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# CONTROL OF LITTER DECOMPOSITION IN A SUBALPINE MEADOW–SAGEBRUSH STEPPE ECOTONE UNDER CLIMATE CHANGE

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*Abstract.* Litter decomposition is an important component of the global carbon and nitrogen cycles. Because climate exerts strong controls over rates of litter decomposition, climate change may alter both cycles. Climate change can influence litter decomposition rates directly, or indirectly through changes in litter quality. The relative importance of climate and litter quality in controlling rates of decomposition varies across ecosystem types. Thus, ecosystem responses to climate change are not readily predictable. This study examines in situ litter decomposition rates of native plant litter of different growth forms (grass, forb, and shrub) in two microclimates (xeric and mesic). In a Colorado subalpine meadow–sagebrush steppe ecotone, a climate-warming treatment was used to determine the influence of litter quality, microclimate, and warming on the rates of decomposition. Three one-year litter bag experiments were performed using senescent leaf litter of the three growth forms from a xeric microclimate (shrub, *Artemisia tridentata*; grass, *Festuca thurberi*; forbs, *Delphinium nuttallianum, Erigeron speciosus*) and a mesic microclimate (shrub, *Pentaphylloides floribunda*; grass, *Festuca thurberi*; forbs, *Erythronium grandiflorum, Ligusticum porteri*). A reciprocal transplant litter experiment was performed in the third year to determine the direct effect of warming on litter quality and subsequent litter mass loss rates. Evidence suggests that decomposition was limited by moisture in the xeric zone and by temperature in the mesic zone. Decomposition rates were strongly correlated with the initial lignin:N ratio of the litter. The forbs had a much lower initial lignin:N ratio and, therefore, decomposed at a much higher rate than did the grasses or shrubs. In a changing climate, initial microclimate and changes in litter quality of the bulk litter produced as a result of shifts in species composition may be more important in determining rates of litter decomposition than the direct effect of warming.

*Key words: carbon cycling; climate change; growth form diversity; litter decomposition; litter quality; nitrogen cycling; sagebrush steppe; soil microclimate; species composition change; subalpine meadow.*

## Introduction

The atmospheric concentration of $CO_2$ is increasing by 1.8 μL/L each year because of anthropogenic emissions. General circulation models (GCMs) predict that this rise in $CO_2$ will increase global mean surface temperatures by 1.5°–3.5°C (Intergovernmental Panel on Climate Change [IPCC] 1995). High-altitude and high-latitude regions are expected to warm disproportionately with rising atmospheric temperatures (IPCC 1995). The temperature increase is expected to directly alter ecosystem processes such as carbon (C) and nitrogen (N) cycling (Bonan and Van Cleve 1992, Jonasson et al. 1993). Impacts may include the modification of litter quality, litter decomposition rates, and nutrient mineralization rates that control the availability and cycling of nutrients (Nadelhoffer et al. 1992, Hobbie 1996). Under increasing atmospheric concentrations of $CO_2$, litter quality may improve (Couteaux et al. 1996), decline (Körner and Miglietta 1994), or remain unchanged, depending on the system (Chu et al. 1996, Franck et al. 1997, Norby et al. 1999). Increasing atmospheric temperatures may alter plant species composition (Chapin and Shaver 1985, Wookey et al. 1993, 1994, Chapin et al. 1995, Harte and Shaw 1995) and therefore alter litter production and quality indirectly through species-specific responses (Hobbie 1992, Cornelissen 1996). Other investigators have discussed these changes for tundra (Shaver and Chapin 1991, Hobbie 1996), grassland (Kemp et al. 1994, Vinton and Burke 1995, Chu et al. 1996), and forest ecosystems (Alban and Pastor 1993, Zou et al. 1995), as the total bulk litter produced varies in litter quality and decomposability with shifts in species composition. Increasing temperatures could increase rates of litter decomposition directly by increasing microbial activity, releasing C and N from the soil organic matter (SOM; Nadelhoffer et al. 1992). Decomposition could also be hindered if litter moisture substantially declines with

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increased temperatures (Berg et al. 1993, Robinson et al. 1995).

Any change in decomposition rates will affect nutrient cycling rates. Experimental evidence indicates that N is limiting to net primary production (NPP) in many terrestrial ecosystems (Shaver and Chapin 1986, McNulty and Aber 1993, Van Der Woude et al. 1994, Shaver and Chapin 1995). Therefore, increases in the availability of N may result in increased biomass production and increased C storage (Shaver and Chapin 1986). The interacting impacts of changes in the soil moisture, precipitation and temperature will determine rates of decomposition, nutrient transformations, N availability, and subsequently NPP (Leadley and Reynolds 1992).

Litter decomposition rates have been shown to be closely correlated with litter quality characteristics and environmental parameters, such as temperature and moisture. Although litter quality refers to the litter's chemical components, it has been defined in various ways. Litter nutrient concentration (Taylor et al. 1989, Stump and Binkley 1993, Berg et al. 1996), soluble carbon fractions (Hobbie 1996), insoluble carbon fractions such as lignin (Meentemeyer 1978), the ratio of lignin to nutrient concentrations (Melillo et al. 1982, Hobbie 1996), and the concentration of phenolics (Aerts and de Caluwe 1997, Steltzer and Bowman 1998) have all been used as indices of litter quality because of their influence on microbial activity and litter decay rates. Both C:N and lignin:N ratios are often used to describe litter quality.

Litter quality characteristics are most useful in describing litter decay rates in environments where climatic and edaphic variables are held relatively constant (Swift et al. 1979). Litter quality variables exert little or secondary control on litter decay rates in ecosystems where this is not the case, particularly in extreme environments (Schaefer et al. 1985, Whitford 1986). In ecosystems where temperature and moisture availability control ecosystem functions, including microbial activity, they will exert strong controls over litter decomposition and decay rates (Swift et al. 1979). For example, patterns of litter decomposition at very dry sites have been found to be influenced more by moisture variation than by litter quality (Dyer et al. 1990, DeSanto et al. 1993, Murphy et al. 1998). A broad-scale analysis of the controls of decomposition across ecosystem types reveals that much of the variation is explained by temperature and moisture (Ryan et al. 1990, Berg et al. 1993).

The degree to which temperature and moisture control decomposition rates across ecosystem types will depend on the litter quality, the degree of climatic variability and severity (Berg et al. 1990, 1993), and edaphic factors. Many studies have attempted to address the relative controls over decomposition by analyzing the difference in decomposition of native plant litter across a climatic gradient (Amundsen et al. 1989, Cepeda-Pizarro and Whitford 1990, Berg et al. 1990, 1993, O'Lear and Seastedt 1994, Kochy and Wilson 1997, Murphy et al. 1998). Others have attempted to identify controls through experimental manipulations (Robinson et al. 1995, Hobbie 1996, Bryant et al. 1998, Williams et al. 1998). Murphy et al. (1998) found moisture to limit decomposition processes along an elevational gradient in a semiarid environment in Northern Arizona. Cepeda-Pizarro and Whitford (1990) found no significant effect of moisture across their moisture gradient in a Chihuahuan desert watershed. In contrast, Kochy and Wilson (1997) found that litter decomposition was more strongly affected by litter quality than by moisture. Because the controls over decomposition have not been uniform across gradient and experimental studies, it is unclear how directional climate change will influence rates of decomposition.

This study examines the effects of litter quality, environmental gradients (vegetation and microclimate), and infrared heating on litter decay rates in a subalpine meadow–sagebrush steppe ecotone to elucidate the relative strengths of these controls over decomposition. This work seeks to explain how increased infrared radiation (IR) comparable to that expected under global climate change influences rates of decomposition directly through soil surface temperature and moisture changes, as well as indirectly through litter quality changes. This study is unique in its exploration of the impact of warming on two different soil microclimates with differing plant assemblages and asks whether rates of decomposition are (1) controlled by soil microclimate conditions, (2) controlled by the litter quality of the dominant growth forms, (3) directly altered by increased infrared heating, and (4) indirectly altered through within-species changes in litter quality.

## METHODS

### *General description*

In simulated-warming plots in a subalpine meadow, we performed three one-year, leaf litter decomposition experiments in 1991, 1992, and 1994, in two different microclimates. Each experiment had two incubation periods (one during the growing season and one during the dormant season) and, therefore, two collection dates (at the end of the growing season and after snowmelt the following spring). Leaf litter was collected from plant representatives of the three predominate growth forms in the meadow: shrubs, forbs, and grasses. This design allowed us to explore the influence of warming, soil microclimate, and litter quality on leaf litter decomposition throughout the course of a year and across consecutive years. Additionally, in 1994, a reciprocal transplant experiment was conducted that allowed us to explore whether there were differences in leaf litter decomposition rates, depending on whether the litter was produced in the presence or absence of the warming treatment. The study site, the heating treatment, the

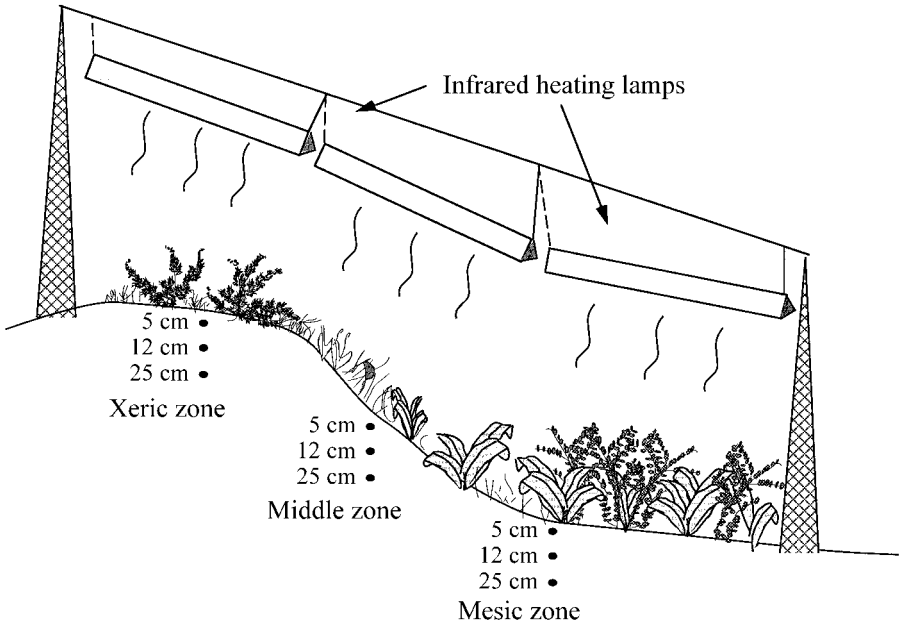


FIG. 1. Plot profile (not to scale). See *Methods: Design of heating experiment.*

microclimates, and the litter collection, incubation, and analysis methods are all described.

### *Study site*

The study site is in a subalpine meadow located at the Rocky Mountain Biological Laboratory, 10 km north of Crested Butte, Colorado, in Gunnison County (latitude 38°53′ N, longitude 107°02′ W, elevation 2920 m). Our meadow lies at the upper elevational boundary of the Great Basin Desert shrubsteppe and supports plant species from both the shrubsteppe and the subalpine meadow ecosystems. It is characterized primarily by vegetation consisting of long-lived perennial herbaceous plants and two woody shrub species. The community is diverse and supports 102 species of forbs. All vegetation in the meadow senesces by the end of the growing season, except the sagebrush (*Artemisia tridentata*), which maintains overwintering leaves.

The soil in the meadow is a well drained, deep, and rocky glacial till (Wilson 1969, Erickson and Smith 1985). Like most subalpine soils, these soils develop in regions of heavy snowfall with short growing seasons, and under grass–shrub cover (Erickson and Smith 1985). Annual precipitation at the site averages 700–750 mm/yr, of which 80% falls as snow. The snow normally melts by mid-May or the beginning of June. Rain falls in summer primarily as late afternoon showers in August.

### *Design of heating experiment*

Five control and five heated plots (3 × 10 m) containing vegetation characteristic of the meadow were located along a ridge and down the length of a slope. A slight arc in the ridge caused a north–south gradient, with the southern-most plot facing 88°E and the northern-most plot oriented at 126°E. Each of the 10 plots spanned an east–west gradient of soil moisture and vegetation, from the upper, xeric zone to the lower, mesic zone (Fig. 1). The xeric zone (at the top of the ridge) was dry and rocky, and the predominant vegetation was *Artemisia tridentata* ssp *vaseyana, Festuca thurberi* Vasey (Poaceae), and a variety of herbaceous perennials, including *Delphinium nuttallianum* Pritzel (Helleboraceae), *Erigeron speciosus* de Candolle (Asteraceae), and *Helianthella quinquenervis* Gray (Asteraceae). The transition zone was situated midway down the ridge at an angle of 20°. Here, the moisture levels were intermediate relative to the xeric and mesic zones (Harte et al. 1995). The vegetation in the middle zone was characteristic of a transition between the xeric and mesic zones, containing species from both. In the mesic zone, the slope was flat, and moisture levels were high relative to the xeric zone. This zone was characterized by the presence of herbaceous perennials, such as *Erythronium grandiflorum* Pursh (Liliaceae), *Potentilla gracilis* Douglas (Rosaceae), *Rhodiola integrifolia* Rafinesque (Crassulaceae), *Veratrum californicus* (Melanthiaceae), and the shrub, *Pentaphylloides floribunda* (Rosaceae, formerly *Potentilla fruticosa*).

For each plot, two 1.6-m electric heaters (Kalglo, Bethlehem, Pennsylvania, USA) were suspended 2.5 m above the soil surface by steel cables in the center of the xeric and mesic zones. The five heated plots received continuous (24 h/d, 365 d/yr) infrared (IR) radiation at an intensity of 15 W/m$^2$, starting on 1 January 1991. On 24 May 1993, we added an additional heater centered above the middle zone and raised the IR output of all heaters to 22 W/m$^2$ (Fig. 1). The heaters produced

no visible radiation (400–700 nm), and the downward flux of far-red wavelengths (700–800 nm) equaled $10^{-6}$ of solar input. This level of IR radiation simulated the net surface warming, due to both the direct effect of a doubling of $CO_2$ and the contribution of the major feedbacks (Intergovernmental Panel on Climate Change 1995). The additional flux above this level was intended to compensate for the lack of convective warming.

Temperature and moisture probes, multiplexers, and data loggers were installed in the summer of 1990 in all plots. Permanently placed thermocouples and calibrated gypsum blocks coupled to multiplexers and data loggers were used to collect soil temperature and moisture every two hours throughout all years. Within each plot, each zone (xeric, transition,and mesic) contained three sets of two probes (one soil temperature and one moisture) at each of three depths (5, 12, and 25 cm; Fig. 1). Harte et al. (1995) discusses the changes in soil microclimate with heating. Only data from the soil surface probe (5 cm) were used in this study.

### *Litter collection and analyses*

Plants were divided into three growth forms: shrubs, graminoids, and forbs. Litter was collected from species with significant biomass and/or specific phenological characteristics (early- or late-season growth). Because the major input of aboveground litter on an annual basis is leaf litter, only leaf litter was collected. Litter collection was separated by zone. In the shrub category, the evergreen sagebrush, *A. tridentata,* was collected in the xeric zone,and the deciduous shrubby cinquefoil, *P. floribunda,* was collected in the mesic zone. The graminoid, *Festuca thurberi* (fescue), was collected in both zones and combined. For each zone, the forb collection included an early-season species and a late-season, high-biomass species. For the xeric zone, these species included *Delphinium nuttallianum* and *Erigeron speciosus,* respectively. For the mesic zone, these species included *Erythronium grandiflorum* and *Ligusticum porteri* Coulter & Rose (Apiaceae), respectively. In the years 1991 and 1992, no late-season species were collected.

Litter was collected as it senesced. The shrub litter was collected as attached, senesced leaves. The graminoid litter was collected as standing dead blades of unknown age, but $<$18 mo. The forb litter included only browned leaves that had recently fallen to the ground. All litter material was dried at 40°C for 24 h. Litter bags (4 $\times$ 10 cm) were made using 0.7-mm nylon screen mesh.

At the end of an incubation period, litter bags were collected, gently scraped to remove surface debris, dried at 50°C, and then brushed lightly to remove remaining debris. Masses of the litter bag contents were measured. After weighing, all samples were ground, milled, and analyzed for C and *N* content using a Carlo Erba NA 1500 Nitrogen Analyzer (Carlo Erba Instruments, Milan, Italy; Giovannini et al. 1985). Subsamples of each initial litter type from each year were analyzed for the acid-insoluble C fraction (lignin), according to the modified acetyl bromide procedure (Iiyama and Wallis 1990). Results from this method have been shown to correlate with those obtained from the forests products method (Effland 1977, Ryan et al. 1990; S. E. Hobbie, *personal communication*). Litter collection dates, litter bag incubation periods, and litter bag collection dates differed slightly from year to year.

### *Effect of heating treatment and growth form on decomposition*

To assess the effect of the heating treatment and growth form on litter decomposition, litter from offsite of the treatment plots was collected in 1991 and 1992, then incubated in the heated and control plots. For the 1991 incubation, litter was collected during the growing season in 1991. Three different species of plants were collected for each zone. In the xeric zone, the litter types included *A. tridentata, F. thurberi,* and *D. nuttallianum.* In the mesic zone, the litter types included *P. floribunda, F. thurberi,* and *E. grandiflorum.* Single-species litter bags were assembled by placing 5 g litter inside and sewing them closed. Eight litter bags per species ($n$ = 3) per zone ($n$ = 2) per treatment ($n$ = 2) per replicate ($n$ = 3) were labeled and placed below the organic layer in each plot $\geq$5 cm outside the shrub canopy for a total of 288 bags. Only six plots were used in the incubations. Four litter bags were collected at the end of the growing season (63 d later), and four were collected after snowmelt at the beginning of the growing season of 1992 (367 d later). The litter bag contents were analyzed as described.

In 1992, litter of the same species was collected and bagged as in 1991. Eight replicate litter bags per species ($n$ = 3) per zone ($n$ = 2) per treatment ($n$ = 2) per replicate ($n$ = 5) were labeled and placed below the organic layer $\geq$5 cm from the shrub canopy in the plots for a total of 480 bags. All 10 plots were used for incubations. There were two collection dates: one at the end of the 1992 growing season (46 d later), and one at the beginning of the 1993 growing season (365 d later). The collected litter bags were analyzed as described.

### *Reciprocal transplants: direct vs. indirect effects*

In 1994, to differentiate the direct effect of heating on litter decomposition rates from the indirect effects (i.e., through changes in litter quality) of the source of the litter (either heated or control plots), a reciprocal transplant experiment was performed. Litter was collected by plot as it senesced and then dried at 50°C during the growing season of 1994. Four different species were collected from each zone. In the xeric zone, the litter types included *A. tridentata, F. thurberi, D. nuttallianum,* and *E. speciosus.* In the mesic zone, the litter types included *P. floribunda, F. thurberi, E. gran-*

*diflorum,* and *L. porteri.* The litter for each species from each plot was mixed: half was placed in bags and returned to the source plot, the other half was placed in bags and placed in paired heated plots. (e.g., litter from plot 1 was incubated in plots 1 and 2). Each bag contained 2 g litter. Eight replicate litter bags per species ($n = 4$) per source treatment ($n = 2$) per zone ($n = 2$) per treatment ($n = 2$) per replicate ($n = 5$) were labeled and placed under the organic layer in the plots for a total of 1280 bags. All 10 plots were used for incubations ($n = 5$). There were two collection dates: half were collected on 13 October 1994 and half on 16 June 1995 (after snowmelt the following spring). The length of the incubation periods of each species depended on its senescence date. The length of the first incubation period by species was as follows: *A. tridentata,* (32 d); *F. thurberi,* (31 d); *D. nuttallianum,* (49 d); *E. speciosus,* (21 d); *P. floribunda,* (32 d); *E. grandiflorum,* (31 d); and *L. porteri,* (39 d).

### *Statistical analyses*

A two-way ANOVA was performed for 1991 and 1992 to determine the effect of litter type and treatment on litter mass and litter N content (as a percentage initial mass or initial N remaining, respectively). For 1994, a three-way ANOVA was employed for each collection separately, using litter mass or N remaining as the dependent variable, litter type (shrub, graminoid, and forb), treatment (heated or control) and source of litter (heated or control) as the independent categorical variables. Additional analyses were performed on the 1994 data to determine the influence of the treatment and litter source on litter mass loss of individual species.

An ANCOVA was used to determine the effect of soil temperature and moisture at 5 cm on litter mass remaining. For the statistical analyses, these soil data were averaged over an incubation period by plot within a zone and used as covariates. The 5-cm data most accurately represent microclimate changes in the litter layer. The winter data (December–late March) were not used because, when temperatures were at or below freezing, the data from the probes were not reliable. With the soil temperature and moisture over the incubation period as the continuous independent variables, and litter type (shrub, graminoid, and forb) as the categorical variable, an ANCOVA was performed for each collection within each year by zone separately and by zones combined.

The effects of litter quality characteristics and growth forms on rates of decomposition were evaluated using the decay constant, *k.* The decay constant is a single variable used to describe litter mass loss over time. It was determined by fitting a single exponential decay function to each species for each treatment, followed by obtaining the slope of the least-squares regression of the natural log of the proportion of the initial mass remaining against time (Weider and Lang 1982):

$$\ln(M_t/M_0) = -kt + c$$

where $M_t$ is the mass at time $t$, $M_0$ is the initial mass, $t$ is time in days, $k$ is the slope of the regression, and $c$ is the intercept of the regression. The single exponential model may not be the best model for describing litter mass loss over time for each of the species used in this study. Other models, including the double exponential decay, asymptotic, or linear models, have been used to describe litter mass loss over time (Parsons et al. 1990, Berg et al. 1996, and Taylor et al. 1989, respectively). This model was used in order to find a single variable ($k$) to facilitate comparisons across species and treatments, not to determine the best model of temporal litter mass loss. Nonlinear regressions were also performed, but estimates of $k$ did not differ from those of the least-squares regressions.

An ANCOVA was used to determine the dependence of $k$ on specific experimental variables. Using the decay constant ($k$) as the dependent variable, litter type (shrub, graminoid, and forb) as the independent categorical variable, and litter quality as the continuous independent variable, an ANCOVA was performed for each year 1991, 1992, and 1994. A separate analysis was done for each litter quality variable, including percent C, percent N, C:N, and lignin:N ratios, by heating treatment on log-transformed data. When significant interactions existed between the categorical variables and the continuous variable (violating the assumption of homogeneity of slopes), decay constants for each litter type were separately regressed against litter quality indices.

All statistical analyses were performed using SYSTAT version 5.2.1 (SYSTAT 1992).

## RESULTS

### *Soil microclimate*

The soil microclimate was significantly influenced by the heating treatment during the snowmelt and the growing season. The snowmelt date was advanced by heating by an average of 11 d in the xeric zone and the mesic zone, over the five year period between 1991 and 1995 (Table 1; Harte et al. 1995). The largest soil temperature difference between the control and heated plots occurred during the period of snowmelt, when the heated treatment temperature obtained a mean value of $\leq$5°C higher than that of the controls and daily-averaged soil-temperature differences between adjacent control and treatment plots was as high as 12°C (Harte et al. 1995). During snowmelt, moisture levels remained at field capacity (48% of dry soil mass) until temperature increases caused evaporative loss.

During the growing season (the period from snowmelt to mid-August) the effect of the heating treatment on soil temperature and moisture was significant, but

TABLE 1. Soil microclimate of a subalpine meadow in Gunnison County, Colorado (USA).

| Year | Xeric zone | | Mesic zone | |
|---|---|---|---|---|
| | Control plots | Heated plots | Control plots | Heated plots |
| Date of snowmelt | | | | |
| 1991 | 135 | 131 | 142 | 133 |
| 1992 | 118 | 112 | 119 | 113 |
| 1993 | 145 | 132 | 150 | 135 |
| 1994 | 133 | 122 | 137 | 130 |
| 1995 | 260 | 140 | 164 | 145 |
| Soil moisture (percentage by mass) | | | | |
| 1991 | 20.7 | 18.1 | 33.7 | 32.1 |
| 1992 | 28.4 | 25.7 | 38.0 | 36.4 |
| 1993 | 18.8 | 17.3 | 29.3 | 28.6 |
| 1994 | 17.3 | 15.7 | 24.0 | 22.0 |
| 1995 | 24.1 | 21.4 | 23.7 | 21.9 |
| Soil temperature (°C) | | | | |
| 1991 | 13.8 | 14.7 | 13.0 | 13.0 |
| 1992 | 12.6 | 13.5 | 12.1 | 12.2 |
| 1993 | 13.7 | 15.1 | 12.8 | 12.8 |
| 1994 | 15.0 | 16.6 | 13.9 | 14.0 |
| 1995 | 13.7 | 14.9 | 12.7 | 12.7 |

*Note:* Soil temperature and moisture values are means of measurements taken every two hours from the soil surface (5 cm), day and night, over the period from the end of snowmelt to mid-August.

less dramatic. The treatment-averaged temperatures at 5 cm were 1.2°C higher in treatment plots, relative to the controls in the xeric zone, and 0.1°C in the mesic zone. The treatment-averaged moistures at 5 cm were 2.2% and 1.5% lower in treatment plots, relative to the control in the xeric and mesic zones, respectively.

### *Litter quality*

Initial litter chemistry varied greatly among growth forms and species (Table 2). Initial litter chemistry also varied from year to year. Generally, the primary determinant of the C:N ratios was the N, content because the C content of the litter was relatively constant (43–50%). The forbs had lower C:N ratios than the graminoids and the shrubs. *Artemisia tridentata* and *F. thurberi* had the highest mean C:N ratios (52.7 and 43.3, respectively) across all three years. The mesic zone shrub, *P. floribunda*, had a much lower mean C:N ratio (24.9). For the forbs, the C:N ratios ranged 10.7–59.9. The early season forbs, *D. nuttallianum* and *E. grandiflorum*, had the lowest C:N ratios (10.7 and 11.8, respectively), while the late season forb, *L. porteri*, had the highest (59.9).

The initial lignin concentrations (reported as percent acid-insoluble carbon) of the litter varied greatly among species (Table 2). The graminoid and late-season forbs had the highest mean lignin concentrations across years (*F. thurberi*, 35.4%; *E. speciosus*, 39.0%; and *L. porteri*, 27.3%). *Festuca thurberi* and *L. porteri* maintained high lignin:N ratios (37.1 and 36.7, respectively). The two shrubs had intermediate lignin concentrations (*A. tridentata*, 15.7%; *P. floribunda*, 18.2%), but the lignin:N ratio for *A. tridentata* was higher (17.3) than *P. floribunda* (10.3). Both early-season forbs had low lignin concentration and much lower lignin:N ratios.

### *Effect of heating treatment and growth form on decomposition*

*Litter mass loss.*—There were few treatment effects on litter mass loss, but the effect of growth form was consistently significant across all years and zones (Table 3). In the xeric zone, with all litter types combined, the treatment effect on mass loss was significant only for the second collection in 1991 (two-way ANOVA, $F = 4.8$, $P = 0.05$, df = 1, 12; Table 3) and 1994 (two-way ANOVA, $F = 9.231$, $P < 0.05$, df = 1, 228; Table 3). Snowmelt date, which depends on treatment, was a statistically significant covariate for mass loss on both dates. There was no treatment effect for the first collections of the xeric zone in any of the years. The mesic zone showed no effect of treatment on litter mass loss for either collection, except the first collection in 1994 (two-way ANOVA, $F = 8.9$, $P < 0.005$, df = 2, 164; Table 3). At that time there was also a significant litter type × treatment interaction (two-way ANOVA, $F = 3.6$, $P = 0.05$, df = 1, 164), most likely resulting from the greater litter mass loss of the forbs compared to the shrubs and graminoids.

Differences in litter mass loss among litter types were much greater than the difference in litter mass loss among heating treatments (Table 3). Within the xeric zone, at each collection in each year, the effect of litter type on mass loss was statistically significant (ANCOVA, $F = 175.5$, $P < 0.05$, df = 2, 289; Table 3). The graminoid experienced the least mass loss, and the forbs the most (Table 3). In all three years, the early-season forbs, *E. grandiflorum* and *D. nuttallianum*, lost 100% of their litter mass within the first year (Table 3). Within the mesic zone, across all three years, the pattern of litter mass loss with litter type was the same: the graminoids decomposed more slowly than the shrubs while the early-season forbs lost all litter mass by the second collection (Table 3). The late-season forbs (*Erigeron speciosus* and *L. porteri*) had less litter mass loss than did the early-season forbs (Table 3). *Erigeron speciosus* and *L. porteri* lost 64.8% and 59.1% of the initial litter by the second collection date (Table 3), whereas *D. nuttallianum* and *E. grandiflorum* both lost 100% (Table 3).

A general linear model built on the entire data set (all years, all collections) for each zone separately indicated that litter type ($F = 68.5$, df = 2, 163), mean temperature ($F = 12.1$, df = 1, 163), and mean moisture ($F = 163.5$, df = 1, 163) through the incubation explained much of the variation in litter mass loss in the mesic zone ($R^2 = 0.606$), as well as litter type ($F = 175.5$, df = 2, 253) and mean moisture ($F = 103.1$, df = 1, 253) in the xeric zone ($R^2 = 0.619$), in the absence of heating. For the years 1991 and 1992, an ANCOVA analysis for the initial

TABLE 2. Initial chemical characteristics of litter in a subalpine meadow (Gunnison County, Colorado, USA).

| Species | Growth form | Source of litter† | Nitrogen (%) | Carbon (%) | C : N | Percent acid-insoluble carbon (lignin) | Lignin : N |
|---|---|---|---|---|---|---|---|
| 1991 Xeric zone | | | | | | | |
| *Artemisia tridentata* | shrub | | 0.9 (0.0) | 48.3 (0.6) | 52.5 (0.6) | 13.1 (0.7) | 14.2 (0.2) |
| *Festuca thurberi* | graminoid | | 1.0 (0.0) | 43.3 (0.1) | 42.7 (0.3) | 34.4 (0.1) | 33.9 (0.0) |
| *Delphinium nuttalliamum* | forb | | 3.9 (0.0) | 41.9 (0.2) | 10.7 (0.2) | 9.4 (0.1) | 2.4 (0.1) |
| 1991 Mesic zone | | | | | | | |
| *Pentaphylloides floribunda* | shrub | | 1.8 (0.0) | 44.0 (0.4) | 24.4 (0.2) | 18.6 (1.0) | 10.3 (0.9) |
| *Festuca thurberi* | graminoid | | 1.0 (0.0) | 43.3 (0.1) | 42.7 (0.3) | 34.4 (0.1) | 33.9 (0.0) |
| *Erythronium grandiflorum* | forb | | 3.3 (0.5) | 39.3 (3.6) | 11.8 (0.9) | 7.6 (1.2) | 2.3 (0.5) |
| 1992 Xeric zone | | | | | | | |
| *Artemisia tridentata* | shrub | | 1.0 (0.0) | 46.4 (0.5) | 47.8 (0.4) | 15.3 (1.3) | 15.7 (0.4) |
| *Festuca thurberi* | graminoid | | 0.9 (0.0) | 40.2 (0.5) | 42.5 (0.8) | 35.6 (0.8) | 37.7 (0.1) |
| *Delphinium nuttallianum* | forb | | 2.3 (0.0) | 38.5 (0.1) | 16.6 (0.1) | 9.1 (0.2) | 3.9 (0.2) |
| 1992 Mesic zone | | | | | | | |
| *Pentaphylloides floribunda* | shrub | | 2.0 (0.0) | 42.9 (0.6) | 21.0 (0.6) | 17.4 (0.4) | 8.5 (0.5) |
| *Festuca thurberi* | graminoid | | 0.9 (0.0) | 40.2 (0.5) | 42.5 (0.8) | 35.6 (0.8) | 37.7 (0.1) |
| *Erythronium grandiflorum* | forb | | 2.7 (0.1) | 39.3 (3.6) | 14.8 (0.1) | 8.0 (0.5) | 3.0 (0.3) |
| 1994 Xeric zone | | | | | | | |
| *Artemisia tridentata* | shrub | control | 0.9* (0.0) | 49.5 (0.4) | 57.6 (1.9) | 18.8* (0.7) | 21.9* (0.4) |
| | shrub | heated | 0.9* (0.0) | 49.7 (0.2) | 53.4 (0.9) | 16.2* (0.2) | 17.4* (0.1) |
| *Festuca thurberi* | graminoid | control | 0.9 (0.0) | 41.2 (0.0) | 44.8 (0.5) | 36.5 (0.6) | 39.6 (0.3) |
| | graminoid | heated | 1.0 (0.0) | 40.9 (0.0) | 43.1 (0.5) | 35.3 (0.2) | 37.1 (0.5) |
| *Delphinium nuttallianum* | forb | control | 2.6 (0.2) | 44.2 (0.3) | 16.7 (0.0) | 8.9 (0.8) | 3.4 (0.5) |
| | forb | heated | 2.5 (0.1) | 44.5 (0.1) | 18.0 (0.0) | 8.6 (0.5) | 3.5 (0.0) |
| *Erigeron speciosus* | forb | control | 2.6 (0.4) | 45.1 (0.3) | 17.1 (3.9) | 40.6 (2.8) | 15.4 (0.5) |
| | forb | heated | 1.9 (0.2) | 44.7 (0.2) | 23.1 (1.9) | 37.3 (1.8) | 19.3 (0.3) |
| 1994 Mesic zone | | | | | | | |
| *Pentaphylloides floribunda* | shrub | control | 1.6 (0.0) | 45.6 (0.0) | 29.2 (0.0) | 18.6 (1.0) | 12.0 (0.4) |
| | shrub | heated | 1.6 (0.0) | 44.7 (0.0) | 27.6 (0.0) | 17.1 (1.3) | 10.6 (0.2) |
| *Festuca thurberi* | graminoid | control | 0.9 (0.0) | 41.2 (0.0) | 44.8 (0.5) | 36.5 (0.6) | 39.6 (0.3) |
| | graminoid | heated | 1.0 (0.0) | 40.9 (0.0) | 43.1 (0.5) | 35.3 (0.2) | 37.1 (0.5) |
| *Erythronium grandiflorum* | forb | control | 1.7 (0.2) | 40.4 (0.6) | 24.3* (2.4) | 7.4 (2.7) | 4.4 (0.1) |
| | forb | heated | 1.3 (0.1) | 40.5 (0.7) | 31.0* (2.3) | 7.5 (1.8) | 5.7 (0.1) |
| *Ligusticum porteri* | forb | control | 0.8 (0.0) | 43.2 (0.4) | 55.3 (2.8) | 29.3 (0.3) | 37.5 (0.3) |
| | forb | heated | 0.7 (0.0) | 42.2 (0.1) | 59.9 (2.3) | 25.2 (1.9) | 35.8 (0.3) |

*Notes:* Values are means (1 SE). For 1991 and 1992 values, $n = 3$. For 1994 values, $n = 5$.
* Statistically significant at $P < 0.05$ (ANOVA for initial litter quality by treatment in 1994).
† Litter source specified for 1994 only; litter for 1991 and 1992 had a common litter source, by species, for all plots.

litter mass remaining indicated that either soil surface temperature or moisture was a significant covariate for the mesic zone for the first collection, but not consistently for the second collection. In contrast, the same analysis indicated that soil surface temperature and moisture were significant covariates for the xeric zone for the second collection, but not for the first collection. In the driest year of the study, 1994, neither temperature nor moisture was a significant covariate in litter mass loss in either zone or collection. When the data from all years are combined and analyzed by zone, temperature ($F = 6.5$, df = 1, 485), moisture ($F = 244.7$, df = 1, 485) and litter type ($F = 194.4$, df = 1, 485) are significant in influencing litter mass loss ($P < 0.010$, for all variables in both zones).

For each species within each year, the regressions of the log-transformation of initial mass remaining against time were all significant ($P < 0.01$; Table 4). This was true for both the control and heated treatments. In some cases, the regression values were lower for the early-season forbs and the graminoid. Because the early-season forbs lost all their mass by the second collection, the decay constant ($k$) calculated using a single exponential decay function underestimated the actual decay rate. In contrast, the graminoid lost mass at a slower rate, and therefore the decay function represented a better fit to mass loss of *F. thurberi* ($R^2 = 0.62$, $P = 0.0010$) than *E. grandiflorum* ($R^2 = 0.42$, $P = 0.0210$; Table 4) in control plots in 1992.

ANCOVAs and stepwise linear regressions to determine characteristics of litter quality that correlate with mass loss over time showed both soluble and insoluble carbon fractions to be highly significant variables across treatments and years (Fig. 2). Only the nitrogen content of the litter was positively correlated with $k$ (Pearson $r = 0.65$, $P < 0.0001$), and it was the only litter quality index that was statistically insignificant in determining decay rates in all years, in both heated and control plots. Determining whether percent C or

TABLE 3. Percentage initial mass remaining by species in 1991, 1992, and 1994, for the xeric and mesic zones.

| Species | Growth form | Treatment | Collection 1 | Collection 2 |
|---|---|---|---|---|
| 1991 Xeric zone | | | | |
| *Artemisia tridentata* | shrub | control | 84.8 (1.0) | 45.5* (0.20) |
| | shrub | heated | 80.4 (0.9) | 40.2* (1.30) |
| *Festuca thurberi* | graminoid | control | 86.0 (0.9) | 66.1 (2.30) |
| | graminoid | heated | 84.1 (3.1) | 62.5 (1.3) |
| *Delphinium nuttallianum* | forb | control | 45.1 (5.2) | 0.0 ··· |
| | forb | heated | 46.3 (2.8) | 0.0 ··· |
| 1991 Mesic zone | | | | |
| *Pentaphylloid floribunda* | shrub | control | 52.6 (1.2) | 22.7 (0.2) |
| | shrub | heated | 50.4 (1.3) | 21.3 (1.3) |
| *Festuca thurberi* | graminoid | control | 84.2 (2.1) | 64.5 (1.8) |
| | graminoid | heated | 83.1 (2.1) | 62.9 (6.6) |
| *Erythronium grandiflorum* | forb | control | 40.9 (0.7) | 0.0 ··· |
| | forb | heated | 41.0 (7.6) | 0.0 ··· |
| 1992 Xeric zone | | | | |
| *Artemisia tridentata* | shrub | control | 72.1 (1.1) | 53.4 (0.2) |
| | shrub | heated | 73.7 (1.3) | 52.4 (1.3) |
| *Festuca thurberi* | graminoid | control | 82.4 (2.2) | 64.0 (1.8) |
| | graminoid | heated | 84.7 (1.6) | 66.0 (6.6) |
| *Delphinium nuttallianum* | forb | control | 31.6 (1.1) | 0.0 ··· |
| | forb | heated | 31.2 (0.4) | 0.0 ··· |
| 1992 Mesic zone | | | | |
| *Pentaphylloides floribunda* | shrub | control | 45.7 (3.0) | 22.4 (1.2) |
| | shrub | heated | 43.2 (1.4) | 21.0 (1.5) |
| *Festuca thurberi* | graminoid | control | 85.2 (1.5) | 65.8 (4.2) |
| | graminoid | heated | 84.6 (2.6) | 66.8 (3.9) |
| *Erythronium grandiflorum* | forb | control | 37.8* (2.8) | 0.0 ··· |
| | forb | heated | 27.4* (3.1) | 0.0 ··· |
| 1994 Xeric zone | | | | |
| *Artemisia tridentata* | shrub | control | 91.6* (1.0) | 69.5* (1.4) |
| | shrub | heated | 89.2* (0.3) | 58.6 (1.3) |
| *Festuca thurberi* | graminoid | control | 96.0 (0.4) | 74.2* (0.9) |
| | graminoid | heated | 95.3 (0.2) | 70.1 (0.8) |
| *Delphinium nuttallianum* | forb | control | 66.6 (1.0) | 0.0 ··· |
| | forb | heated | 64.1 (0.9) | 0.0 ··· |
| *Erigeron speciosus* | forb | control | 83.0 (0.4) | 38.3* (1.2) |
| | forb | heated | 82.8 (0.1) | 35.5 (0.6) |
| 1994 Mesic zone | | | | |
| *Pentaphylloides floribunda* | shrub | control | 84.5* (0.6) | 30.6* (0.9) |
| | shrub | heated | 78.2 (1.5) | 25.3 (0.6) |
| *Festuca thurberi* | graminoid | control | 94.3 (0.3) | 72.0 (0.5) |
| | graminoid | heated | 94.6 (0.5) | 71.2 (1.3) |
| *Erythronium grandiflorum* | forb | control | 67.1 (1.5) | 0.0 ··· |
| | forb | heated | 69.0 (2.7) | 0.0 ··· |
| *Ligustucum porteri* | forb | control | 78.1 (2.1) | 45.6* (1.2) |
| | forb | heated | 77.7 (3.0) | 39.7 (1.6) |

*Note:* Data are means (1 SE) in heated plots and control plots at each collection date.
* $P < 0.05$.

percent lignin was more important in determining $k$ was confounded by the highly negative correlation between $k$ and both the litter quality indexes percent C and percent lignin (Pearson $r = -0.55$, $P < 0.0001$; and $r = -0.70$, $P < 0.0001$, respectively; Fig. 2). Stepwise linear regressions identified both characteristics as highly significant in determining mass loss. In addition, litter indexes C:N and Lignin:N were highly correlated with one another (Pearson $r = 0.75$, $P < 0.0001$). Litter type was highly significant in determining the decay rates across years and treatments (Fig. 2).

*Litter nitrogen changes*.—There was no effect of treatment on net nitrogen immobilization/release, except in 1994 (Table 5). In 1994, net N immobilization was less in the heated plots, relative to the controls in both the xeric zone and the mesic zone (two-way ANOVA, $F = 13.2$, $P = 0.0007$, df = 1, 48; and two-way ANOVA, $F = 22.1$, $P < 0.0001$, df = 1, 44; respectively).

Species and litter types differed significantly in their timing and pattern of nitrogen release at each collection in all three years (Table 5). There were also differences within species across years. Most of the species showed net sequestration of N on the first collection and a greater N sequestration by the second collection (Table 5). The notable exceptions were the early-season forbs, which exhibited either no change in N content or net N loss by

TABLE 4. Decay constants, *k*, evaluated as slopes from regressions of log-transformed litter mass (proportion of initial mass remaining) against time, with regressions performed separately for each species, treatment type, and zone.

| Year | Species | Source of litter† | *N* | Control | | Heated | |
|---|---|---|---|---|---|---|---|
| | | | | $R^2$ | $k$ ($d^{-1}$) | $R^2$ | $k$ ($d^{-1}$) |
| Xeric zone | | | | | | | |
| 1991 | *Artemisia tridentata* | | 9 | 0.91 | 0.0010 | 0.90 | 0.0013 |
| | *Festuca thurberi* | | 9 | 0.95 | 0.0011 | 0.90 | 0.0013 |
| | *Delphinium nuttallianum* | | 6 | 0.90 | 0.0131 | 0.97 | 0.0125 |
| 1992 | *Artemisia tridentata* | | 15 | 0.86 | 0.0016 | 0.90 | 0.0016 |
| | *Festuca thurberi* | | 15 | 0.70 | 0.0013 | 0.90 | 0.0013 |
| | *Delphinium nuttallianum* | | 9 | 0.99 | 0.0154 | 0.99 | 0.0155 |
| 1994 | *Artemisia tridentata* | control | 15 | 0.98 | 0.0013 | 0.98 | 0.0019 |
| | | heated | 15 | 0.98 | 0.0017 | 0.98 | 0.0021 |
| | *Festuca thurberi* | control | 15 | 0.99 | 0.0011 | 0.99 | 0.0013 |
| | | heated | 15 | 0.95 | 0.0010 | 0.93 | 0.0013 |
| | *Delphinium nuttallianum* | control | 10 | 0.99 | 0.0084 | 0.99 | 0.0091 |
| | | heated | 10 | 0.93 | 0.0077 | 0.96 | 0.0088 |
| | *Erigeron speciosus* | control | 15 | 0.99 | 0.0031 | 0.99 | 0.0034 |
| | | heated | 15 | 1.00 | 0.0033 | 0.99 | 0.0040 |
| Mesic zone | | | | | | | |
| 1991 | *Pentaphylloides floribunda* | | 9 | 0.91 | 0.0037 | 0.91 | 0.0038 |
| | *Festuca thurberi* | | 9 | 0.89 | 0.0008 | 0.83 | 0.0010 |
| | *Erythronium grandiflorum* | | 6 | 0.99 | 0.0159 | 0.74 | 0.0166 |
| 1992 | *Pentaphylloides floribunda* | | 15 | 0.85 | 0.0037 | 0.85 | 0.0039 |
| | *Festuca thurberi* | | 15 | 0.62 | 0.0010 | 0.85 | 0.0011 |
| | *Erythronium grandiflorum* | | 10 | 0.42 | 0.0210 | 0.69 | 0.0227 |
| 1994 | *Pentaphylloides floribunda* | control | 15 | 1.00 | 0.0040 | 0.99 | 0.0045 |
| | | heated | 15 | 0.99 | 0.0038 | 0.99 | 0.0048 |
| | *Festuca thurberi* | control | 15 | 0.99 | 0.0012 | 0.98 | 0.0012 |
| | | heated | 15 | 0.99 | 0.0012 | 0.94 | 0.0012 |
| | *Erythronium grandiflorum* | control | 8 | 0.97 | 0.0119 | 0.99 | 0.0128 |
| | | heated | 8 | 0.99 | 0.0134 | 0.93 | 0.0156 |
| | *Ligusticum porteri* | control | 12 | 0.94 | 0.0027 | 0.95 | 0.0033 |
| | | heated | 12 | 0.93 | 0.0028 | 0.96 | 0.0033 |

† Litter source specified for 1994 only; litter for 1991 and 1992 had a common litter source, by species, for all plots.

the first collection and complete N loss by the second collection, across all three years. The graminoid and the shrubs had no net N loss over the incubations. *A. tridentata* and *F. thurberi* had the highest net N sequestration, as high as 138% and 162% above initial, respectively, by the second collection in the 1992 experiment (Table 5). Of the late-season forbs, *L. porteri* immobilized more N than it released, and *E. speciosus* had no change in N content at the time of the second collection from the beginning of the incubation.

### *Reciprocal transplants: effect of heating treatment on litter quality and decomposition*

*Litter quality.*—Only three of the species produced litter that differed in quality depending on the treatment (Table 2). *Artemisia tridentata* had significantly lower lignin concentrations in the heated plots relative to the controls (16.6% vs. 18.8%, respectively; ANOVA, $F = 13.2$, $P = 0.006$, df = 1, 8) and, therefore, lower lignin:N ratios (17.4 vs. 21.9, respectively; ANOVA, $F = 15.8$, $P = 0.004$, df = 1, 8). It also had lower C:*N* ratios (Table 2). The C:N ratio of *E. grandiflorum* was significantly higher in the heated plots (31.0 vs. 24.3; ANOVA, $F = 118.3$, $P < 0.05$, df = 1, 6), and there was a trend towards higher lignin:N (ANOVA, $F = 3.63$, $P < 0.10$, df = 1, 6). The late-season forb *L. porteri* had a C content that was significantly lower in the heated plots,plus a strong trend ($P < 0.06$) towards lower lignin. The remainder of the species showed no differences in initial litter chemical characteristics due to the treatment of the source plot.

*Litter mass loss.*—There were both significant incubation treatment and source treatment effects on litter mass loss in the reciprocal transplant experiment (Fig. 3). There were fewer treatment and litter source effects in the first collection relative to the second (Fig. 3). *A. tridentata*, *F. thurberi*, *E. speciosus*, and *E. grandiflorum* had mass loss rates that were significantly affected by the treatment of the source of the litter (two-way ANOVA, $F = 82.5$, $P < 0.0001$, df = 1, 16; two-way ANOVA, $F = 109.8$, $P = 0.005$, df = 1, 16; and two-way ANOVA, $F = 5.1$, $P < 0.0001$, df = 1, 16; respectively). In each case, the litter from the heated source lost the greatest mass (Fig. 3), although these litter losses were not always associated with a higher quality of litter produced in the heated plots (Table 2).

In the xeric zone, *A. tridentata* had significantly greater mass loss in the heated plot relative to the control in both collections (two-way ANOVA, $F = 7.0$, $P = 0.0175$, df

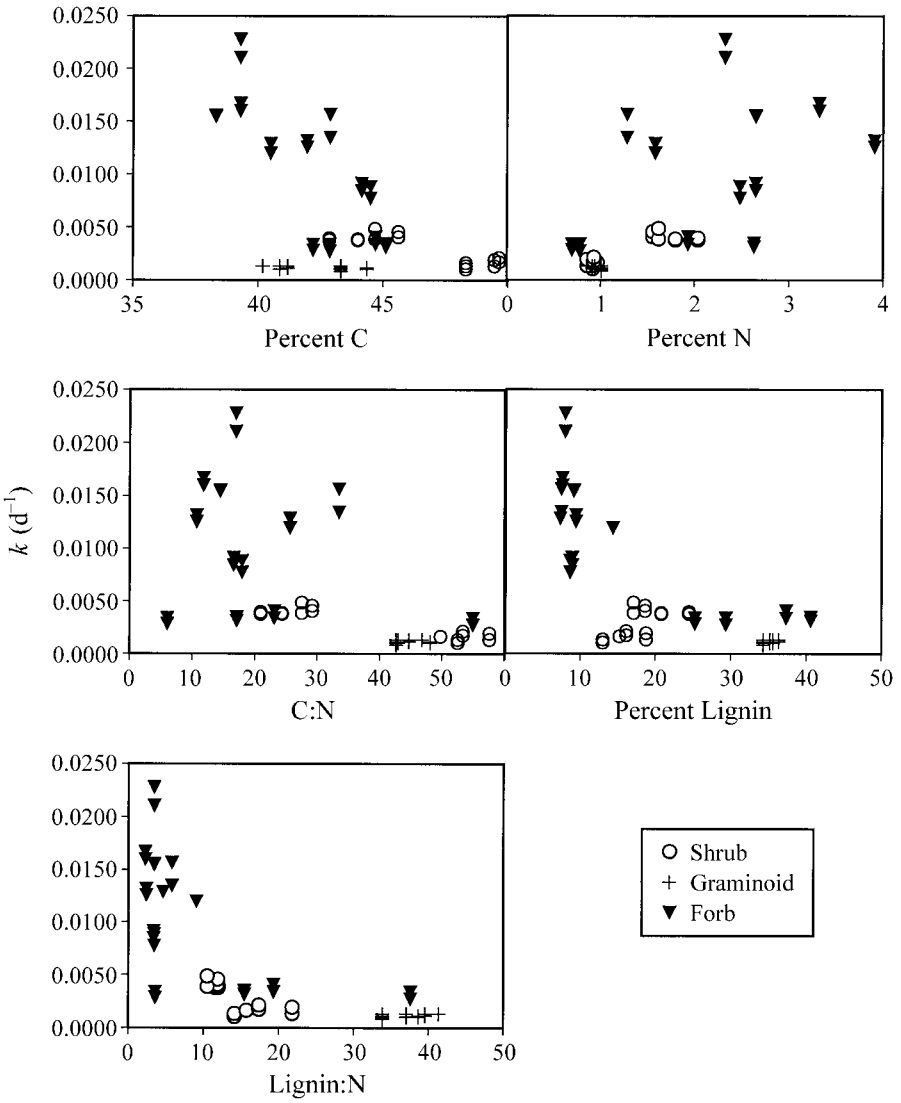


FIG. 2. Litter decay constants ($k$) vs. litter quality variables (Percent C, Percent N, C:N, Percent Lignin, and Lignin:N) by growth forms (shrub, open circles; graminoid, plus sign; and forb, solid triangle) for all three years.

= 1, 16; and two-way ANOVA, $F = 232.5$, $P < 0.0001$, df = 1, 16; respectively) and the loss was correlated with lower C:N and lignin:N ratios in the litter from the heating treatment. As in the previous years, *A. tridentata* lost much less mass over the course of the year than did the forbs (Fig. 3). Likewise, *E. speciosus* had significantly greater mass loss in the heated plots relative to the controls (two-way ANOVA, $F = 175.2$, $P < 0.0001$, df = 1, 16; Fig. 3) and a significant litter source effect (two-way ANOVA, $F = 109.8$, $P < 0.0001$, df = 1, 16; Fig. 3), but there was no significant difference in the initial litter by source (Table 2).

In the mesic zone, *P. floribunda* lost more mass in the heated plots relative to the control in both collections (first collection—two-way ANOVA, $F = 32.9$, $P < 0.0001$, df = 1, 16; second collection—two-way ANOVA, $F = 78.4$, $P < 0.0001$, df = 1, 16; Fig. 3). Although there was a trend towards a lower lignin:N ratio in the litter from the heated plots (Table 2), there was no litter source effect in either collection. *L. porteri* lost significantly more mass in the heated plots during the second incubation (Fig. 3). In the mesic zone, only *E. grandiflorum* had significant mass loss due to the litter source (two-way ANOVA, $F = 5.1$, $P = 0.05$, df = 1, 16). The litter of *E. grandiflorum* had a significantly lower C:N ratio when the source of the litter was the heated plots.

*Litter nitrogen changes*.—There were no significant treatment effects on litter N content within either zone of the first collection (Fig. 4). In the second collection, *A. tridentata*, *E. speciosus*, *P. floribunda*, and *L. porteri* all had greater release of N when incubated in the heated plots relative to the controls. Only *E. speciosus* had a litter N content that was significantly influenced by the source treatment of the litter (Fig. 4).

TABLE 5. Percentage initial N remaining by species in 1991, 1992, and 1994, for the xeric and mesic zones.

| Species | Growth form | Treatment | Collection 1 | Collection 2 |
|---|---|---|---|---|
| 1991 Xeric zone | | | | |
| *Artemisia tridentata* | shrub | control | 105.4 (9.2) | 124.1 (5.74) |
| | shrub | heated | 110.1 (3.0) | 132.9 (2.07) |
| *Festuca thurberi* | graminoid | control | 115.8 (8.2) | 145.1 (4.04) |
| | graminoid | heated | 108.9 (9.9) | 130.7 (11.86) |
| *Delphinium nuttallianum* | forb | control | 86.6 (6.1) | 0.0 ··· |
| | forb | heated | 82.7 (12.2) | 0.0 ··· |
| 1991 Mesic zone | | | | |
| *Pentaphylloides floribunda* | shrub | control | 93.4 (2.4) | 121.7 (3.2) |
| | shrub | heated | 92.7 (3.2) | 113.4 (3.5) |
| *Festuca thurberi* | graminoid | control | 114.9 (6.0) | 132.4 (4.4) |
| | graminoid | heated | 109.9 (5.5) | 125.3 (7.0) |
| *Erythronium grandiflorum* | forb | control | 113.3 (2.9) | 0.0 ··· |
| | forb | heated | 109.9 (8.5) | 0.0 ··· |
| 1992 Xeric zone | | | | |
| *Artemisia tridentata* | shrub | control | 110.0 (0.9) | 135.2 (6.2) |
| | shrub | heated | 107.4 (2.5) | 141.2 (5.4) |
| *Festuca thurberi* | graminoid | control | 115.0 (3.9) | 162.2 (7.1) |
| | graminoid | heated | 113.9 (7.1) | 162.1 (10.2) |
| *Delphinium nuttallianum* | forb | control | 65.6 (2.1) | 0.0 ··· |
| | forb | heated | 54.2 (5.3) | 0.0 ··· |
| 1992 Mesic zone | | | | |
| *Pentaphylloides floribunda* | shrub | control | 104.4 (1.5) | 115.2 (3.6) |
| | shrub | heated | 100.1 (1.4) | 110.6 (5.6) |
| *Festuca thurberi* | graminoid | control | 108.1 (3.4) | 152.9 (9.1) |
| | graminoid | heated | 112.9 (2.7) | 156.1 (7.9) |
| *Erythronium grandiflorum* | forb | control | 65.6* (1.9) | 0.0 ··· |
| | forb | heated | 54.2* (4.7) | 0.0 ··· |
| 1994 Xeric zone | | | | |
| *Artemisia tridentata* | shrub | control | 143.8 (8.9) | 130.4* (10.3) |
| | shrub | heated | 143.4 (9.0) | 117.3 (3.6) |
| *Festuca thurberi* | graminoid | control | 120.6 (0.3) | 115.6 (5.2) |
| | graminoid | heated | 157.7 (3.2) | 144.3 (4.4) |
| *Delphinium nuttallianum* | forb | control | 103.9 (3.3) | 0.0 ··· |
| | forb | heated | 98.8 (8.3) | 0.0 ··· |
| *Erigeron speciosus* | forb | control | 86.4 (8.4) | 100.7* (3.6) |
| | forb | heated | 93.7 (4.6) | 84.9 (8.6) |
| 1994 Mesic zone | | | | |
| *Pentaphylloides floribunda* | shrub | control | 101.4 (2.5) | 122.8* (3.5) |
| | shrub | heated | 95.9 (2.5) | 115.1 (3.0) |
| *Festuca thurberi* | graminoid | control | 120.6 (2.7) | 145.5 (8.6) |
| | graminoid | heated | 118.6 (3.8) | 152.5 (4.8) |
| *Erythronium grandiflorum* | forb | control | 100.6 (13.0) | 0.0 ··· |
| | forb | heated | 101.3 (14.9) | 0.0 ··· |
| *Ligustucum porteri* | forb | control | 181.2 (11.8) | 107.3* (9.2) |
| | forb | heated | 178.6 (26.1) | 113.7 (6.6) |

*Note:* Data are means (1 SE) in heated plots and control plots at each collection date.
* $P < 0.05$.

## DISCUSSION

Increasing atmospheric temperature may alter C and N cycling through changes in decomposition. This study evaluated how C and N cycling may be altered (1) directly, through changes in soil temperature and moisture that alter rates of litter mass loss; (2) indirectly, through the effects of warming on plant litter quality; and (3) indirectly, through warming impacts on plant community structure and subsequent changes in plant litter quality. The results of our investigation of these issues in a subalpine meadow indicate the following: (1) soil temperature and moisture contribute to litter decomposition, but their relative importance depends on the time of the season and initial soil microclimate; (2) litter quality of the dominant growth forms, particularly lignin:N, was the primary determinant of litter mass loss; (3) the effects of additional infrared radiative flux had no consistent and significant effect on litter mass loss; and (4) there is potential for a slight increase in litter quality of the litter produced under warming. The relative importance of these four factors in controlling litter decomposition rates will depend on the temporal scale. On a short time scale (months to years) under a warming climate, soil moisture availability and litter quality will be important in determining patterns of decomposition. When these results are

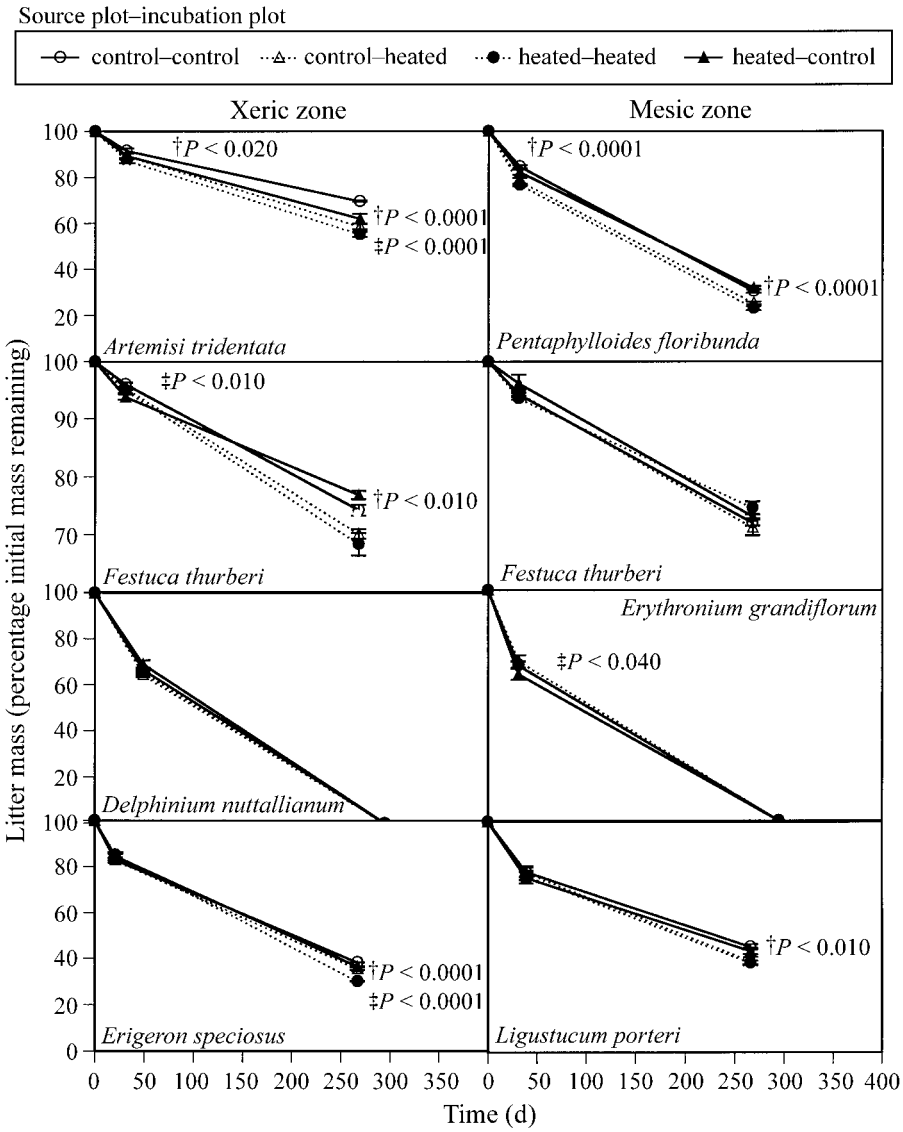


FIG. 3. Reciprocal transplant experiment. Percentage initial mass remaining by species in 1994 for the xeric and mesic zones. Data are means ($n = 5$) ± 1 SE for litter from control plots incubated in the control plots (open circles), litter from control plots incubated in the heated plots (open triangles), litter from heated plots incubated in the heated plots (solid circles), and litter from heated plots incubated in the control plots (solid triangles). A dagger symbol (†) indicates a statistically significant incubation treatment effect, and a double dagger (‡) indicates a significant effect of the treatment of the litter source.

combined with previous findings that suggest a potential shift from a forb-dominated to a shrub-dominated plant community (Harte and Shaw 1995), this study suggests that on long time scales (decades to centuries), the balance among factors affecting litter quality may be more important in controlling C and N cycling than abiotic factors such as temperature and moisture.

### *Soil microclimate controls over decomposition*

*Litter mass loss in the absence of climate warming.*—The influence of the surface soil temperature and moisture on litter mass loss was temporally segregated by collection across the two zones. The mass loss in the mesic zone was significantly affected by surface soil temperature and/or moisture during the growing season with few effects during winter and early spring, whereas the opposite was true for the xeric zone in which soil microclimate affected mass loss during the winter and early spring with little influence during the growing season. The exception to this pattern was in 1994, the driest year, in which neither soil temperature nor moisture explained the variation in mass loss in either zone or time of season.

The patterns in 1991 and 1992 are most readily ex-

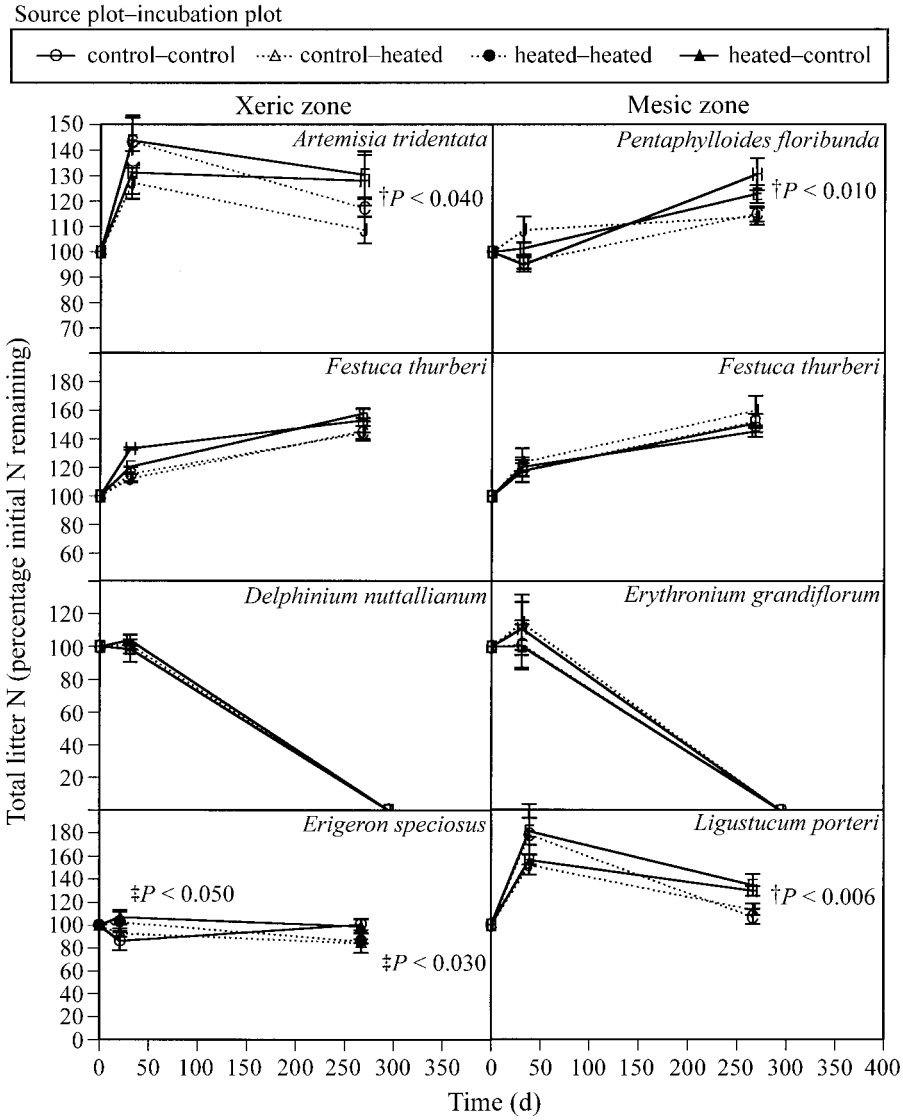


FIG. 4. Reciprocal transplant experiment: percentage initial N remaining by species in 1994 for the xeric and mesic zones. Data are means ($n = 5$) ± 1 SE for litter from control plots incubated in the control plots (open circles), litter from control plots incubated in the heated plots (open triangles), litter from heated plots incubated in the heated plots (solid circles), and litter from heated plots incubated in the control plots (solid triangles). A dagger symbol (†) indicates a statistically significant incubation treatment effect, and a double dagger (‡) indicates a significant effect of the treatment of the litter source.

plained by differences in initial soil microclimate conditions that provide favorable conditions for decomposition processes to occur. Litter mass loss rates are influenced greatly by moisture, because microbial activity is highly sensitive to soil microclimate conditions (Howard and Howard 1979). Generally, microbial activity is optimal at soil water potential of −0.05 MPa and decreases as the soil becomes waterlogged near 0.00 MPa or too dry near −1.5 MPa (Griffin 1981). At the subalpine site, soil water potential becomes unfavorable for microbial activity in the xeric zone by mid-July (<10% soil moisture or near −1.5 MPa) and in both zones at snowmelt (>40% soil moisture or >[−0.05] MPa). For decomposition rates to increase under climate warming, there will need to be an increase in surface soil temperature without soil drying that prohibits microbial activity.

*Litter mass loss with climate warming.*—Many studies on the impacts of climate warming on ecosystem processes have reported large temperature effects on litter mass loss (Hornsby et al. 1995, Hobbie 1996) and C and *N* cycling (Marion and Black 1987, Nadelhoffer et al. 1991, Hobbie 1996) with simulated climate warming. While the warming treatment alone was generally not significant in explaining the litter mass remaining, increased IR radiation did influence the soil tempera-

ture and moisture. The magnitude and direction of the change depends on initial microclimate conditions, interannual climate variability and vegetation cover (Harte et al. 1995). Since both soil moisture and temperature affect microbial activity, the IR warming treatment should influence decomposition. The overall effect depends on whether drying accompanies the warming. Harte et al. (1995) found that the IR treatment primarily promoted soil warming treatment in the xeric zone and both soil warming and drying in the mesic zone. As a result, either temperature or moisture alone consistently explained a significant amount of the variation in this study, while the IR treatment did not. Surface soil moisture at a 5-cm depth was significant in explaining litter mass loss in many of the analyses. When combined with litter type, soil temperature and moisture explained >60% of the variation in litter mass loss in both zones.

In the mesic zone, there was a consistent, significant effect of treatment on mass loss during the growing season. As the growing season progressed, the soils in the mesic zone became less saturated, and the increased IR was partitioned between increasing soil temperature and driving evaporative loss of moisture from the soil. This created conditions favorable for microbial activity and, thus, increased mass loss rates in the mesic zone. In contrast, there was little litter mass loss with the increased IR in the late fall, the winter, and the spring past snowmelt. During snowmelt, the mesic zone soils are at field water capacity and maintain water potentials above the optimum for microbial activity (greater than −0.050 MPa) associated with decomposition processes. During this period in the mesic zone, there are no changes in decomposition rates, because the additional IR radiation serves to increase evaporative loss only, and does not increase the temperature of the soil (Harte et al. 1995).

In the xeric zone, there was no effect of soil temperature and moisture on mass loss during the growing season. Because the soils are well drained and soil water potentials at the surface become very low during the second half of the growing season (less than −1.0 MPa), the additional IR energy primarily serves to increase the soil temperature. The soils of the xeric zone experience soil water potential below the optimum for microbial activity (less than −0.5 MPa) for most of the growing season. Additional moisture inputs by precipitation events during the growing season allow for sporadic but temporary conditions that are favorable for litter decomposition at the soil surface. In contrast, there was a significant effect of the treatment on mass loss during the winter and early spring. The xeric zone is well drained, and soil field capacity is transient. Increased IR radiation serves to raise soil temperature and rates of litter mass loss during the period immediately following snowmelt. Others have found similar patterns of decomposition at snowmelt when the surface soil moisture is high and soil temperature is increasing (O'Lear and Seastedt 1994).

Overall, the annual decomposition rates between the two zones are comparable within litter types. The soil microclimate interacts with the treatment effect to determine the temporal pattern of litter loss. The complexity of this microclimate–treatment interaction is not replicated in laboratory incubation and greenhouse experiments because there is no allowance for evaporative loss, soil drying, soil saturation, or diurnal temperature and moisture fluctuations (Marion and Black 1987, Hornsby et al. 1995, Hobbie 1996). Because of this, in situ field experiments are more likely to capture the complexity of ecosystem responses to climate warming.

On a broad-scale, the extent to which climate warming affects decomposition rates will depend substantially on the moisture regime of the ecosystem (Murphy et al. 1998). In ecosystems such as the Great Basin Sagebrush Steppe, where summer precipitation events are sporadic and the water table is deep, a rise in temperature may not substantially influence decomposition rates because of the low soil moisture. Patterns of decomposition at very dry sites have been found to be influenced more by moisture variations than by litter quality (Dyer et al. 1990, DeSanto et al. 1993, Murphy et al. 1998). In mesic ecosystems, such as the subalpine meadow, a warming climate and a lengthening of the growing season should greatly increase annual rates of decomposition.

### *Litter quality controls over decomposition*

*Litter quality controls over litter mass loss in the absence of climate warming.*—Differences in species litter quality were related to growth form. The graminoid and shrub litter were more resistant to decay than that of the forbs. Their litter tissues retained a higher lignin and carbon content and a lower N content. Others have found similar differences among growth forms (Chapin et al. 1996, Hobbie 1996).

Like other experimental reports (Cotrufo and Ineson 1996, Franck et al. 1997, McTiernan et al. 1997), there was no one initial chemical characteristic of the litter that served as the best predictor for determining decay rates across species and microclimates. All C fractions, including total C and total lignin, were significantly negatively correlated with $k$. Across all years and zones, percent lignin and lignin:N ratios were consistently highly significant, whereas percent C and C:N ratios were significant to a lesser degree and exhibited lower consistency. Initial N concentration was insignificant in explaining the variation in decay rates among species.

*Litter quality controls over litter mass loss with climate warming.*—There was some evidence of increasing litter quality with the heating treatment in *A. tridentata, P. floribunda, E. grandiflorum,* and *L. porteri. Artemisia tridentata* had lower lignin and C concen-

tration in its tissues when produced in the heating treatment. As a result, *A. tridentata* litter produced in heated plots had higher rates of decomposition than that produced in the controls. A few studies have documented increased litter quality and subsequent increased mass loss in litter produced at relatively dry sites (Vitousek et al. 1994, Austin and Vitousek 1998). These studies found that when litter of *Metrosideros polymorpha* produced at a wet site and a dry site were decomposed at a common site, litter from the dry site decomposed much more rapidly. This more rapid decomposition of litter from dry sites correlated with a strong decrease in leaf lignin content (Austin and Vitousek 1998).

If the sites are getting drier, it is expected that over time lignin will decline significantly. Eventually this should lead to faster decomposition, unless it gets so dry that moisture is limiting. Our data suggest a trend in the direction of decreased lignin in the heated plots, but our small sample sizes may not have been large enough to detect an effect. It is possible that the more rapid decomposition associated with increasing litter quality in the heated plots may counteract the slowing decomposition due to decreased soil moisture and species compositional changes. The mesic and xeric zones were not strikingly different from one another in controls over decomposition, as might be predicted by ecological theory. In other mesic systems, the initial nitrogen content of the litter has been shown to strongly influence the rate of decomposition (Melillo et al. 1982, Taylor et al. 1989, Harmon et al. 1990), while in xeric systems, abiotic factors such as moisture, temperature, and weathering play key roles (Whitford et al. 1981, Schaefer et al. 1985, Amundson et al. 1989). This study, like recent studies on semiarid systems, found that the control over decomposition is unique in that it combines features of both mesic and xeric systems (Murphy et al. 1998). Indeed, for both zones, the general linear model that best describes the pattern of litter mass loss has as its main components moisture and initial lignin:N ratio.

The main distinguishing response of litter decay between the two microclimates under warming was the timing of the litter mass loss with respect to the time of season. Because C and N release from litter increase as linear functions of both season length and temperature, and as a parabolic function of soil moisture content (Moorhead and Reynolds 1993), this difference may become important in a changing climate. If rates of litter decomposition increase with warming in a mesic subalpine meadow, the turnover time of C and N within the litter compartment will decrease. This has the potential to decrease storage of both C and N, which could alter the timing and availability of N for plant growth. In contrast, in the xeric regions dominated by sagebrush, an increase in temperature will likely decrease soil moisture and rates of decomposition during the growing season, which has the potential to increase N sequestration in the litter layer. Indeed, the zonal patterns found here could be strengthened under a warming scenario that includes an increase in the growing season length, changes in precipitation patterns, and alterations of species composition.

### *Implications for ecosystem responses to climate change*

Interspecific differences in litter mass loss and N release were much greater than differences between the control and heated treatments. This study concurs with growing evidence that, as the atmosphere warms, changes in plant community composition may strongly influence changes in C and N cycling (Pastor and Post 1988, Chapin et al. 1996, Hobbie 1996). Experimental evidence suggests subalpine plant community structure will respond to warming with an increase in shrub biomass, relative to forb and graminoid biomass (Harte and Shaw 1995; see also Chapin et al. [1995] for tundra). This change in community structure has the potential to increase storage of C and N for three reasons. First, soil organic matter (SOM) decomposition rates do not appear to change with increased IR radiation in this system (Saleska et al. 1999). Second, the turnover time for C and N of the system will increase, because the shrubs are long lived and allocate a large proportion of their biomass to woody tissues that do not senesce annually. Third, the total litter produced by the shrubs has a much slower decay rate than litter of forbs. These three factors combined have the potential to increase soil C and N storage, although the second factor has the potential to increase storage over a longer period of time.

Nitrogen turnover rates should also be affected by changes in litter composition. Both the shrub and the graminoid litter immobilized N, while the forb litter released a significant percentage of the total initial nitrogen content within the one-year incubations (Fig. 4). Many studies in temperate zones have reported a period of nitrogen sequestration (Staaf and Berg 1981, Pastor et al. 1987, Melillo et al. 1989, Takeda 1995) following a short period of nitrogen release from the litter (Berg and McClaugherty 1989, Berg and Tamm 1994, Monleon and Cromack 1996). With increased shrub abundances, relative to forb, and a subsequent increase in shrub litter, there may be longer periods of N sequestration in the litter layer. Because this study had no incubation longer than one year, the duration of net N sequestration in the litter layer remains uncertain.

This study most likely underestimates the magnitude of the effect of warming on decomposition rates through changes in litter quality. First, the decomposition experiments did not include the woody stems that decompose more slowly. Secondly, the research does not take into account the potential decrease in litter quality through increased carbon fixation with increasing atmospheric $CO_2$ concentrations (Owensby 1993, Berntson and Bazzaz 1996, Cotrufo and Ineson 1996, Franck et al. 1997); however, there is evidence

that suggests this effect may not be significant (Hirschel et al. 1997, Norby et al. 1999).

Under climate warming, the combined long-term effects of decreasing litter quality through changes in community composition and decreasing soil moisture may be a decrease in decomposition rates. This decrease in litter decomposition rates has the potential to decrease nitrogen turnover rates and increase soil C storage. This effect may be slightly modified by increasing litter quality as soils become drier. Of course, long-term changes in soil carbon storage will depend on how climate change influences many other processes that control carbon pools, including rates of photosynthesis, plant respiration, decomposition of litter derived from other tissues, and decomposition of substrates remaining from the initial decomposition of litter. For leaf litter, the results of this study suggest that the direct impacts of increasing temperature on rates of litter decomposition will be less important in subalpine ecosystems than the indirect impacts of changes in soil moisture and plant species composition.

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