

Decomposition of litter produced under elevated CO₂: Dependence on plant species and nutrient supply

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Abstract. We investigated the effect of CO₂ concentration and soil nutrient availability during growth on the subsequent decomposition and nitrogen (N) release from litter of four annual grasses that differ in resource requirements and native habitat. *Vulpia microstachys* is a native grass found on California serpentine soils, whereas *Avena fatua*, *Bromus hordeaceus*, and *Lolium multiflorum* are introduced grasses restricted to more fertile sandstone soils (Hobbs & Mooney 1991). Growth in elevated CO₂ altered litter C:N ratio, decomposition, and N release, but the direction and magnitude of the changes differed among plant species and nutrient treatments. Elevated CO₂ had relatively modest effects on C:N ratio of litter, increasing this ratio in *Lolium* roots (and shoots at high nutrients), but decreasing C:N ratio in *Avena* shoots. Growth of plants under elevated CO₂ decreased the decomposition rate of *Vulpia* litter, but increased decomposition of *Avena* litter from the high-nutrient treatment. The impact of elevated CO₂ on N loss from litter also differed among species, with *Vulpia* litter from high-CO₂ plants releasing N more slowly than ambient-CO₂ litter, whereas growth under elevated CO₂ caused increased N loss from *Avena* litter. CO₂ effects on N release in *Lolium* and *Bromus* depended on the nutrient regime in which plants were grown. There was no overall relationship between litter C:N ratio and decomposition rate or N release across species and treatments. Based on our study and the literature, we conclude that the effects of elevated CO₂ on decomposition and N release from litter are highly species-specific. These results do not support the hypothesis that CO₂ effects on litter quality consistently lead to decreased nutrient availability in nutrient-limited ecosystems exposed to elevated CO₂.

Introduction

Increases in CO₂ emissions to the atmosphere since the mid-1800s have led to concentrations of atmospheric CO₂ unequalled in the last 160,000 years (Post et al. 1990). In order to predict the long-term trajectory of atmospheric CO₂, we must understand the response of long-term carbon cycling to elevated CO₂. The two major control points in the terrestrial carbon cycle are carbon

gain by plant production and carbon release by decomposition. Of these two processes, the response of decomposition to elevated CO₂ is less well understood but is crucial to predictions of long-term changes in carbon storage in ecosystems (Dixon & Turner 1991; Comins & McMurtrie 1993).

Litter quality plays a major role in controlling decomposition rate. Elevated atmospheric CO₂ can affect litter quality by altering tissue concentrations of nutrients (Norby et al. 1986; Billes et al. 1990; Garbutt et al. 1990; Brown 1991; Mooney et al. 1991; Lindroth et al. 1993) or refractory compounds such as lignin (Norby et al. 1986; Bazzaz 1990; Lambers 1993) or by increasing the ratio of root litter to shoot litter (Cotrufo & Ineson 1995). Changes in initial litter quality under elevated CO₂ can also affect soil respiration rates and alter soil microfaunal interactions (Melillo et al. 1982; Coûteaux et al. 1991). Published studies of CO₂ effects on litter decomposition report a range from a 30% increase in decomposition to a 60% decrease, indicating that CO₂ effects on litter decay rates are sensitive to many factors, including initial litter quality (Cotrufo et al. 1994; Cotrufo & Ineson 1995), plant nutrient availability (Kemp et al. 1994), and soil fauna (Coûteaux et al. 1991; O'Neill 1994). Because most ecosystems exhibit some degree of nutrient limitation (Vitousek & Howarth 1991), the response of the biosphere to elevated CO₂ may be constrained by nutrient supply (Mooney et al. 1991; Shaver et al. 1992). Thus, an understanding of the interaction between nutrient levels and the CO₂ response of decomposition is critical to long-term predictions of ecosystem response to elevated CO₂.

The goal of this experiment was to determine the effect of rising atmospheric CO₂ on plant litter quality and decomposition (litter C loss and N release) to predict more accurately the role of soil processes as biological feedbacks in the global carbon cycle. We examined this effect as a function of both soil nutrient level during plant growth and species traits. We hypothesized that elevated CO₂ would reduce litter decomposition and N release, due to reduced litter quality (increased C:N ratio). We expected CO₂ effects on C:N ratio to be particularly pronounced at high nutrient availability and in species with large growth responses to elevated CO₂.

Methods

We studied four annual grasses that differ in resource requirements and occurrence on nutrient-limited serpentine soil. *Vulpia microstachys* is native to California and is typically the dominant grass on California serpentine (Mooney et al. 1986; Huenneke et al. 1990). *Lolium multiflorum* and *Bromus hordaceus* are invasive European grasses that appear infrequently on serpentine soils but invade with fertilization (Huenneke et al. 1990). *Avena fatua*,

another invasive Mediterranean grass, is ubiquitous in California grasslands on more fertile soils but is normally absent on serpentine (Hickman 1993). These four species were chosen to characterize species effects on nitrogen release from decomposing litter in response to elevated CO₂ and nutrient addition.

Plants were grown in open-top chambers at the Jasper Ridge Biological Preserve near Stanford, California, using the Microecosystems for Climate Change Analysis (Field et al. 1996). Each species was grown in monoculture in tubes 1 m deep and 20 cm in diameter in a 2-way factorial design (nutrients × CO₂) during the 1992–1993 growing season, with 7 replicates of each treatment. CO₂ treatments were ambient and ambient + 350 ppm CO₂, and fertilization treatments were unamended serpentine soil and serpentine soil supplemented with 20 g/m² each of nitrogen, phosphorus, and potassium as Osmocote 120-day slow-release fertilizer. Comparable nutrient amendment increased aboveground biomass production to levels found in non-serpentine grasslands (McNaughton 1968; Turitzin 1982; Huenneke et al. 1990). Unamended soils had 3.8 mg N/g soil and 0.5 mg P/g soil (Kjeldahl digestion). Soil pH was 5.5–6.5 (Luo et al. 1994).

Seeds were sown in October 1992, and senescent plant roots and shoots were collected in May 1993 (the end of the growing season for these early-season annuals) for use in this decomposition study. Plant material was dried at 65 °C and weighed. A subsample of roots and shoots from each treatment was ground to a fine powder and analyzed for C and N content by combustion in an elemental analyzer (Roboprep, Europa Scientific). The remaining material from the 7 replicates of each treatment was mixed thoroughly (separate mixtures for shoot and root litter), and then 5 subsamples were removed from each mixture for this decomposition study.

Root and shoot litter from each species were allowed to decompose for 5 months in microcosms using the following experimental design (Hobbie, in press): The material was cut in 0.5 cm lengths, weighed, and placed into nylon mesh litter bags with separate compartments for roots and shoots (total root + shoot mass, 0.4 g/bag). Root and shoot material was partitioned according to the root:shoot ratio exhibited by each species growing under the treatment from which it was harvested (Table 1). Top-soil (top 20 cm) collected from a serpentine grassland at Morgan Hill, California, was air dried, sifted to remove rocks, and weighed (~65 g) into 1 L glass jars. The soil was then watered to approximately 65% of water-holding capacity and incubated for two weeks. Throughout incubation and during the entire experiment, the jars were covered with a fitted plastic film wrap (Handiwrap) that allowed exchange of CO₂ and O₂ but prevented water loss. After the 2-week incubation, litter bags were placed midway between the soil surface and the bottom of the jar

Table 1. Root:shoot dry weight ratios from four annual grasses grown in ambient and elevated CO₂ and fertilized and unfertilized serpentine soil measured at the end of the growing season (data from Field et al., in preparation). Values are means \pm SE ($n = 6$ to 7).

	Plant root:shoot dry weight ratio			
	Unfertilized soil		Fertilized soil	
	350 ppm CO ₂	700 ppm CO ₂	350 ppm CO ₂	700 ppm CO ₂
<i>Avena</i>	0.49 \pm 0.09	0.43 \pm 0.03	0.33 \pm 0.01	0.33 \pm 0.03
<i>Bromus</i>	0.73 \pm 0.14	0.77 \pm 0.07	0.44 \pm 0.04	0.51 \pm 0.04
<i>Lolium</i>	0.56 \pm 0.08	0.94 \pm 0.09	0.39 \pm 0.04	0.45 \pm 0.06
<i>Vulpia</i>	0.35 \pm 0.04	0.36 \pm 0.07	0.27 \pm 0.03	0.23 \pm 0.03

(approximately 1 cm total soil thickness), with 5 replicate litter bags for each treatment.

The jars were incubated in the dark at 20 °C for five mo before harvest. Root and shoot litter was recovered separately, then oven dried (65 °C) and weighed. Litter samples were ground to a fine powder and analyzed for C and N content by combustion, gas-chromatography (Carlo-Erba).

It was difficult to remove mineral soil from the recovered litter samples, so the measured litter mass was corrected for mineral soil contamination based on the measured final litter %C (with mineral soil contamination), initial litter %C, and soil %C. Final litter mass was calculated assuming constant litter and soil %C.

Nitrogen release from the litter after the five months – presented as milligrams N per gram initial litter – was calculated by subtracting final litter N (final litter mass times final litter N concentration, both corrected as above for mineral soil contamination) from initial litter N (initial litter mass times initial litter N concentration).

Root and shoot C:N and whole-microcosm (root + shoot) litter decomposition and N release were analyzed in 3-way analyses of variance (ANOVAs) with CO₂, nutrients, and species as the main effects. Data for all tests passed Cochran's test for homogeneity of variances (Winer et al. 1991). Because the CO₂ \times Nutrient \times Species interaction was significant for both decomposition and N release, each species was also analyzed separately in 2-way ANOVAs. Tukey's *post hoc* multiple range tests were used to compare the four species under common nutrient and CO₂ treatments. To determine differences between root and shoot decomposition and N release, and whether these responded differently to CO₂ and nutrient effects, litter decomposition and N release were also analyzed in 3-way split-plot ANOVAs, with main effects as above and plant fraction (root and shoot) as the within-plot effect.

Table 2. *P*-values from 3-way ANOVAs showing the effects of growth CO₂ concentration, soil nutrient availability, and plant species on litter C:N, mass loss, and N release.

Source of variation	C:N shoots	C:N roots	Mass loss	Nitrogen loss
	<i>P</i> -value			
CO ₂	0.933	0.043	0.099	0.512
NPK	0.054	0.001	0.021	0.417
Species	0.001	<0.001	0.002	0.005
CO ₂ × NPK	0.427	0.391	0.036	0.725
CO ₂ × Species	0.037	<0.001	<0.001	<0.001
NPK × Species	<0.001	0.073	0.005	0.004
CO ₂ × NPK × Sp.	0.044	0.096	0.017	<0.001

Pearson correlations were used to examine relationships between litter C:N, decomposition, and N release to determine whether differences in C:N ratio among species or treatments could explain the overall patterns in decomposition and N release that we observed. Because our major interest was in comparisons across species and treatments we used mean values of each parameter for each species-treatment combination. The correlation analysis was done separately for shoots and roots.

Results

The effect of elevated CO₂ on litter C:N ratio was relatively small and depended strongly on species (CO₂ × species interactions; Table 2, Figure 1). Elevated CO₂ caused the expected increase in litter C:N ratio only in *Lolium* shoots and roots and actually decreased shoot C:N in *Avena* at high nutrients (Table 3, Figure 1). Nutrient addition decreased C:N in *Avena* shoots and roots but increased C:N ratio in *Vulpia* shoots (Table 3, Figure 1)

Species differed in decomposition, but the differences depended on CO₂ and nutrient treatments (Figure 2), as indicated by the strong CO₂ × species interactions (Table 2). Differences were often especially strong between the native grass *Vulpia* and the three non-native species *Avena*, *Bromus*, and *Lolium*. Growth under elevated CO₂ decreased decomposition in *Vulpia* at both nutrient levels but increased decomposition in *Avena* at high nutrients and in *Lolium* at low nutrients (CO₂ × NPK interactions; Figure 2, Table 3). Nutrient addition increased subsequent decomposition of *Avena*, particularly in litter from high-CO₂-grown plants and decreased subsequent decomposition in *Vulpia* litter from both CO₂ levels, and of *Lolium* litter from high CO₂ (Figure 2, Table 3). Decomposition of litter from ambient CO₂ under

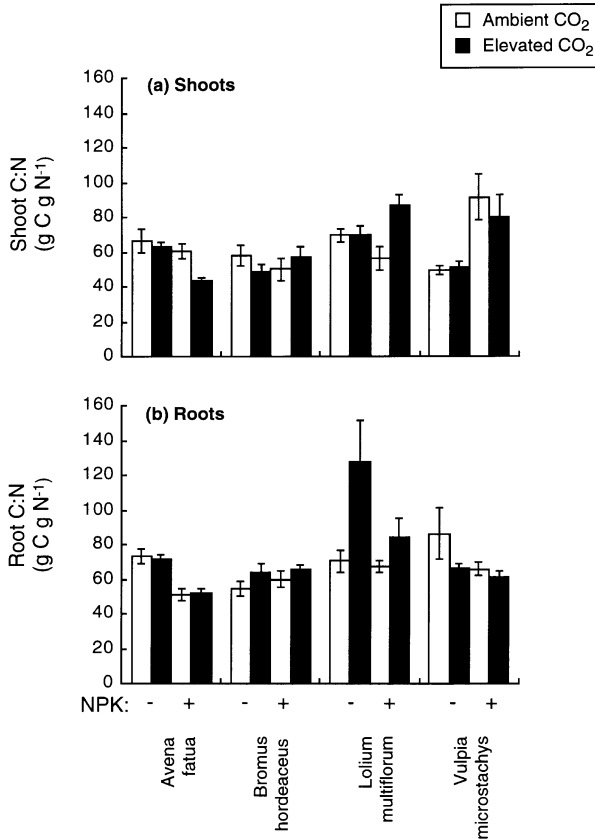


Figure 1. Effect of growth CO₂ concentration and soil nutrient (NPK) availability on (a) shoot and (b) root carbon to nitrogen ratio (gC/gN) at the end of the growing season. Data are means \pm SE ($n = 5$ to 7).

both nutrient conditions did not differ between *Avena*, *Bromus* and *Lolium*, but *Vulpia* litter decomposed significantly faster than the other three (Figure 2). In response to growth at low nutrients and elevated CO₂, *Lolium* litter decomposed the fastest, *Avena* litter the slowest, while *Vulpia* and *Bromus* litter were intermediate. Finally, for plants grown under elevated CO₂ and high nutrients, litter decomposition did not differ among the four species. Thus, while species differed in litter decomposition, the nutrient and CO₂ treatments often eliminated or even reversed these differences.

As with species differences in mass loss, N release from litter during decomposition varied strongly among species and nutrient treatments in response to elevated CO₂ (Figure 3, Table 2; CO₂ \times NPK \times species interaction). Indeed, the pattern for each species was unique. *Vulpia* litter from

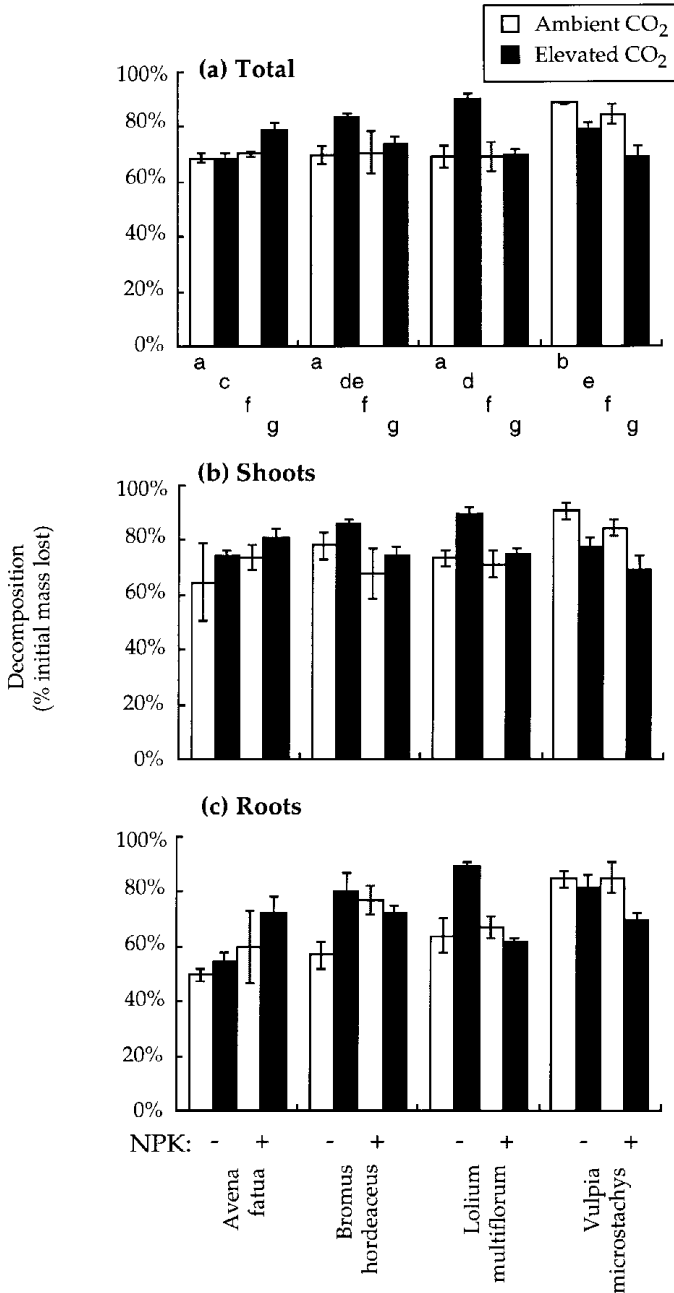


Figure 2. Effect of growth CO₂ concentration and growth soil nutrient (NPK) availability on litter mass loss after 5 months of decomposition in (a) total (whole bag) litter, (b) shoot litter, and (c) root litter. Data are means \pm SE ($n = 5$). For total litter mass loss, means in the same CO₂ and nutrient treatment with a common letter do not differ (Tukey's *post hoc* multiple range test, $P < 0.05$).

Table 3. *P*-values from 2-way ANOVAs showing the effects of growth CO₂ concentration and soil nutrient availability on litter C:N, mass loss, and N release for 4 annual grasses.

	Source of variation		
	CO ₂	NPK	CO ₂ × NPK
	<i>P</i> -value		
Shoot C:N			
<i>Avena</i>	0.020	0.004	0.121
<i>Bromus</i>	0.819	0.931	0.181
<i>Lolium</i>	0.009	0.698	0.010
<i>Vulpia</i>	0.596	0.001	0.510
Root C:N			
<i>Avena</i>	0.940	<0.001	0.738
<i>Bromus</i>	0.118	0.462	0.656
<i>Lolium</i>	0.015	0.115	0.163
<i>Vulpia</i>	0.115	0.105	0.313
Mass loss			
<i>Avena</i>	0.063	0.012	0.046
<i>Bromus</i>	0.077	0.337	0.245
<i>Lolium</i>	0.007	0.112	0.010
<i>Vulpia</i>	0.001	0.040	0.387
N release			
<i>Avena</i>	0.004	0.001	0.006
<i>Bromus</i>	0.585	0.657	0.019
<i>Lolium</i>	0.549	0.263	0.001
<i>Vulpia</i>	0.004	0.799	0.001

high-CO₂ plants lost much less N (particularly from the low-nutrient treatment) compared to litter from low-CO₂ plants (Figure 3, Table 3; CO₂ × NPK interaction). The same inhibitory effect of CO₂ on N release was observed in *Lolium*, but only at high nutrients. In contrast, growth under elevated CO₂ dramatically increased N release from *Avena* litter, particularly in litter from the high-nutrient treatment and from *Bromus* litter (low-nutrient treatment only) (CO₂ × NPK interaction).

Nutrient addition also caused no simple overall effect in litter N release. Rather, changes under fertilization interacted with CO₂ and species (Table 2). In *Avena*, growth under high nutrients stimulated N release from litter, particularly in elevated-CO₂ litter (Figure 3, Table 3; CO₂ × NPK interaction). Nutrient addition increased N release from *Bromus* and *Lolium* litter from the ambient-CO₂ treatment, but decreased it in litter from the elevated-CO₂ treatment (CO₂ × NPK interaction). In contrast, nutrient addition decreased N release from *Vulpia* litter from the ambient-CO₂ treatment.

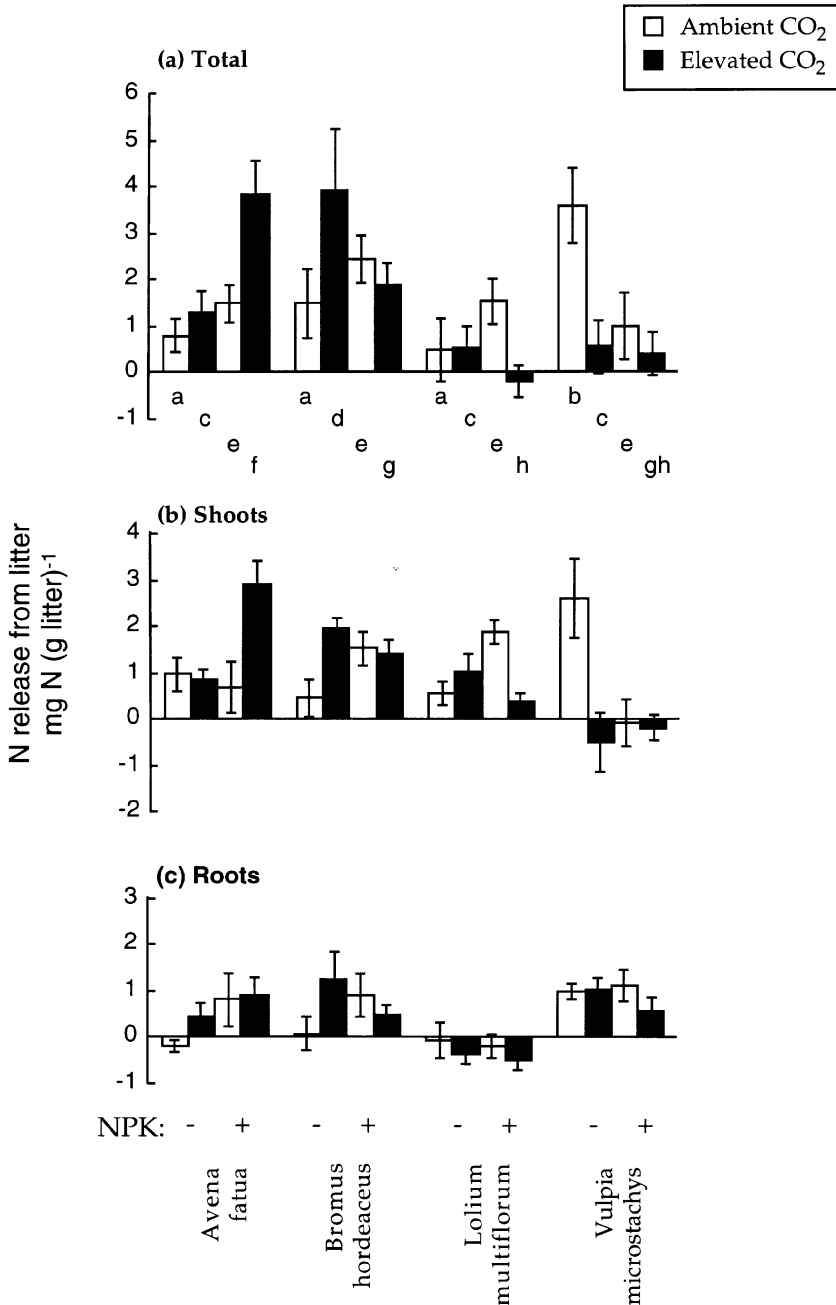


Figure 3. Effect of growth CO₂ concentration and growth soil nutrient (NPK) availability on N release from litter after 5 months of decomposition in (a) total (whole bag) litter, (b) shoot litter, and (c) root litter. Data are means \pm SE ($n = 5$). For total litter N release (a), means in the same CO₂ and nutrient treatment with a common letter do not differ (Tukey's *post hoc* multiple range test, $P < 0.05$). N release from the litter is represented by positive values; net N immobilization in litter (from soil) by negative values.

Though species differed in N release from litter, the direction and magnitude of these differences depended on the CO₂ and nutrient treatments in which the litter was produced (Figure 3, Table 2). For example, of the four grasses at low nutrients, *Vulpia* had the highest N release from litter in the ambient-CO₂, ambient-NPK treatment but relatively low N release from high-CO₂ litter (Figure 3). Of the four grasses grown at high nutrients, N release was highest from *Avena* litter in elevated CO₂, but was relatively low from *Avena* litter grown under ambient CO₂. Thus, growth CO₂ and soil-nutrient conditions strongly determined species differences in N release from litter.

In general, root litter decomposed more slowly and released N more slowly than did shoot litter ($p < 0.001$ for the plant-part effect for each process in 3-way split-plot ANOVA; detailed statistics not shown). However, rates of root and shoot litter decomposition and N loss were not different in some cases, and the magnitude of the difference varied among treatments (Figures 2, 3). For example, *Vulpia* litter did not differ in decomposition rate between roots and shoots, whereas root litter of *Avena* always decomposed more slowly than did shoot litter. The relative decomposition rate of roots and shoots depended on treatment in *Bromus* and *Lolium*. For all species except *Vulpia*, root litter released less N than did shoot litter (Figure 3); roots even immobilized N in some cases. In *Vulpia*, root litter released more N than shoot litter; *Vulpia* shoot litter immobilized N except in the ambient CO₂ and nutrient treatment (Figure 3). For the other three species, the magnitude of the difference between root and shoot N release was larger under some nutrient, CO₂, and species combinations. In summary, although roots decomposed and released N more slowly than shoots in most cases, the magnitude of this difference depended on species, nutrients, and CO₂ treatments.

Litter C:N was a poor predictor of mass loss and N release. Shoot C:N explained 21% of the variance in shoot N release ($P = 0.04$), with higher shoot C:N corresponding with lower N release. In contrast, shoot C:N was not significantly related to shoot mass loss ($P = 0.67$), nor was root C:N significantly related to mass loss ($P = 0.16$) or N release ($P = 0.70$). Thus, in our experiment where there were relatively small treatment and species differences in C:N ratio, factors in addition to tissue C:N must have contributed to species differences in mass loss and litter N release and to changes in these parameters caused by nutrients and elevated CO₂.

Discussion

Perhaps the most striking result of our study was the strong difference among species in the effect of elevated CO₂ on subsequent litter decomposition and N release, even though all study species were annual grasses grown under the

same conditions. Contrary to our initial hypothesis, litter from plants grown under elevated CO₂ often decomposed more rapidly than did litter of ambient-CO₂-grown plants. This occurred at high nutrients in *Avena* and at ambient nutrients in *Bromus* and *Lolium*. The stimulation of decomposition by growth under elevated CO₂ may reflect accumulation of carbohydrates or other labile carbon substrates. Only the native grass *Vulpia* showed the expected decrease in mass loss from litter produced under elevated CO₂. Similarly, the effects of elevated CO₂ on N release were complex, depending on soil nutrient availability and plant species. Growth of plants under elevated CO₂ caused litter to release N more rapidly in *Avena* and more slowly in *Vulpia*, although, for all species, the CO₂ effect on N release was strongly affected by nutrient treatment.

Previous studies also show conflicting evidence for reduced decomposition and N mineralization rates in high-CO₂-grown litter. Boerner & Rebeck (1995) report a decrease in both mass loss and in N release in yellow poplar leaves from seedlings grown in elevated CO₂. Cotrufo & Ineson (1995) report a decrease in mass loss of elevated-CO₂ birch roots but no change in elevated-CO₂ spruce roots. Kemp et al. (1994) found no significant effects of elevated CO₂ on decomposition of *Andropogon gerardii*, *Sorghastrum nutans*, and *Poa pratensis* litter produced in tallgrass prairie. Norby & O'Neill (1991) also found no significant effect of elevated CO₂ on the decomposition of *Populus* leaf litter. Finally, Coûteaux et al. (1991) report a retarded weight loss of elevated-CO₂ sweet-chestnut leaf litter decomposed in soil fauna of low diversity but an increased weight loss with more complex soil fauna. Because species differ so strongly in CO₂ effects on decomposition, there is currently little support for the hypothesis that elevated CO₂ will consistently reduce nutrient availability in ecosystems through reductions in litter quality (Bazzaz 1990; Field et al. 1992; Boerner & Rebeck 1995), particularly when CO₂ has relatively small effects on C:N ratio.

The significant differences between shoot and root litter in C:N ratio, decomposition rate, and N release suggest that responses of litter decomposition and N release to elevated CO₂ may be strongly influenced by root:shoot ratio, which depends on species traits and nutrient availability as well as CO₂ level.

Past studies of litter decomposition of elevated-CO₂ litter have shown litter C:N ratio to be a good predictor of mass loss and nutrient release rates (Taylor et al. 1989; Cotrufo et al. 1994). Cotrufo & Ineson (1995) found that initial litter C:N accounted for 63% of the variation in mass loss in elevated-CO₂ litter from birch and spruce roots, and was a better predictor of mass loss than %N. Studies involving C:N ratios in elevated-CO₂ litter have reported a range of results, including no change in leaf-litter quality (Norby & O'Neill 1991);

an increase in shoot C:N but no change in root C:N (Chu et al. 1992); and an increase in root C:N in both low N environments (Curtis et al. 1990; Barnes & Pfirrmann 1992; Kohen et al. 1992; Cotrufo & Ineson 1995) and high N environments (Kohen et al. 1992; Diaz et al. 1993). In our study, the CO₂ effects on initial litter C:N were relatively small so that other (unmeasured) factors apparently exerted greater effect on decomposition and N release. For example, elevated CO₂ caused a decline in lignin concentration of *Avena fatua* (Chu et al., in press). Similarly, there was no effect of elevated CO₂ on C:N ratio of aboveground litter of the total community in California serpentine and sandstone grasslands (Hungate et al., in press a), and Kemp et al. (1994) found species differences to be a greater controlling factor than changes in litter chemistry for litter decomposition and nutrient release in elevated-CO₂ litter. In summary, our results and the literature do not support predictions that CO₂-induced declines in foliar N content will result in consistent and predictable decreased litter decomposition and nutrient release rates (Field et al. 1992; Lambers 1993; Boerner & Rebeck 1995).

The strong species differences in CO₂ effects on decomposition and N release from litter that we observed have important implications for future changes in species composition of annual grasslands in California. Because *Bromus* can invade serpentine soil when nutrient availability is high (Huenneke et al. 1990), elevated CO₂ could favor its success by increasing litter turnover and N release. In contrast, because *Vulpia* can thrive at extremely low nutrient levels characteristic of serpentine soil (Huenneke et al. 1990), decreased N release from *Vulpia* litter in elevated CO₂ could reduce the ability of *Bromus* to invade serpentine, favoring *Vulpia*. The relative importance of these opposing CO₂ effects on N release during decomposition will depend on the CO₂-stimulation of biomass for these species, and on how these species compete under elevated CO₂, and thus their respective contributions to the litter pool. The invasive species tend to show a larger biomass response to elevated CO₂ (Hungate et al., in press b), suggesting that the positive feedback to nutrient availability through increased decomposition of *Bromus* litter may override the negative feedback to nutrient availability through decreased decomposition in *Vulpia* litter. If so, elevated CO₂ has the potential to replace fertilization as a window through which *Bromus* could invade serpentine grassland. As serpentine grasslands are one of the few repositories of native California grasses (Huenneke et al. 1990), such changes in species composition could have important implications for conservation.

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