages are taken from *Pinus edulis, Juniperus monosperma,* and *Bouteloua gracilis,* since these litters were placed at each site. Error bars show +1 SE.

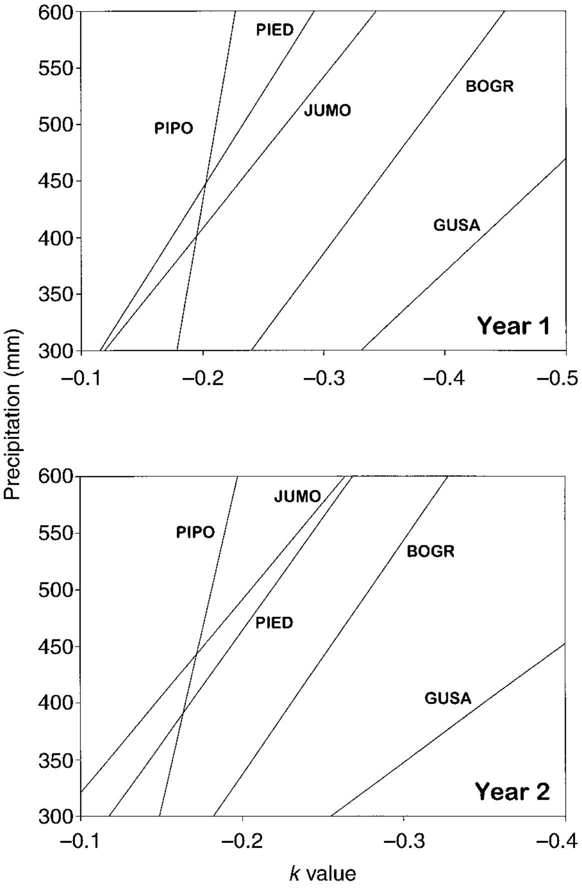

FIG. 6. Linear relationships between decay rates (*k* values) for five litter types and precipitation across the environmental gradient for year 1 (top) and year 2 (bottom) of the study: *Pinus edulis* (PIED), *Juniperus monosperma* (JUMO), *Pinus ponderosa* (PIPO), *Bouteloua gracilis* (BOGR), and *Gutierrezia sarothrae* (GUSA).

measured variable to some other attribute that we did not quantify. Gallardo and Merino (1993) determined that leaf ''toughness'' was the main controller of decomposition after 1 yr in Mediterranean ecosystems in southwest Spain. We hypothesize that litter decomposition in semiarid regions is best described by a two-stage model (Berg and Agren 1984, Harmon et al. 1990) that switches from the early stage of decay to the later stage after a majority of the labile material has been decomposed (~12 mo for *B. gracilis,* and sometimes >24 mo for *P. edulis, J. monosperma,* and *P. ponderosa*). Unlike other two-stage models that describe nutrient limitation as the factor controlling the early stage of decomposition, we propose a decay model that is controlled by the availability of easily degradable carbon compounds and periodic precipitation events. A two-stage model would follow the actual decay dynamics more closely, providing a more comprehensive description of the switching between the early and late phases of decomposition.

The correlation between initial litter chemistry and mass loss allows us to make some assumptions about the decomposer community. The applicability of a litter-quality variable indicates that bacteria and/or fungi are the dominant decomposers in these ecosystems. In mesic systems, the microbial community has a dominant role in decomposition, and litter quality is an accurate predictor of decomposition rates. In arid systems, mass loss is dominated by microinvertebrates, and litter-quality variables may not apply (Schaefer et al. 1985, Cepeda-Pizarro and Whitford 1989). While microinvertebrates are an important component of the decomposer community in these systems (Price 1973, Whitford 1987), the litter supported a substantial fungal component (K. L. Murphy, *personal observation*). Additionally, Klopatek et al. (1994) indicated that the bacterial component is dominant at all the sites in our study area and that the fungal component only becomes significant at the upper elevation site (PP). Thus, the litter types with the higher lignin values would tend to be decomposed faster at that site by lignin-degrading fungi (Berg et al. 1996). This suggests that decomposition in semiarid systems is functionally similar to that of mesic systems.

The nutrient status and climate of these semiarid systems present some important differences from mesic systems. In mesic systems, the litter nitrogen content has a significant influence on the rate of decomposition (Melillo et al. 1982, Blair 1988, Taylor et al. 1989, Harmon et al. 1990). However, pinyon–juniper communities are generally considered to be at least partially nitrogen limited (Klopatek et al. 1990), and based on their nutrient-use efficiency (R. T. Conant, *unpublished data*), it did not appear from our data that initial nitrogen was controlling the process of decomposition. This is despite the fact that total soil N was generally <0.1% in the interspaces where the litter bags were located. While nitrogen dynamics are undoubtedly important in these systems, climatic stress in the form of moisture limitation overrides the importance of nutrient limitation. During periods of high precipitation, nitrogen is added in the precipitation water or translocated from the soil into the litter and immobilized by the microbial component. We have found that this coincides with periods of increased mass loss and with the greatest amount of nitrogen immobilization (Murphy 1995). Conversely, we found that extended periods without precipitation induced nitrogen mineralization from the litter (*unpublished data*), along with a decreased rate of decomposition. This indicates that although the initial nitrogen content of the litter was not statistically correlated with mass loss in these ecosystems, it is still important in the process of decomposition, but its importance is dictated by moisture conditions and the microbial community.

Although our data suggest that the decomposer community in these systems is more similar to mesic systems than to arid systems, output from the model developed by Meentemeyer (1978) (which bases predictions on mesic ecosystems) does not fit with our data as it did for Aerts (1997). The model underestimates mass loss for each of our species under several climatic conditions, which may be due in part to the influence of microinvertebrates in the decomposition process (Santos and Whitford 1981, Whitford et al. 1981, Whitford 1987). This suggests that decomposition in our study area imitates decomposition in arid systems. However, in contrast to those patterns reported by Whitford et al. (1986), decomposition is linked closely to precipitation events and subsequent soil moisture reserves.

It is apparent that decomposition in these semiarid ecosystems is unique, taking on some of the characteristics of both arid and mesic systems. We hypothesize that the decomposition process in these regions is transitional between the two variations of the same basic process. As described earlier, similar studies analyzing the effect of different climates on decomposition have had differing results. Once again there is a disparity between arid lands, which show no differences in the rate of decomposition along moisture and temperature gradients, and mesic climates, which differ according to small increases in temperature and/or moisture. Our data from this experiment showed that the fastest rate of decomposition was observed at the higher elevations of the study area, despite the cooler temperatures. Our findings agree with those of Amundson et al. (1989), who found that microbial respiration increased at higher elevations along a semiarid gradient. This is confirmed by studies of Conant et al. (*in press*), who found that soil respiration at our sites was 2.5 times greater at the ponderosa pine site than at the desert scrub site. Litter decomposition and the associated soil microbial respiration may comprise as much as 50% of the soil respiration at the ponderosa pine sites. We conclude that in the semiarid ecosystem types that we examined, moisture limits decomposition to the extent that minor changes in temperature (1–2°C) have little, if any, effect on the rate of mass loss.

This finding has important implications for the effect of climate change on semiarid systems. In these systems, changes in temperature alone may have a minimal direct impact on carbon storage and flux. The importance of increasing temperature may be limited to the effect that temperature has on moisture availability. Locally, the effect of increasing temperature may be limited to changes in evapotranspiration and the accompanying changes in decomposition. On a regional scale, changes in precipitation patterns resulting from increased temperature will have more important consequences for decomposition and thus for carbon storage than the direct effect of temperature.

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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.

Allen, S. E. 1989. Chemical analysis of ecological materials. Second edition. Blackwell Scientific, Boston, Massachusetts, USA.

Amato, M., R. B. Jackson, J. H. A. Butler, and J. N. Ladd. 1983. Decomposition of plant material in Australian soils. II. Residual organic $^{14}$C and $^{15}$N from legume plant parts decomposing under field and laboratory conditions. Australian Journal of Soil Research **21**:563–570.

Amundson, R. G., O. A. Chadwick, and J. M. Sowers. 1989. A comparison of soil climate and biological activity along an elevational gradient in the eastern Mojave Desert. Oecologia **80**:395–400.

Anderson, J. M. 1991. The effects of climate change on decomposition processes in grassland and coniferous forests. Ecological Applications **1**:326–347.

Berg, B., and G. Agren. 1984. Decomposition of needle litter and its organic chemical components: theory and field experiments. Long-term decomposition in a Scots pine forest. III. Canadian Journal of Botany **62**:2880–2888.

Berg, B., G. Ekbohm, M. Johansson, C. McClaugherty, F. Rutigliano, and A. Virzo de Santo. 1996. Maximum decomposition limits of forest litter types: a synthesis. Canadian Journal of Botany **74**:659–672.

Berg, B., et al. 1993*a*. Litter mass loss rates in pine forests of Europe and eastern United States: some relationships with climate and litter quality. Biogeochemistry **20**:127–159.

Berg, B., K. Hannus, T. Popoff, and O. Theander. 1982*a*. Changes in organic chemical components of needle litter during decomposition. Long-term decomposition in a Scots pine forest. I. Canadian Journal of Botany **60**:1310–1319.

Berg, B., P.-E. Jansson, and C. McClaugherty. 1990. Climate variability and litter decomposition, results from a transect study. Pages 250–269 *in* Landscape—ecological impact of climate change. IOS, Washington, D.C., USA.

Berg, B., C. McClaugherty, and M.-B. Johansson. 1993*b*. Litter mass-loss rates in late stages of decomposition at some climatically and nutritionally different pine sites. Long-term decomposition in a Scots pine forest. VIII. Canadian Journal of Botany **71**:680–692.

Berg, B., and H. Staaf. 1980. Decomposition rate and chemical changes of Scots pine needle litter. II. Ecological Bulletin **32**:373–390.

Berg, B., B. Wessen, and G. Ekbohm. 1982*b*. Nitrogen level and decomposition in Scots pine litter. Oikos **38**:291–296.

Blair, J. M. 1988. Nitrogen, sulfur, and phosphorus dynamics in decomposing deciduous leaf litter in the southern Appalachians. Soil Biology and Biochemistry **20**(5):693–701.

Cepeda-Pizarro, J. G., and W. G. Whitford. 1989. Decomposition patterns of surface leaf litter of six species along a Chihuahuan Desert watershed. American Midland Naturalist **123**:319–330.

Conant, R. T., J. M. Klopatek, R. C. Malin, and C. C. Klopatek. *In press.* Carbon pools and processes along an environmental gradient in northern Arizona. Biogeochemistry.

Currie, W. S., and J. D. Aber. 1997. Modeling leaching as a decomposition process in humid montane forests. Ecology **78**:1844–1860.

deCatanzaro, J. B., and J. P. Kimmins. 1985. Changes in the weight and nutrient composition of the litter fall in three forest ecosystem types on coastal British Columbia. Canadian Journal of Botany **63**:1046–1056.

Effland, M. J. 1977. Modified procedure to determine acid insoluble lignin in wood and pulp. TAPPI (Technical Association of the Pulp and Paper Industry) **60**(10):143–144.

Fogel, R., and K. Cromack, Jr. 1977. Effect of habitat and substrate quality on Douglas-fir litter decomposition in western Oregon. Canadian Journal of Botany **55**:1632–1640.

Gallardo, A., and J. Merino. 1993. Leaf decomposition in two Mediterranean ecosystems of southwest Spain: influence of substrate quality. Ecology **74**:152–161.

Harmon, M. E., G. A. Baker, G. Spycher, and S. E. Greene. 1990. Leaf-litter decomposition in the *Picea*/*Tsuga* forests of Olympic National Park, Washington, U.S.A. Forest Ecology and Management **31**:55–66.

Hart, S. C., M. K. Firestone, and E. A. Paul. 1992. Decomposition of ponderosa pine needles in a Mediterranean-type climate. Canadian Journal of Forest Research **22**:306–314.

Houghton, J. T., B. A. Callander, and S. K. Varney. 1992. Climate change 1992: the supplementary report to the IPCC scientific assessment. Cambridge University Press, Cambridge, UK.

IPCC (Intergovernmental Panel on Climate Change). 1996. IPCC working group I: summary for policy makers. http://www.unep.ch/ipcc/ipcc95.html.

Kearney, T. H., and R. H. Peebles. 1960. Arizona flora. University of California Press, Berkeley, California, USA.

Klopatek, J. M., J. M. King, R. T. Conant, K. L. Murphy, R. A. Malin, and C. C. Klopatek. 1998. Implications of patterns of carbon pools and fluxes across a semiarid environmental gradient. Landscape and Urban Planning **39**:309–317.

Klopatek, J. M., C. C. Klopatek, and L. F. DeBano. 1990. Potential variation of nitrogen transformations in pinyon–juniper ecosystems resulting from burning. Biology and Fertility of Soils **10**:35–44.

Klopatek, C. C., K. L. Murphy, J. Rosen, J. R. Obst, and J. M. Klopatek. 1994. Preliminary results of decomposition and cellulose degradation along an environmental gradient in northern Arizona. Pages 46–53 *in* Desired future conditions for pinon–juniper ecosystems. General Technical Report RM-258. USDA Forest Service, Fort Collins, Colorado, USA.

Klopatek, C. C., E. G. O'Neill, D. W. Freckman, C. S. Bledsoe, D. C. Coleman, D. A. Crossley, Jr., E. R. Ingham, D. Parkinson, and J. M. Klopatek. 1992. The sustainable biosphere initiative: a commentary from the U.S. Soil Ecology Society. Bulletin of the Ecological Society of America **73**: 223–228.

LIDET (Long-Term Intersite Decomposition Experiment Team). 1995. Meeting the challenge of long-term, broadscale ecological experiments. Publication Number 19. LTER Network Office, Seattle, Washington, USA.

McClaugherty, C. A., J. Pastor, J. D. Aber, and J. M. Melillo. 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. Ecology **66**:266–275.

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.

Merrill, W., and E. B. Cowling. 1966. Role of nitrogen in wood deterioration: amounts and distribution of nitrogen in tree stems. Canadian Journal of Botany **44**:1555–1580.

Millar, H. C., F. B. Smith, and P. E. Brown. 1948. The rate of decomposition of various plant materials in soils. Journal of the American Society of Agronomy **20**:914–923.

Mitchell, J. F. B., S. Manabe, V. Melsheko, and T. Tokioka. 1990. Equilibrium climate change—and its implications for the future. Pages 131–172 *in* J. T. Houghton, G. J. Jenkins, and J. J. Ephraums, editors. Climate change: the IPCC scientific assessment. Cambridge University Press, Cambridge, UK.

Murphy, K. L. 1995. The effects of climate and litter quality on litter decomposition along an elevational gradient. Thesis. Department of Botany, Arizona State University, Tempe, Arizona, USA.

Olson, J. S. 1963. Energy storage and balance of producers and decomposers in ecological systems. Ecology **44**:322–331.

Parton, W. J., D. S. Ojima, C. V. Cole, and D. S. Schimel. 1994. A general model for soil organic matter dynamics: sensitivity to litter chemistry, texture, and management. Pages 147–167 *in* Quantitative modeling of soil forming processes. Soil Science Society of America Special Publication 39, Madison, Wisconsin, USA.

Price, D. W. 1973. Abundance and vertical distribution of microarthropods in surface layers of a California pine forest soil. Hilgardia **42**:121–147.

Running, S. W., and E. R. Hunt, Jr. 1993. Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global-scale models. Pages 141–158 *in* J. E. Ehleringer and C. B. Field, editors. Scaling physiological processes; leaf to globe. Academic Press, New York, New York, USA.

Santos, P. F., and W. G. Whitford. 1981. The effects of microarthropods on litter decomposition in a Chihuahuan Desert ecosystem. Ecology **62**:654–663.

SAS Institute. 1989. SAS/STAT guide for personal computers: Version 6 edition. SAS Institute, Inc., Carey, North Carolina, USA.

Schaefer, D., Y. Steinberger, and W. G. Whitford. 1985. The failure of nitrogen and lignin decomposition in a North American desert. Oecologia **65**:383–386.

Schinner, F. 1982. Soil microbial activities and litter decomposition related to altitude. Plant and Soil **65**:87–94.

Schlesinger, W. H. 1977. Carbon balance in terrestrial detritus. Annual Review of Ecological Systems **8**:51–81.

Schlesinger, W. H., and M. M. Hasey. 1981. Decomposition of chaparral shrub foliage: losses of organic and inorganic constituents from deciduous and evergreen leaves. Ecology **62**:762–774.

Steinberger, Y., A. Shmida, and W. G. Whitford. 1990. Decomposition along a rainfall gradient in the Judean desert, Israel. Oecologia **82**:322–324.

Stohlgren, T. J. 1988. Litter dynamics in two Sierran mixed conifer forests. II. Nutrient release in decomposing leaf litter. Canadian Journal of Forest Research **18**:1136–1144.

Swift, M. J., O. W. Heal, and J. M. Anderson. 1979. Decomposition in terrestrial ecosystems. University of California Press, Berkeley, California, USA.

Taylor, B. R., D. Parkinson, and W. F. J. Parsons. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. Ecology **70**:97–104.

Waring, R. H., and W. H. Schlesinger. 1985. Forest ecosystems: concepts and management. Academic Press, San Diego, California, USA.

Whitford, W. G. 1987. Soil fauna as regulators of decomposition and nitrogen cycling in pinyon–juniper ecosystems. Pages 365–368 *in* Proceedings: Pinyon–Juniper Conference General Technical Report INT-215. USDA Forest Service Intermountain Experiment Station, Ogden, Utah, USA.

Whitford, W. G., V. Meentemeyer, T. R. Seastedt, K. Cromack, Jr., D. A. Crossley, Jr., P. Santos, R. L. Todd, and J. B. Waide. 1981. Exceptions to the AET model: deserts and clear-cut forest. Ecology **62**:275–277.

Whitford, W. G., Y. Steinberger, W. MacKay, L. W. Parker, D. W. Freckman, J. A. Wallwork, and D. Weems. 1986. Rainfall and decomposition in the Chihuahuan Desert. Oecologia **68**:512–515.