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Diverse mechanisms for CO_2 effects on grassland litter decomposition

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Abstract

The ongoing increase in atmospheric CO_2 concentration ($[CO_2]$) can potentially alter litter decomposition rates by changing: (i) the litter quality of individual species, (ii) allocation patterns of individual species, (iii) the species composition of ecosystems (which could alter ecosystem-level litter quality and allocation), (iv) patterns of soil moisture, and (v) the composition and size of microbial communities. To determine the relative importance of these mechanisms in a California annual grassland, we created four mixtures of litter that differed in species composition (the annual legume *Lotus wrangelianus* Fischer & C. Meyer comprised either 10% or 40% of the initial mass) and atmospheric $[CO_2]$ during growth (ambient or double-ambient). These mixtures decomposed for 33 weeks at three positions (above, on, and below the soil surface) in four types of grassland microcosms (fertilized and unfertilized microcosms exposed to elevated or ambient $[CO_2]$) and at a common field site. Initially, legume-rich litter mixtures had higher nitrogen concentrations ([N]) than legume-poor mixtures. In most positions and environments, the different litter mixtures decomposed at approximately the same rate. Fertilization and CO_2 enrichment of microcosms had no effect on mass loss of litter within them. However, mass loss was strongly related to litter position in both microcosms and the field. Nitrogen dynamics of litter were significantly related to the initial [N] of litter on the soil surface, but not in other positions. We conclude that changes in allocation patterns and species composition are likely to be the dominant mechanisms through which ecosystem-level decomposition rates respond to increasing atmospheric $[CO_2]$.

Keywords: California, decomposition, elevated CO_2, global change, grassland, litter quality, nitrogen

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Introduction

The response of litter decomposition to the ongoing increase in atmospheric $[CO_2]$ will either affect the global carbon cycle directly, by altering the total mass of carbon that is bound in litter and soil organic matter, or indirectly, by altering the availability of nitrogen to plants and decomposers, and thus affecting productivity. Potential mechanisms through which rising $[CO_2]$ could alter decomposition rates include the following:

1 Changes in litter chemistry of individual species. Some previous experiments found decreases in quality indices (e.g. decreases in %N, and increases in C:N and lignin:N) of litter produced in enriched-CO_2 environments (Melillo 1983; Coûteaux *et al*. 1991; Cotrufo *et al*. 1994; Kemp *et al*. 1994), which led to speculation that rising $[CO_2]$ will slow decomposition, increasing the mass of litter and soil carbon pools, and decreasing nutrient availability (Norby *et al*. 1986; Lambers 1993).

2 Changes in ecosystem-level litter quality due to CO_2-induced shifts in plant species composition (O'Neill 1994). Kemp *et al*. (1994) suggest that shifts in the relative biomass of C3 and C4 grasses could change decomposition rates in prairies and marshes, because these groups of grasses differ in their decomposibility. CO_2-driven increases in the abundance of late-season annuals (Field

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et al. 1996) and the N-fixer *Lotus wrangelianus* (Thayer *et al*. submitted) may change the average litter quality of California grasslands.

3 Changes in allocation patterns, which affect both litter quality (Seastedt 1988; Franck *et al*. 1997) and the proximity of litter to soil. Under most conditions, litter that is buried or mixed with soil decomposes more quickly than litter that is placed on the soil surface, which in turn decomposes more quickly than litter that is suspended above-ground (Douglas *et al*. 1980; Deshmukh 1985; Thurow 1989). In California grassland, these three categories roughly correlate with root litter, which is buried, leaf litter, which reaches the soil surface quickly, and stem litter, which remains standing long after the plants have senesced. The rise in [CO_2] may alter allocation patterns directly, as individual species alter their structure, or indirectly, as a consequence of shifts in species dominance.

4 Increases in soil moisture due to higher water use efficiency by plants. Fredeen *et al*. (1997) reported increases in the late-season soil moisture of a California grassland under elevated [CO_2]. In an open-top chamber experiment on N-fertilized tallgrass prairie, Rice *et al*. (1994) observed increased microbial activity in the top 5 cm of soil under elevated [CO_2], and suggested that higher moisture levels could be responsible.

5 Increased available substrate for microbes. CO_2-driven increases in root:shoot ratios, rhizodeposition and root exudation can provide microbes with additional carbon, increasing soil microbial biomass and thus microbial C and N sequestration (Díaz *et al*. 1993). As this growing pool of microbial biomass turns over, N mineralization increases, potentially leading to higher N availability (Zak *et al*. 1993). Changes in resource availability could affect decomposition by influencing microbes' choice of substrates. If litter and root inputs increase in quantity or C:N ratio, microbes will consume (and thus decompose) more soil organic matter to obtain sufficient N (van de Geijn & van Veen 1993). Conversely, if an increase in the C:N ratio of soil organic matter results in N-limitation of microbial populations, litter decomposition could slow under elevated [CO_2]. Changes in the plant species composition of an ecosystem can also alter soil N cycling (Hungate *et al*. 1996).

We decomposed mixed-species litter in litter bags to study the relative importance of these mechanisms in California annual grasslands. To study mechanisms 1 and 2, we compared short-term decomposition of four separate mixtures of litter, which differed in [CO_2] during growth and species composition. By monitoring decomposition of these mixtures in fertilized and unfertilized grassland microcosms at ambient and twice-ambient [CO_2], and in a field plot, we were able to assess the relative importance of mechanisms 4 and 5. Our design compelled us to examine the cumulative effects of these two mechanisms, rather than examining each independently. To assess the relative importance of mechanism 3, we placed litter bags in three types of microsites designed to simulate standing dead, surface-level, and buried litter. By placing shoot litter in all three positions, we were able to assess the relative importance of position for decomposition without confounding the study with differences in litter type.

Materials and methods

Study site and design

Our study was part of the Jasper Ridge CO_2 Experiment, which took place at Jasper Ridge Biological Preserve near Stanford, Calif., USA (37°24'N, 122°14'W, 105 m elevation). The site has a Mediterranean climate, with cool, wet winters and hot, dry summers. Most of our study was conducted in large (1.3 m square) open-top chambers supplied with either ambient air or ambient air plus 350 ppm CO_2 (Field *et al*. 1996). Microcosms for our experiment were contained in 48 polyvinyl chloride tubes, which stood 0.95 m tall by 0.2 m in diameter. Each tube contained 49 cm of shredded sandstone-derived topsoil on a base of 45 cm of crushed sandstone rock subsoil. We divided 24 of the microcosms among three chambers that received ambient air, and placed the remaining 24 microcosms in three CO_2-enriched chambers. Half of the tubes in each CO_2 treatment received 20 g m^{-2} of N, P, and K in the form of 120-day release fertilizer (Osmocote 14–14–14, Grace Sierra Horticultural Products Co., Milpitas, CA). We seeded tubes with five species representative of typical California annual grasslands on 19 October 1995 (Table 1). Seeds were sown around templates that covered two 6.5 cm by 6.5 cm patches of soil 4 cm apart. We weeded other species out of the microcosms over the course of the growing season, with the exception of *Lolium multi-*

Table 1 Seeding densities in the microcosms

Species	Seeds planted	Target # of plants
Avena barbata Link	20	19
Bromus hordeaceus L.	50	45
Hemizonia congesta ssp. *luzulifolia* (DC.) Babc. & H.M. Hall	22	4
Lotus wrangelianus	7	7
Nassella pulchra (A. Hitchc.) Barkworth	11	7

florum Lam., which appeared at similar densities in all tubes.

We established a common garden field site in sandstone grassland about 100 m from the microcosm chambers. Within this site, we chose 12 locations on a 4-m × 5 m grid to receive litter bags, with no two locations closer than 1 m.

Litter types and placement

During the 1994–5 season, plant material for this study grew in microcosms identical to those used for the unfertilized treatment above. The microcosms received a total seasonal water input of 923 mm. Plant communities featured the same species as listed above, minus *Lolium*, with identical plant densities over slightly more area (no templates were used). Plant shoots were harvested on 29 June 1995, at which time tissue of most species had fully senesced.

Fully senescent shoot tissue (hereafter litter) was air-dried and sorted into *Lotus* and non-*Lotus* litter, grown in ambient and high [CO_2]. Within each category, litter was cut into lengths of approximately 5 cm and mixed. Litter bags received 0.5 ± 0.004 g of material from either the high-[CO_2]-grown or ambient-[CO_2]-grown pools. Bags contained a ratio of non-*Lotus*: *Lotus* material of either 9 : 1 or 6 : 4 by mass, typical of the *Lotus* fraction in microcosms grown in ambient [CO_2] in a dry year, and elevated [CO_2] in a wet year, respectively.

We used three types of litter bags: nylon mesh (6 cm × 6 cm, mesh size 0.27 mm), stainless steel (7 cm × 7 cm, mesh size 0.48 mm), and nylon netting (9 cm × 9 cm, mesh size 0.63 mm). These litter bags were chosen to minimize the influence of the bag on microsite conditions while minimizing soil contamination of the samples in each of three microsites. We placed two sets of the three types of bags in each microcosm and at each field location. Two nylon mesh bags were buried vertically, with the top edge at surface level. Two stainless steel bags were placed on the soil surface at least 4 cm apart, in the former location of the templates (see above – except for field sites, where bags were slid through the litter layer to the soil surface), and two nylon netting bags were hung 5 cm above the soil surface from separate bamboo stakes. All six bags in a given microcosm or field plot contained the same species ratio, with one set of bags in the three locations containing litter from plants grown at ambient [CO_2] and the other containing high-[CO_2]-grown litter, to the extent that our supply of litter permitted. Litter bags were put in position 14–16 November 1995, before any seeds in the microcosms had germinated. Six samples of each mixture were kept in the laboratory as controls.

Measurements and analyses

We used time domain reflectometry (TDR; technique described in greater detail in Field *et al*. 1997) to periodically measure the water content of topsoil during the latter portion of the growing season. Half of the microcosms in each CO_2 and nutrient treatment were equipped with vertically orientated stainless steel rods that served as wave guides for the TDR measurements.

Litter bags were collected on 5–6 July 1996. At this time litter was removed from bags, brushed free of soil, air-dried, and weighed. A fraction of the samples was dried for 48 h at 65 °C and reweighed to determine % moisture. Oven-dry weights of the remaining samples were calculated based on the % moisture in oven-dried samples. All controls and samples were then ground through a 20 mesh screen in a Wiley mill, ground again in a ball mill, and dried at 65 °C.

We determined carbon and nitrogen contents of subsamples of material from each litter bag and control using an elemental analyser (NA-1500, Carlo Erba Instruments, Milan, Italy). To correct for contamination of samples by mineral soil, we determined the C concentration of topsoils in the various treatments, and calculated final litter masses on the assumption that mineral soil contamination was solely responsible for any declines in the carbon concentration of the samples from the control values. Results from this correction technique agree closely with results obtained from ash corrections (Dukes, unpubl. data).

We followed the acetyl bromide digestion protocol of Chu *et al*. (1996) to determine the lignin concentration of control litter.

Results were analysed with one-, two-, and three-way analyses of variance (ANOVAS), as indicated. Mass loss percentages were log transformed before analysis. Data from anovas with significant results ($P < 0.05$) passed Cochran's (1951) test for homogeneity of variances. We used simple regression to test for relationships between the initial chemical composition of litter mixtures and their decomposition and N release rates. Turnover rates (k) were calculated based on the equation $M_t = M_0 e^{-kt}$, where t=time (years), M_t=litter mass at time t, and M_0=initial litter mass.

Results

Litter chemistry

Legume-rich litter mixtures had higher N concentrations and lower C:N ratios than legume-poor litter mixtures (Tables 2, 3). Of the legume-poor mixtures, high-[CO_2]-

% *Lotus*	ppm CO_2	Litter quality index		
		%N	C/N	% Lignin
10	350	0.34 ± 0.01	130 ± 5	7.0 ± 0.8
	700	0.38 ± 0.02	115 ± 6	5.8 ± 0.6
40	350	0.42 ± 0.02	105 ± 4	5.9 ± 0.8 ($n = 5$)
	700	0.42 ± 0.01	105 ± 4	6.0 ± 0.6 ($n = 5$)

Table 2 Litter quality indices for grassland litter mixtures composed of 10% and 40% *Lotus wrangelianus* by weight, and grown in ambient and elevated CO_2. Values are means ± SE ($n = 6$, except where noted)

Table 3 *P*-values from 2-way ANOVAS showing the effects of species composition and CO_2 concentration on litter %N, C:N, and % lignin

Litter quality index	Source of variation (*P*-values)		
	Species	CO_2	Species × CO_2
% N	<0.001	0.133	0.136
C:N	0.002	0.126	0.131
% Lignin	0.524	0.406	0.361

grown litter had a marginally higher N concentration than low-[CO_2]-grown litter (one-way ANOVA: $F = 4.790$, $P = 0.0535$). Litter mixtures did not differ in lignin content (Tables 2, 3).

Soil moisture

Soil moisture in the top 13.5 cm of the microcosms was affected by NPK fertilization, but not by CO_2 enrichment (Fig. 1). Early in the season, fertilized microcosms dried out faster than unfertilized microcosms. Nutrient-amended microcosms were significantly drier on 5 of 7 measurement dates before the end of April (two-way ANOVA, $P < 0.05$). This trend reversed later in the season, and unfertilized microcosms were significantly drier on 11 June. While CO_2-enriched microcosms tended to be wetter than ambient microcosms for most of the growing season, these differences were not statistically significant.

Mass loss

In this experiment, litter position had the greatest and most consistent influence on mass loss. Species composition and CO_2 conditions during growth of the litter had minor and inconsistent effects on mass loss that were not always related to differences in measured litter chemistry variables. During decomposition, neither atmospheric [CO_2] nor nutrient availability affected mass loss rates.

In the microcosms, differences due to litter quality were small and position-dependent. Of the above-ground litter bags in unfertilized microcosms, legume-rich mixtures lost mass more quickly than legume-poor mixtures (Tables 4, 5 and Fig. 2a). Species composition and CO_2 origin of litter did not affect mass loss from mixtures on the soil surface (Table 4, Fig. 2a). Species composition did not affect decomposition of buried litter mixtures that had been grown at high [CO_2]. However, legume-poor litter grown at low [CO_2] lost mass more slowly than legume-rich litter even though the difference in the proportion of legumes was much smaller between these mixtures than the high-[CO_2]-grown mixtures. Of the buried legume-rich mixtures, litter grown at ambient [CO_2] decomposed faster than litter grown under elevated [CO_2] (Tables 4, 5 and Fig. 2a). Mass loss of above-ground and buried mixtures was weakly related to the initial %N and C:N of litter. For above-ground litter, initial %N and C:N explained 11% ($P < 0.01$) and 8% ($P < 0.01$) of the variance in mass loss, respectively. For buried litter, both initial %N and C:N explained 4% of the variance in mass loss ($P = 0.04$ in each case). At both positions, %N was positively correlated with mass loss and C:N was inversely related. Mass loss from surface mixtures was not significantly related to measured litter chemistry variables.

In the field, species composition and CO_2 origin of litter did not affect mass loss from mixtures in any of the litter positions (Tables 4, 5 and Fig. 2a), and mass loss was not related to measured litter chemistry variables.

Because several treatments of low-[CO_2]-grown litter were missing from our originally planned factorial design, we limited our analysis of the effect of environmental variables to high-[CO_2]-grown litter. Litter position strongly affected mass loss rates of mixtures in the field ($F = 41.291$, $P < 0.0001$) and in the microcosms (Table 6). However, soil fertilization and atmospheric [CO_2] during decomposition did not affect mass loss of litter in microcosms (Table 6).

Nitrogen dynamics

Nitrogen dynamics of the litter mixtures did not parallel mass loss dynamics. While N dynamics of litter on the soil surface were correlated significantly with initial litter N concentration, this relationship did not hold for litter

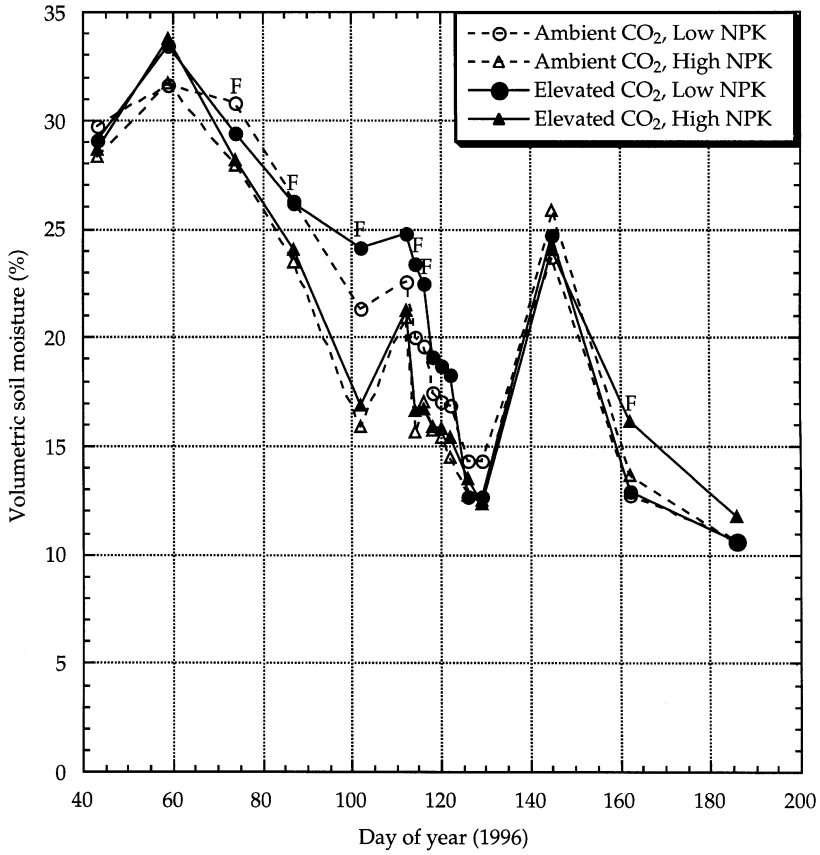

Fig. 1 Mean ($n = 6$) % volumetric soil moisture in the top 13.5 cm of microcosms over the latter portion of the 1996 growing season. Dates on which fertilized and unfertilized treatments significantly differed (2-way ANOVA, $P < 0.05$) have been marked with the letter F. Interactions and differences between CO_2 treatments were never significant.

Table 4 *P*-values from ANOVA showing the effects of species composition and CO_2 concentration during tissue growth on % mass loss of litter (log transformed) in three positions in microcosms and the field

	Source of variation (*P*-value)			
Litter position[1]	Species	CO_2	Species × CO_2	ANOVA type
M, Above-ground[2]	0.004	0.364	0.056	2-way
M, Surface	0.431	0.992	0.304	2-way
M, Below-ground	0.504[3], 0.046[4]	0.039[5]		1-way
F, Above-ground	0.123[3]	0.416[6]		1-way
F, Surface	0.296	0.059	0.102	2-way
F, Below-ground	0.759[3], 0.514[4]	0.656[5]		1-way

[1]Key: *M*, litter decomposed in microcosms; *F*, litter decomposed in field. [2]Comparison of litter mixtures in unfertilized microcosms only. [3]Comparison of high-CO_2-grown litter mixtures. [4]Comparison of low-CO_2-grown litter mixtures. [5]Comparison of legume-rich litter mixtures. [6]Comparison of legume-poor litter mixtures.

in other positions. Litter that was in close proximity to the soil of fertilized microcosms immobilized more N than litter in the same position in unfertilized microcosms.

In the microcosms, the importance of litter quality varied with litter position. Among the legume-poor mixtures in hanging bags, low-[CO_2]-grown legume-poor litter immobilized N, while high-[CO_2]-grown legume-poor litter did not (Fig. 2b, Table 7). CO_2 conditions during growth did not affect N dynamics of legume-rich litter. In surface bags, litter grown at low [CO_2] immobilized more N than litter grown at high [CO_2], and legume-poor litter immobilized more N than legume-rich litter (Table 7). In buried bags, N dynamics did not vary among litter types (Table 7). Nitrogen dynamics were significantly related to the initial N

Table 5 Turnover rates (k) of four litter types decomposed in different environments. These values overestimate actual decomposition rates at the study site because this experiment was conducted primarily during the region's wet season

Decomposition environment[1]	Litter type (% *Lotus*, CO_2 level during growth)			
	10, low	10, high	40, low	40, high
Above-ground, field	0.58	0.54	–	0.63
Above-ground, nc	0.38	0.37	0.43	0.49
Above-ground, nC	0.43	0.4	0.42	0.48
Above-ground, Nc	0.43	0.38	–	0.51
Above-ground, NC	0.43	0.38	–	0.47
Surface, field	1.02	0.78	0.97	0.95
Surface, nc	0.53	0.64	0.59	0.57
Surface, nC	0.53	0.54	0.59	0.55
Surface, Nc	0.55	0.62	0.62	0.59
Surface, NC	0.7	0.56	0.61	0.61
Buried, field	1.28	1.24	1.21	1.26
Buried, nc	1.31	1.33	1.49	1.23
Buried, nC	1.27	1.13	1.47	1.3
Buried, Nc	1.29	1.19	1.35	1.42
Buried, NC	1.3	1.29	1.32	1.16

[1]Decomposition environment expressed as litter position and environmental conditions (n=unfertilized, N=fertilized, c=ambient air, C=ambient air + 350 ppm CO_2).

Table 6 *P*-values from 3-way ANOVAS showing the effect of environmental factors (litter position, fertilizer addition, and CO_2 concentration during decomposition) on % mass loss and % initial N of litter in the microcosms

Source of variation	% mass loss	% initial N remaining
Litter position	< 0.001	< 0.001
NPK	0.637	< 0.001
CO_2	0.279	0.259
Pos. × NPK	0.817	< 0.001
Pos. × CO_2	0.454	0.667
NPK × CO_2	0.977	0.712
Pos. × NPK × CO_2	0.486	0.499

concentration of litter in surface ($r^2 = 0.226$, $P < 0.0001$), but not above-ground or buried litter bags. Surface mixtures with higher initial N contents were more likely to release N (Fig. 2b).

Nitrogen dynamics of litter in the field resembled those of litter in microcosms. In hanging bags, legume-poor litter released N if grown in high [CO_2] and immobilized N if grown in low [CO_2] (Fig. 2b, Table 7). Of the high-[CO_2]-grown litter at this position, legume-poor mixtures lost N while legume-rich mixtures did not, with a marginally significant species effect. Of the legume-poor litter on the soil surface, low-[CO_2]-grown mixtures immobilized more N than high-[CO_2]-grown mixtures (Fig. 2b, Table 7). Legume-rich mixtures released N at approximately the same rate. There were no differences in N release rates among litter mixtures buried in the field. As in the microcosms, initial litter N concentration was significantly related to N dynamics of litter in the surface position only ($r^2 = 0.621$, $P < 0.0001$), where litter with higher initial N concentrations was more likely to release N (Fig. 2b).

Nitrogen dynamics of litter were not affected by the CO_2 concentration of the decomposition environment (Table 6). Litter that was buried under or placed on the soil surface of NPK-fertilized microcosms immobilized more N than litter in unamended microcosms (Fig. 2b, Table 6). Fertilization did not affect N dynamics in hanging mixtures (2-way ANOVA, $P = 0.95$).

Discussion

Although the rise in atmospheric [CO_2] has the potential to alter litter decomposition rates through many mechanisms, our results indicate that few of these mechanisms will drive biologically significant changes. Changes in biomass allocation and litterfall timing have the greatest potential to alter litter decomposition rates in California grasslands.

Litter quality

Most previous experiments that have examined the potential response of decomposition to elevated [CO_2] have focused on a single mechanism: the response of the litter quality of individually-grown plants of a single species to elevated [CO_2]. Results of a few studies have led to the conclusion that the N

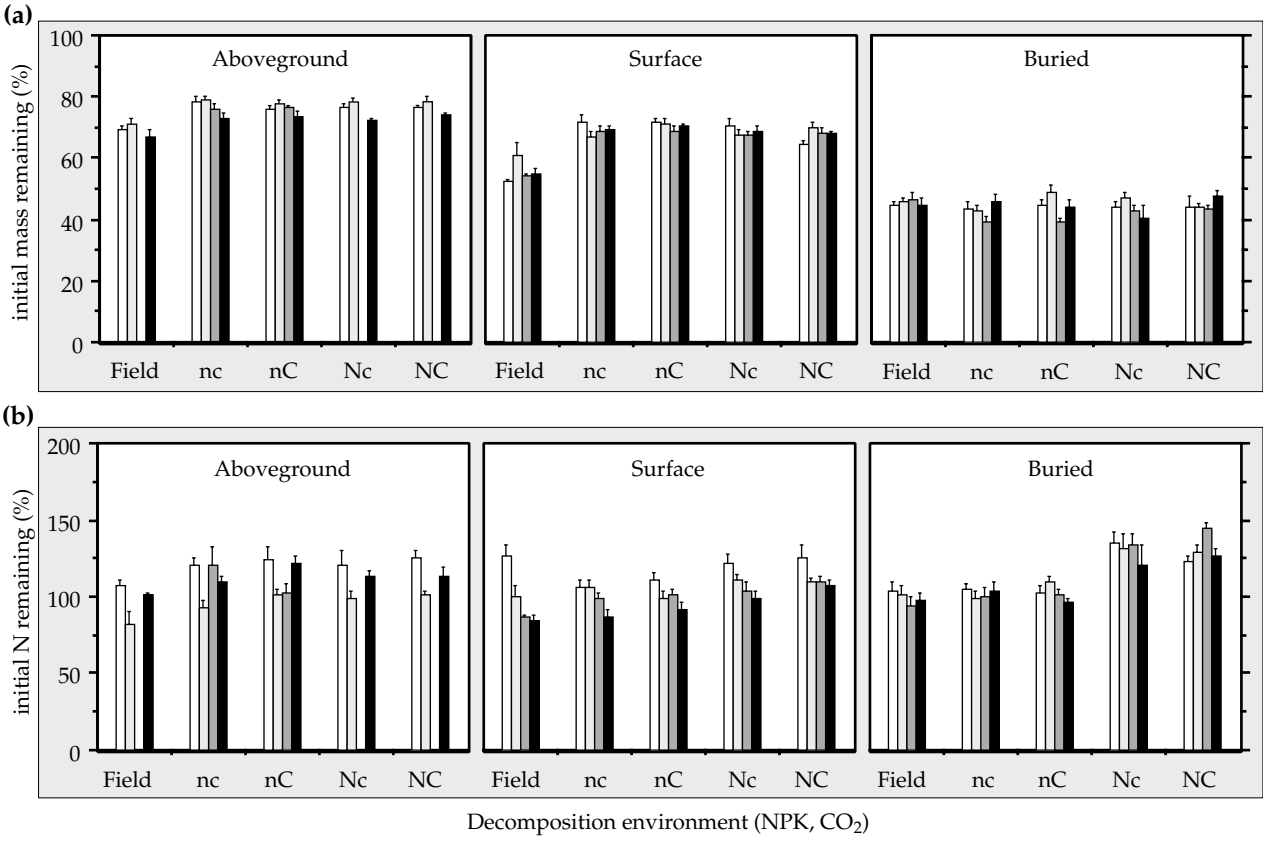

Fig. 2 Mean (± SE, $n = 6$) % (a) initial mass remaining and (b) initial N remaining of litter mixtures containing 10% (white and light grey bars), or 40% (dark grey and black bars) *Lotus wrangelianus* by mass, and grown in either ambient (white and dark grey bars) or elevated (light grey and black bars) CO_2 concentrations. Each set of bars depicts values representing the different litter types in one of five decomposition environments [four types of microcosms: unfertilized (n) and NPK fertilized (N) microcosms in ambient (c) or CO_2-enriched (C) atmospheres, plus a common field site (Field)]. Each panel depicts values representing the litter in one of three positions (above-ground, surface, or buried). In the buried position, ambient-[CO_2]-grown litter mixtures identified as containing 10% *Lotus* (white bars) mistakenly received a total of 0.20 g *Lotus* and 0.45 g non-*Lotus* litter (creating a 31% *Lotus* mixture). Initial %N and C:N for these mixtures were calculated using a simple mixing model.

concentration and decomposition rate of litter decrease when plants are grown under elevated [CO_2] (e.g. Cotrufo *et al*. 1994; Cotrufo & Ineson 1995), but other studies have found small, species-dependent changes in litter quality and decomposition rates (e.g. Kemp *et al*. 1994; Ball & Drake 1997; Franck *et al*. 1997; Hirschel *et al*. 1997; Gahrooee 1998). Even when the litter chemistry of a species clearly responds to elevated [CO_2], this litter may decompose faster than ambient-grown litter in some environments and slower in others, depending on the decomposer community (Coûteaux *et al*. 1991) or on the location and its accompanying climate (Robinson *et al*. 1997).

In this study, we found little change in the litter chemistry of communities grown under different CO_2 conditions when the species composition of the litter was held constant. In one case, we observed a trend toward an *increase* in the N concentration (and a decrease in C:N) of litter grown under elevated [CO_2]. We offer two possible explanations for this trend. First, the N concentration of *Avena barbata* litter may increase when the species is grown under elevated [CO_2]. When grown in nutrient-amended serpentine soil, a closely related species (*Avena fatua*) decreased its C:N ratio in both green tissue (Chu *et al*. 1996) and litter (Franck *et al*. 1997) in response to elevated [CO_2]. Secondly, nitrogen fixed by *Lotus wrangelianus* (Thayer *et al*. submitted) may have become available to other species. This legume was more abundant in CO_2-enriched microcosms. The stimulation of legume growth also affects the litter chemistry of the community directly, as is evident from the difference in N concentration between legume-rich and legume-poor litter mixtures. This highlights an important point: shifts in the species composition of communities

Table 7 *P*-values from ANOVAS showing the effects of species composition and CO_2 concentration during tissue growth on % initial N remaining of litter in three positions in the microcosms and in the field

Litter position[1]	Source of variation			ANOVA type
	Species	CO_2	Species × CO_2	
M, Above-ground[2]	0.448	0.044	0.004	2-way
M, Surface	< 0.001	0.001	0.618	2-way
M, Below-ground	0.379[3]	0.232[4]		1-way
F, Above-ground	0.051[3]	0.018[5]		1-way
F, Surface	< 0.001	0.024	0.050	2-way
F, Below-ground	0.574[3]	0.728[4]		1-way

[1]Key: *M*, litter decomposed in microcosms; *F*, litter decomposed in field. [2]Comparison of litter in unfertilized microcosms. [3]Comparison of high-CO_2-grown litter mixtures. [4]Comparison of legume-rich litter mixtures. [5]Comparison of legume-poor litter mixtures.

will probably have more important effects on the litter chemistry of those communities than will the direct effects of rising [CO_2] on the litter chemistry of individual species.

Mass loss

Although litter mixtures clearly differed in N concentration, litter [N] had little influence on the decomposition rates of the mixtures. Legume-rich mixtures lost mass more quickly than legume-poor mixtures when they were suspended above-ground in the microcosms, but not when they were placed on the soil surface, and not in the field. CO_2 conditions during tissue growth significantly affected mass loss in only one case, that of legume-rich litter buried in the microcosms. The litter chemistry properties that we measured do not explain this difference.

Elevated-[CO_2]-driven changes in the physico-chemical environment and in the population size and species composition of the decomposer community can affect decompositon rates through a number of mechanisms. Elevated CO_2 levels generally increase the water-use efficiency of plants, leading to increased soil moisture in California grasslands (Field *et al*. 1997; Fredeen *et al*. 1997) and some other ecosystems (e.g. Bremer *et al*. 1996). Wetter soils accelerate decomposition, especially of buried detritus. Increased carbon exudation and rhizodeposition under elevated [CO_2] often stimulate increases in microbial biomass (Hungate *et al*. 1997), which could increase decomposition rates (Zak *et al*. 1993). Elevated [CO_2] also affects microbial species composition (Hungate *et al*. 1999; Rillig *et al*. 1999), which could alter the efficiency with which different substrates are decomposed (Jones *et al*. 1998). In this study, the combination of observed changes in soil moisture and any (unmeasured) changes in the microbial community did not affect mass loss from litter in any treatment. This contrasts with the findings of Jones *et al*. (1998), who postulated that increases in the abundance of cellulose decomposers under elevated [CO_2] accelerated the decomposition of cotton strips in their model ecosystems.

The most striking differences in decomposition in our experiment were not caused by elevated [CO_2], but by litter position. While it is not surprising that decomposition rates were correlated with the proximity of litter to soil, these results highlight the potential of elevated-[CO_2]-driven shifts in allocation or the timing of litterfall to alter decomposition rates. Our study did not examine the relative importance of the changes in litter quality that accompany shifts in allocation (but see Franck *et al*. 1997).

By drying air-exposed litter, rapid within-canopy airflow in the chambers probably minimized differences in decomposition between suspended and surface litter, and slowed decomposition at these positions in microcosms relative to rates in the field.

N dynamics

Although the species composition and CO_2 origin of litter mixtures made little difference for mass loss rates, they were correlated with N dynamics. In microcosms and in the field, N dynamics of litter on the soil surface were strongly related to the litter's initial N concentration. Litter with a higher initial N content was more likely to release N. This trend suggests that an increase in litter N concentration, whatever the mechanism, could increase the rate at which that N once again becomes available to plants and microbes. If *Lotus wrangelianus* or other N-fixing species increase their dominance in California grasslands as the atmospheric [CO_2] increases (Thayer *et al*. 1999), N availability may increase through

two mechanisms: an increase in the total pool of fixed N due to a faster rate of symbiotic fixation, and a decrease in the proportion of circulating N that is locked up by plant litter as N mineralization accelerates. Any increase in N availability could relieve hypothesized (Schimel 1995) increases in N limitation under elevated [CO_2]. This experiment illustrates consequences of litter N status at a single timepoint, however, and the net process of N immobilization by and release from litter is neither linear nor monotonic. Thus, our results on litter N dynamics should be interpreted with caution.

Litter position made little difference for N dynamics in unfertilized microcosms. Fertilization of microcosms increased N immobilization by litter that was in contact with soil. Despite this increase in immobilization, N availability did not limit decomposition of surface or buried litter. This result is consistent with results from many other studies that have found changes in litter nutrient dynamics, but not mass loss, in fertilized treatments (e.g. Holland & Coleman 1987; Hobbie & Vitousek 1999).

Rising atmospheric [CO_2] will have a range of effects on litter decomposition, but few of these are likely to be important in California grasslands. The most consequential CO_2-driven changes for decomposition rates will be those that alter allocation, which controls litter position. In grasslands and other ecosystems, these changes are likely to be more sensitive to shifts in species dominance than shifts in allocation patterns of individual species. Changes in species composition have the greatest potential to alter the nutrient dynamics and litter quality of California grasslands.

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