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ECOSYSTEMS

Elevated Carbon Dioxide and Litter Decomposition in California Annual Grasslands: Which Mechanisms Matter?

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ABSTRACT

To date, most research that has examined the effect of elevated atmospheric carbon dioxide concentration ([CO_2]) on litter decomposition has focused on changes in the leaf litter quality of individual species. Results from California grasslands indicate that other CO_2 responses may have greater consequences for decomposition rates. For instance, CO_2-driven changes in either species dominance or patterns of biomass allocation would alter both the quality and the position of grassland litter. We review the results from studies in California grasslands to identify the mechanisms that affect grassland litter decomposition. We use a simple calculation that integrates the results of two studies to identify three mechanisms that have the potential to substantially alter decomposition rates as the atmospheric [CO_2] rises.

Key words: allocation; elevated CO_2; litter decomposition; litter position; litter quality; plant litter; serpentine grassland; soil microbiota; soil moisture; species composition.

INTRODUCTION

Over the last decade, research investigating the effects of elevated atmospheric carbon dioxide concentrations ([CO_2]) on litter decomposition has focused on changes in the quality and mass loss rates of litter from individual species (O'Neill and Norby 1996). This focus reflects the history of the field. Early observations of decreases in the nitrogen (N) concentration of green leaves under elevated [CO_2] (see Cotrufo and others 1998 for a review) led to speculation that litter quality would also decline (Strain and Bazzaz 1983).

It is now apparent that the rise in [CO_2] will not consistently decrease litter quality across species or ecosystems (Norby and others 2001), although changes in the litter chemistry of individual species are likely to affect litter decomposition rates of some ecosystems (Cotrufo and others 1994; Cotrufo and Ineson 1996; Franck and others 1997). In other ecosystems, the most important effects of elevated CO_2 on decomposition may be indirect (Figure 1). For instance, a rise in [CO_2] might decrease the success of an abundant species, which would alter ecosystem-level litter chemistry. Elevated [CO_2] can also lead to changes in the physical and biotic aspects of the environment and alter biomass allocation patterns. These changes all have the potential to affect litter decomposition, but they have not been examined until recently.

The Jasper Ridge CO_2 Experiment took place in 1992–97 at Jasper Ridge Biological Preserve, which is located on the San Francisco Peninsula in central

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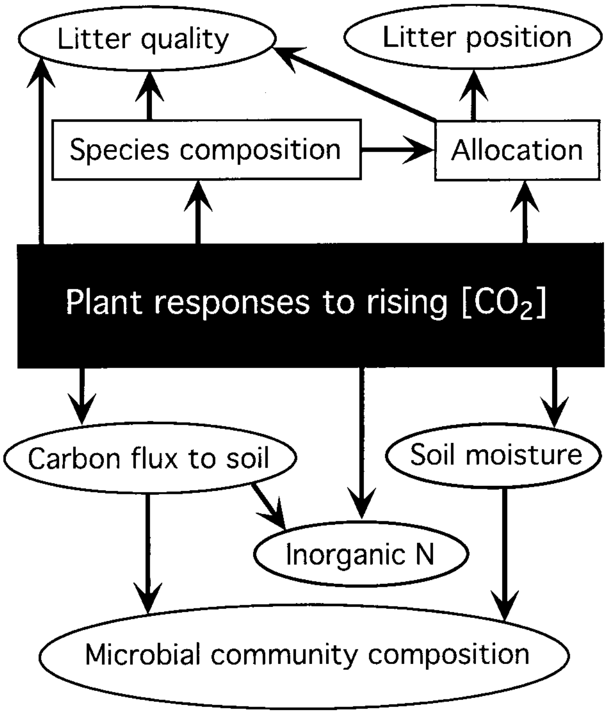

Figure 1. Conceptual diagram of mechanisms through which responses of plants to rising [CO_2] may alter litter decomposition rates. Circled properties directly affect decomposition.

California, USA. This region has a Mediterranean climate and receives a mean annual precipitation of 667 mm. Two types of grassland, which differ in species composition and soil type, grow in close proximity on this preserve. The more extensive grassland is composed primarily of European annual grasses growing on moderately fertile sandstone-derived soils. In contrast, the nutrient-poor soils of the neighboring serpentine grassland are covered by dense stands of spring-flowering native annual forbs. Among these carpets of early-season annuals grow various densities of summer-flowering native annuals and more widely spaced perennial bunchgrasses (McNaughton 1968).

For the Jasper Ridge CO_2 Experiment, plots in each of these types of grasslands were enclosed in small open-top chambers and fumigated with either ambient or CO_2-supplemented air for 5 years. In addition, microcosms were exposed to ambient and CO_2-enriched air in open-top chambers (Field and others 1996). Several studies within this larger experiment examined mechanisms through which elevated [CO_2] could impact decomposition. Other studies of California grassland species also offered insights into the topic. Here we summarize and integrate results from several studies to provide a comprehensive assessment of the potential impact of rising [CO_2] on decomposition in California grasslands on both sandstone and serpentine soils. In the conclusion, we discuss how findings from these grasslands relate to those from other terrestrial ecosystems.

DIRECT EFFECTS ON LITTER QUALITY

In these California grasslands, the effect of elevated [CO_2] on litter quality varies among plant species but is very small on litter of mixed species grown in communities. Our discussion of the effects of elevated [CO_2] on litter quality focuses on tissue carbon–nitrogen (C:N) ratio, because this parameter is often a better indicator of decomposition rates of herbaceous plant tissues than lignin concentration or lignin:N ratio (Taylor and others 1989). In monocultures of serpentine and sandstone annuals grown with high and low nutrient availability, the effects of elevated [CO_2] on live and senescent tissue C:N ratios were quite variable among species, and this variation obscured any consistent effect of elevated [CO_2]. For example, among six annual grasses and forbs, only senesced roots of *Lolium multiflorum* and *Lasthenia californica* showed the predicted increase in C:N ratio in response to elevated [CO_2], and senesced shoots of *Avena fatua*, when grown with supplemental nutrient fertilizer, actually had a lower C:N ratio in elevated compared to ambient [CO_2] (Franck and others 1997; B. A. Hungate unpublished) (Figure 2). The C:N ratios of litter of *Plantago erecta* and *Bromus hordeaceus* were not significantly affected by growth in elevated [CO_2] at either high or low soil nutrient levels, and CO_2 enrichment tended to decrease C:N of senesced roots of *Vulpia microstachys* (B. A. Hungate unpublished; Franck and others 1997) (Figure 2A and B). Species within plant functional types—for example, grass versus forb, invasive versus native—did not clearly exhibit similar responses to elevated [CO_2]; rather, species responses were individualistic. The effects of elevated [CO_2] on litter C:N were dampened in mixed-species litter of above- and belowground tissues collected from microcosms grown with either ambient or supplemental nutrient fertilizers (circles in Figures 2A and B). Similarly, 3 years of data on aboveground litter collected from the field experiment showed no significant effects of elevated [CO_2] on litter C:N in either sandstone or serpentine grasslands (Figure 2C). Thus, while elevated [CO_2] caused some species-specific changes in tissue C:N when grown in monoculture, these effects were largely absent at the community level and when plants were grown under field conditions.

Root and shoot litter generated from plants grown in monoculture and decomposed in laboratory microcosms showed that growth in elevated [CO_2] caused species-specific changes in litter decomposition (Franck and others 1997). Litter of *A. fatua* from plants grown in elevated [CO_2] at high nutrients decomposed more quickly compared with low-[CO_2]–grown *A. fatua*—a change that is consistent with the lower litter C:N ratio in this species caused by elevated [CO_2]. However, CO_2-induced changes in litter decomposition did not consistently relate to the effects of elevated [CO_2] on litter C:N ratio. Specifically, *V. microstachys* was the only species for which growth in elevated [CO_2] consistently decreased the rate of decomposition and associated N mineralization, even though elevated [CO_2] actually tended to decrease the litter C:N ratio in this species. The lack of correlation between effects of elevated [CO_2] on C:N ratio—which is a standard index of litter quality (Taylor and others 1989)—and mass loss was probably due to the poor predictive value of the litter quality index in this particular system; across all litter types in this study, C:N ratio was not significantly related to mass loss (Franck and others 1997).

In summary, the overall effects of elevated [CO_2] on litter decomposition were quite small. When elevated [CO_2] did have an effect, the changes were not clearly related to shifts in litter C:N ratio. In these serpentine monocultures, the effects of elevated [CO_2] on decomposition differed not only in magnitude but also in sign. Thus, it is likely that changes in species composition in response to elevated [CO_2] could have a large effect on decomposition rates.

Results from experiments at the community level provide little support for a CO_2-driven decrease in

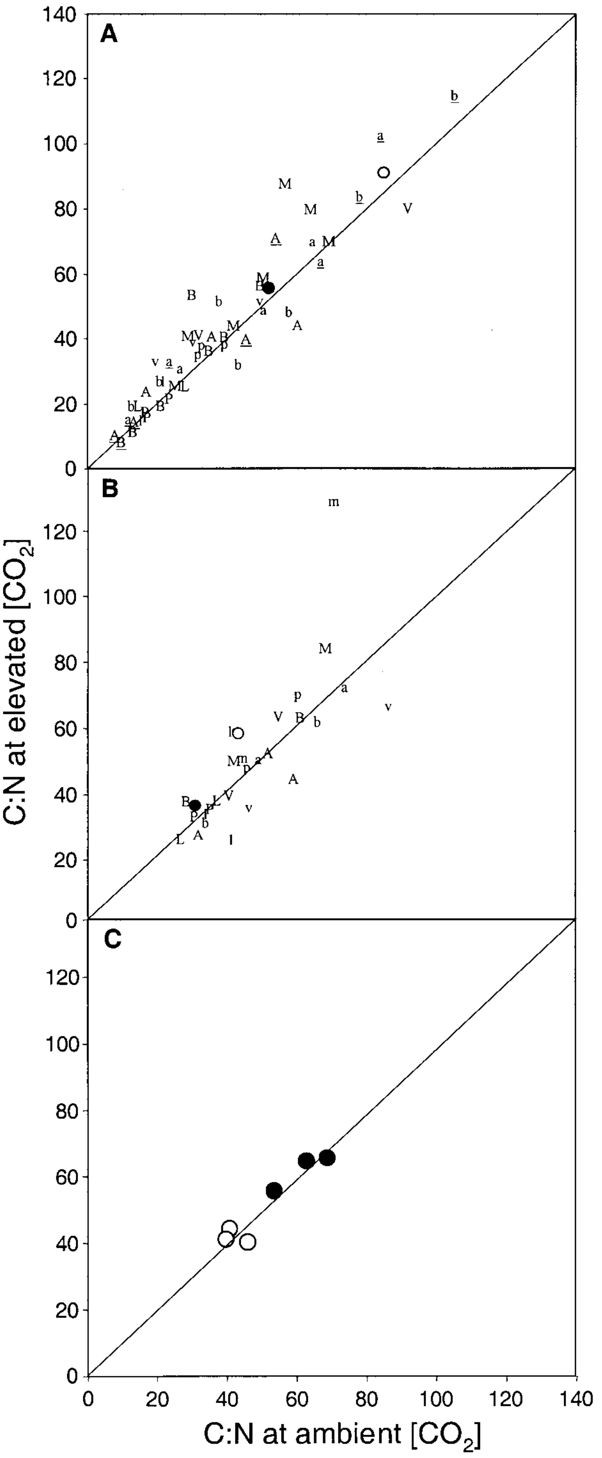

Figure 2. The effect of elevated [CO_2] on tissue and litter carbon–nitrogen ratio (C:N), expressed as C:N in elevated [CO_2] as a function of C:N in ambient [CO_2] for (**A**) shoots and (**B**) roots of single species grown in monoculture (letters) or mixed communities (underlined letters) with ambient (lower case) or supplemental (upper case) NPK fertilizer (+ 20 g m^{-2} y^{-1}) (Franck and others 1997; Hungate and others 1996; B. A. Hungate unpublished). Species are indicated as follows: *Avena fatua* (A or a), *Bromus hordeaceous* (B or b), *Lasthenia californica* (L or l), *Lolium multiflorum* (M or m), *Plantago erecta* (P or p), and *Vulpia microstachys* (V or v). Within a species and nutrient treatment, high C:N values indicate senescent tissue, whereas low C:N values indicate live tissue. Also shown are C:N values for (**A**) shoots and (**B**) roots of mixed-species litter from microcosm experiments with ambient (open circles) or + 20 g m^{-2} NPK (filled circles) fertilizer (Hungate and other 1997c; Dukes and Field 2000). (**C**) C:N ratios of mixed-species litter collected from the field open-top chamber experiment from the sandstone (filled circles) and serpentine (open circles) grasslands in January 1993, 1994, and 1995. In each panel, the solid line shows the 1:1 relationship.

decomposition rates, but they do show that changes in the quality and quantity of litter can alter soil N transformations during the early season. During the 10 days following the first autumn rains, microbial immobilization of tracer $^{15}NH_4^+$ was higher in the microcosms with elevated [CO_2]-grown litter than in those with ambient [CO_2]-grown litter, likely a consequence of increased root mass and a slightly increased root C:N caused by elevated [CO_2] (Hungate and others 1997c). However, growth in elevated [CO_2] had no effect on the mass loss of mixed-species litter (Dukes and Field 2000). In this case, small or species-dependent effects of elevated [CO_2] on litter quality (Figure 2A and B) diminished the effect at the community level, leading to no change in decomposition rates. We conclude that elevated [CO_2] does not consistently decrease litter quality and subsequent decomposition in these grassland ecosystems.

INDIRECT EFFECT ON LITTER QUALITY

Species Composition

Although the direct responses of litter quality to elevated [CO_2] may have important consequences for biogeochemical processes, the indirect effects, such as changes in species composition, may be of equal or even greater consequence. In communities where species differ in litter quality, CO_2-driven changes in species dominance have the potential to alter decomposition rates. In the elevated [CO_2] treatments of the Jasper Ridge CO_2 Experiment, the most frequently observed shifts in species composition were increases in the dominance of annual legumes and late-flowering forbs (Chiariello and Field 1996; Field and others 1996; N. R. Chiariello and others unpublished).

Late-flowering annual forbs can produce half of the total aboveground biomass in serpentine grasslands, and they produce up to about 10% of the total biomass in sandstone grasslands (Field and others 1996; N. R. Chiariello and others unpublished). These species appear to respond to the increase in summer water availability that accompanies elevated [CO_2] (Chiariello and Field 1996). In a 1994 microcosm experiment, elevated [CO_2] increased the density ($P < 0.02$) and biomass ($P < 0.09$) of *Hemizonia congesta* ssp. *luzulifolia* in mixed-species communities on serpentine soil, but the increase in *Hemizonia's* proportional contribution to total community biomass was small (increases of less than 1% and approximately 3% in two different community types) (Chiariello and Field 1996). In the early years of the field experiment, elevated [CO_2] did not cause a significant change in the total aboveground biomass production of either type of grassland before senescence of the dominant grassland species. However, after senescence of the grasses, elevated [CO_2] increased production of the most common late-flowering forbs on both serpentine and sandstone soils (Field and others 1996). The abundance of these species, *Calycadenia multiglandulosa* on serpentine soils and *H. congesta* on sandstone soils, declined in the chambered plots in subsequent years. It is suspected that the decline was a result of poor pollination; both species are self-sterile, and pollinator access to the insides of the chambers was at least partially restricted. By 1997, a self-compatible late-flowering species, *Epilobium brachycarpum*, had become abundant in the serpentine plots, where it tended to produce more biomass under elevated [CO_2] (N. R. Chiariello and others unpublished).

Increases in the prevalence of late-season annuals will alter the litter chemistry of California grasslands, because these species differ from other species in their litter chemistry (Hooper and Vitousek 1998). However, it is not clear whether these changes will lead to increased or decreased decomposition rates. Whereas leaf litter of the native late-flowering forb *H. congesta* decomposes more slowly than that of the dominant grass (*A. barbata*), litter from the introduced late-season forb *Centaurea solstitialis* decomposes more rapidly (Figure 3).

Legumes, which generally make up a small fraction of the aboveground biomass in these grassland ecosystems, might become more abundant under elevated [CO_2] (Verville 1999; S. S. Thayer and others unpublished). In a microcosm experiment with grassland communities growing in different moisture regimes on both soil types, elevated [CO_2] dramatically stimulated the growth of a native legume, *Lotus wrangelianus*. Carbon dioxide enrichment significantly increased the contribution of this species from 8% to 22% of aboveground community biomass in droughted sandstone microcosms and from 22% to 34% in the wettest treatment (S. S. Thayer and others unpublished). Although the proportion of total biomass contributed by *L. wrangelianus* also increased under elevated [CO_2] in serpentine microcosms, the change was less dramatic. By the 1997 harvest of the field experiment, elevated [CO_2] had significantly increased the biomass and density of legumes (primarily *L. wrangelianus*) on both soil types (N. R. Chiariello and others unpublished). However, because legumes remained a much smaller proportion of total aboveground biomass in the field (generally less than 1%), their potential influence on soil pro-

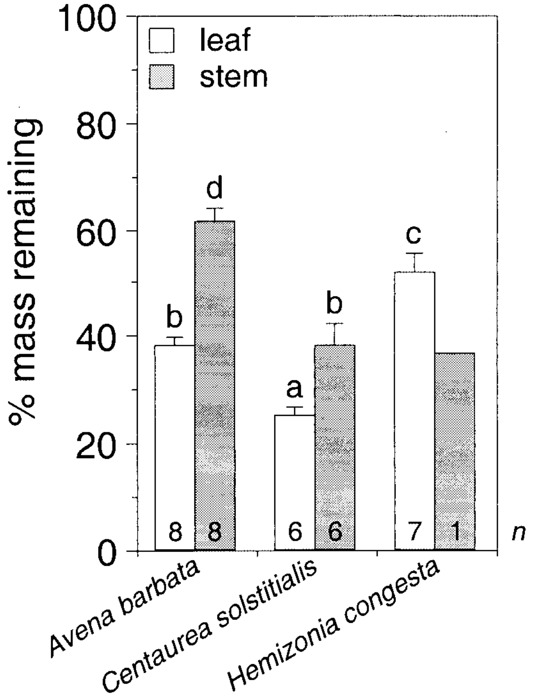

Figure 3. Percent ash-free mass remaining of litter from three species. Plants were grown in ambient [CO_2]. Litter decomposed for 14 months in stainless steel mesh (0.5-mm) bags that were placed on the soil surface in grassland at Jasper Ridge Biological Preserve. Sample size is given at the bottom of each bar. Bars labeled with different letters differ significantly (ANOVA, $P = 0.0001$, followed by the Student-Newman-Keuls test, $\alpha = 0.05$. *Hemizonia* stems were excluded from the analysis due to the lack of replication). Data from J. Dukes (unpublished).

cesses may be limited. Litter from *L. wrangelianus* is relatively N-rich compared with that of the dominant grass species on these soils (Dukes and Field 2000).

Dukes and Field (2000) expected decomposition rates of shoot litter to accelerate as the proportional contribution of *L. wrangelianus* to the total litter pool increased. They assembled multispecies mixtures of litter containing either 10% or 40% *L. wrangelianus* and allowed them to decompose in common environments for 33 weeks. The mixtures differed in litter chemistry, with significantly higher concentrations of N in the legume-rich litter mixture. This difference in litter chemistry did not induce consistent or substantial differences in decomposition rate, possibly because both types of litter had relatively high C:N ratios, or because the incubation time was too short for differences to appear. Although differences in mass loss were small and inconsistent, clear differences in N dynamics emerged. When litter was placed on the soil surface, legume-rich mixtures released N faster than the legume-poor litter mixtures. This result suggests that an increase in legume abundance could lead to a rise in N availability in the grasslands through two mechanisms. First, the increase in legume abundance could increase ecosystem-level N fixation, directly increasing the pool of available N in the ecosystem (see also Verville 1999). Second, litter from *L. wrangelianus* may release N more quickly than litter from other species, increasing the pool of obtainable N for plants and microbes.

Allocation

The rise in atmospheric [CO_2] may affect ecosystem-level biomass allocation through two mechanisms (Figure 1): directly, by altering the proportion of carbon and nutrients that individual species allocate to different organs, or indirectly, by altering the relative abundance of species that have different allocation patterns. Similarly, there are two mechanisms through which changes in allocation patterns can influence litter decomposition (Figure 1). First, because plant parts differ in chemical composition, they differ in their intrinsic decomposability. Increased allocation to a relatively recalcitrant plant part reduces the overall decomposition rate of the plant. Second, allocation patterns determine the initial position, and thus the surrounding environment, of litter. Litter position is an important determinant of initial decomposition rates in California grassland (Dukes and Field 2000).

The results of one study conducted at Jasper Ridge suggest that rising [CO_2] is unlikely to cause significant direct changes in the root versus shoot allocation of many California grassland species. Of six species that were grown in fertilized and unfertilized serpentine soil, only *Lolium multiflorum* in unfertilized soil significantly altered its root:shoot ratio in response to elevated [CO_2] (Joel 2000) (Figure 4).

In the short term, the rise in [CO_2] may be more likely to affect allocation to leaves versus stems than roots versus shoots. By slowing the drawdown of soil moisture, elevated [CO_2] appears to increase the summer growth of late-flowering annuals. At this time of year, stem growth exceeds leaf growth in many of these species, so the increase in late-season growth should lead to decreased leaf:stem ratios. This phenomenon is apparent in the nonnative late-season annual *Centaurea solstitialis*, which, when grown in single-species microcosms on sandstone soils, allocated 26% of its aboveground biomass to stems under ambient [CO_2] and 38% under elevated [CO_2]. The increase in stem biomass com-

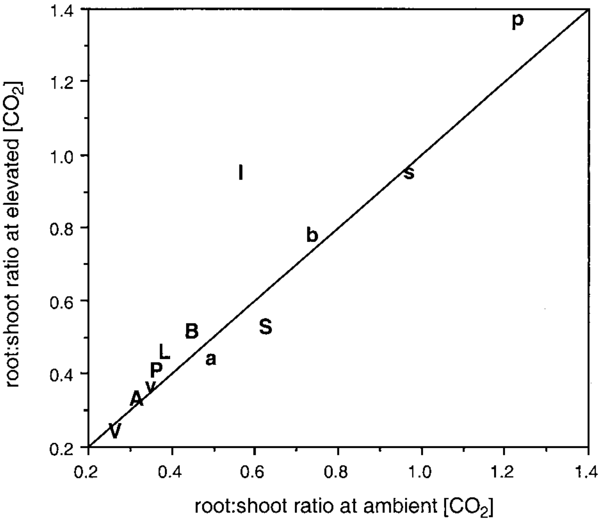

Figure 4. Root:shoot ratio responses of six species to elevated [CO_2], expressed as root:shoot in elevated [CO_2] as a function of root:shoot in ambient [CO_2]. All species were grown as monocultures in serpentine soil microcosms.: A, *Avena barbata*; B, *Bromus hordeaceus*; L, *Lolium multiflorum*; S, *Lasthenia californica*; P, *Plantago erecta*; V, *Vulpia microstachys*. Uppercase letters represent data from microcosms fertilized with N, P, and K. Lowercase letters represent data from unfertilized microcosms. The solid line shows the 1:1 relationship. Data from Joel (2000).

prised 71% of the aboveground biomass stimulation for monocultures of this species on sandstone soils and 60% on serpentine soils (J. S. Dukes unpublished). Because the increased growth of late season annuals can constitute the bulk of the biomass stimulation in these ecosystems (Field and others 1996), an increase in stem tissue of late-season annuals may account for much of the total biomass increase in California annual grassland.

CO_2-driven changes in the leaf:stem ratios of plants occur in other functional groups but they are generally less dramatic. In a series of microcosm studies, Joel and others (2001) documented allocation patterns of species that were grown as monocultures in a factorial combination of ambient and elevated [CO_2] and nutrient availability. Several species—including *Avena barbata, Bromus hordeaceus, Lasthenia californica*, and *Lolium multiflorum*—altered their allocation to leaves or stems in response to increased nutrient availability, but only one species—*B. hordeaceus*—significantly altered its allocation to leaves and stems under elevated [CO_2]. High [CO_2] caused *B. hordeaceus* to increase its allocation to stems in both fertilized serpentine monocultures and sandstone soil–based communities. In a separate microcosm study, J. H. Verville (unpublished) found that elevated [CO_2] decreased the leaf:stem ratio of both grass species (*A. barbata* and *B. hordeaceus*) that were grown in mixed-species communities on sandstone-derived soil (Figure 5).

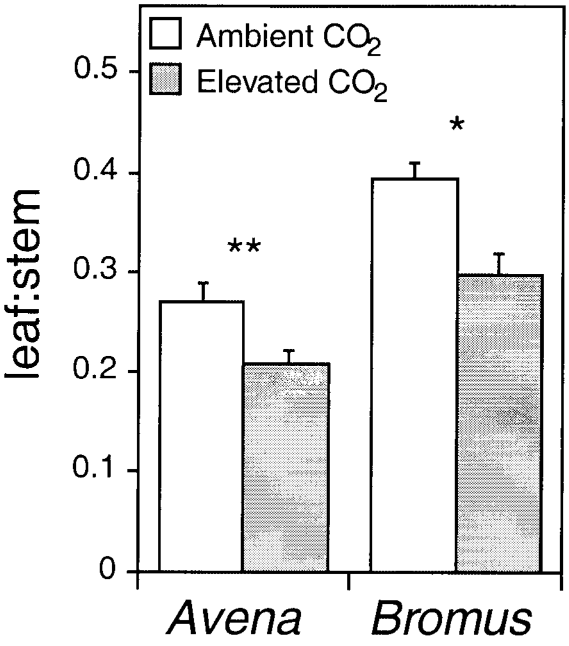

Figure 5. Leaf:stem ratios of two grass species (*Avena barbata* and *Bromus hordeaceus*) grown in polycultures. Polycultures grew in microcosms on sandstone-derived soil and were exposed to either ambient or ambient + 350 ppm CO_2. Asterisks denote significant differences between CO_2 treatments: *$P < 0.05$; **$P < 0.01$ Data from J. H. Verville (unpublished).

Rising [CO_2] could indirectly alter the ecosystem-level root:shoot and leaf:stem ratios by facilitating changes in species dominance (Figure 1). As shown in Table 1, root:shoot allocation varies widely among California grassland species (and depends strongly on soil fertility) (Figure 4). Gulmon and others (1983) studied three annuals growing in serpentine grassland. These native forbs illustrate the magnitude of variation among species in leaf:stem ratios. Typical of many late-season annuals, *H. congesta* grows in rosette form until May, when it develops a stem that eventually comprises most of its biomass. Stem tissue makes up a substantial and constant fraction (approximately 35%) of total biomass during the growth of *Clarkia rubicunda*, which flowers in midsummer. In contrast, very little biomass is allocated to stems by the earliest-flowering of the species, *Plantago erecta*. Annual grasses differ less dramatically than annual forbs in their allocation patterns. Stems comprised approximately two-

Table 1. Percent of Total Plant Biomass Contributed by Roots of California Grassland Species at the End of the Growing Season

Species	Type of Plant	Type of Experiment[a]	% Roots	Reference
Bromus hordeaceus	annual grass	Pot	20	Armstrong 1991
Elymus multicetus	perennial grass	Pot	55	Armstrong 1991
Eschscholzia californica	perennial forb	Pot	57	Armstrong 1991
Hemizonia congesta ssp. *luzulifolia*	late-flowering annual forb	Pot	19	Armstrong 1991
Plantago erecta	early-flowering annual forb	Pot	26	Gulmon and others 1983
Bromus diandrus	annual grass	Pot	11	Holmes and Rice 1996
Nassella pulchra	perennial grass	Pot	29	Holmes and Rice 1996
Avena fatua	annual grass	Pot	33	Joel and others 2001
Bromus hordeaceus	annual grass	Pot	42	Joel and others 2001
Calycadenia multiglandulosa	late-flowering annual forb	Pot	42	Joel and others 2001
Lasthenia californica	early-flowering annual forb	Pot	49	Joel and others 2001
Lolium multiflorum	annual grass	Pot	36	Joel and others 2001
Plantago erecta	early-flowering annual forb	Pot	55	Joel and others 2001
Vulpia microstachys	annual grass	Pot	26	Joel and others 2001
Clarkia rubicunda	mid-flowering annual forb	Field	7	King and Roughgarden 1983
Plantago erecta	early-flowering annual forb	Field	14	King and Roughgarden 1983

Comparisons among species are best made within single experiments, because different researchers used different soils and root harvesting techniques.

[a] *All plants were grown in ambient [CO_2] without nutrient amendments. Plants in pot studies were grown as monocultures in serpentine soil, except for those studied by Holmes and Rice, which were grown in a sandy loam, and those studied by Armstrong, which were grown in sand.*

thirds of the nonreproductive aboveground biomass in all four of the annual grass species studied by Joel and others (2001).

Allocation patterns directly influence the process of decomposition by moderating ecosystem-level litter quality. Changes in allocation patterns are accompanied by corresponding changes in litter quality because plant parts differ in their chemical composition (Hooper and Vitousek 1998) and vulnerability to attack by decomposers. Franck and others (1997) decomposed root and shoot litter of four annual grass species in common environments and observed that, in general, root litter decomposed and released N more slowly than shoot litter. J. S. Dukes (unpublished) observed that, for the grass *A. barbata* and the forb *C. solstitialis*, stem litter decomposed more slowly than leaf litter over 1 year (Figure 3).

Litter Position

Allocation patterns also control the decomposition process by determining the environment in which litter eventually decomposes. A change in allocation to shoots and roots alters the ratio of buried litter to litter that decomposes aboveground. For forbs that either grow leaves in a rosette or drop their leaves from the stem upon senescence, the pattern of allocation to leaves versus stems determines the initial ratio of litter that decomposes close to the ground to litter that is suspended above the soil surface. For instance, most of the leaf biomass of *H. congesta*, *C. multiglandulosa*, and *C. solstitialis* is contained in rosettes that develop and remain near the soil surface. However, stems of these and other late season annuals often remain standing in the grasslands for many months after the plants have senesced (J. S. Dukes unpublished).

Differences in litter position strongly affect litter decomposition rates in California annual grasslands. In a 33-week litterbag study, litter that was suspended aboveground in the field decomposed 36% more slowly than litter placed on the soil surface, which decomposed 14% more slowly than litter buried just beneath the soil surface (Dukes and Field 2000) (Figure 6).

These results indicate that by changing the initial position of litter, decreases in the leaf:stem ratio of *H. congesta* and other forbs would slow litter decomposition in California grasslands. We would expect this change to be more pronounced in serpentine grasslands, where late-season annuals are abundant, than in more fertile grasslands, where late-season annuals comprise a smaller portion of the total aboveground biomass. Recent increases in the

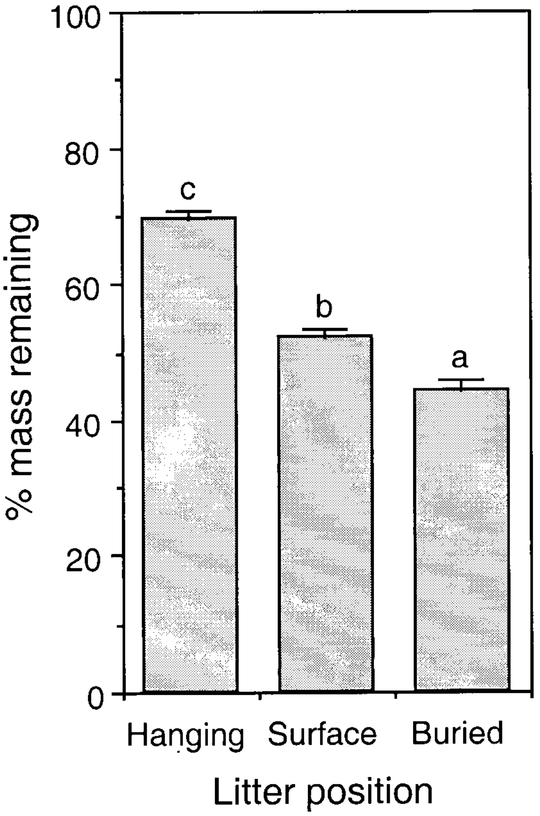

Figure 6. Percent mass remaining of ambient-[CO_2]-grown, mixed-species shoot litter at three positions. Litter decomposed in the field for 33 weeks. Data from Dukes and Field (2000). Bars labeled with different letters differ significantly (ANOVA, $P < 0.0001$, followed by the Student-Newman-Keuls test, $\alpha = 0.05$).

abundance of the biological invader *C. solstitialis* in California grasslands (Maddox and Mayfield 1985; Pitcairn and others 1998) may have both accelerated decomposition (Figure 3) and increased the sensitivity of decomposition to elevated [CO_2] by altering the ecosystem-level allocation response to CO_2.

CHANGES IN THE DECOMPOSITION ENVIRONMENT

Increased Carbon Input to Soil

The increase in atmospheric [CO_2] may also influence litter decomposition through changes in the decomposition environment. For instance, by increasing the flow of carbon (C) to soil through root exudation and root turnover (van Veen and others 1991; Hungate and others 1997b), elevated [CO_2] can alter the balance and availability of C and nutrients for decomposer microorganisms in the rhizosphere. Two experiments conducted in California grasslands directly addressed the idea that elevated [CO_2] alters soil C turnover through changes in C input to soil. In the first, a pulse label of $^{13}CO_2$ was used to trace subsequent C release from labeled litter (Hungate and others 1997b). In the second, serpentine and sandstone communities, both comprising C_3 plants, were grown in a soil developed under C_4 grasses, thereby providing a ^{13}C signature that distinguished plant-derived from soil-derived C (Cardon 1996; Cardon and others 2001). Monitoring CO_2 efflux and its isotope composition in these experiments provided a way to partition soil respiration into its various components. In both cases, elevated [CO_2] increased the relative contribution of root-derived C to soil respiration, consistent with an increase in root respiration, exudation, and turnover in elevated [CO_2] (Hungate and others 1997b; Cardon and others 2001).

Elevated [CO_2] also caused indirect effects on decomposition in these experiments. In the experiment with C_4 soil, when nutrient availability was high, elevated [CO_2] depressed the microbial decomposition of older soil organic matter (SOM), measured as a reduction in the flux of CO_2 from soil carrying the C_4 isotopic signature. The effects of elevated [CO_2] on the decomposition of older SOM were similar under the low-nutrient conditions, with a tendency for reduced decomposition of C_4 SOM under high [CO_2] (Cardon and others 2001). These results are consistent with the idea that increased rhizodeposition in elevated [CO_2] causes microorganisms to switch from utilizing older soil organic matter to the more labile root-derived carbon substrates (Kuikman and Gorissen 1993). In the $^{13}CO_2$ pulse experiment, monitoring of CO_2 efflux and its ^{13}C composition a year later showed that decomposition of the previous year's litter was unaffected by elevated [CO_2] under nutrient-rich conditions, whereas litter decomposition was depressed by elevated [CO_2] under nutrient-poor conditions. In this case, the high proportion of *Vulpia microstachys* may have had an effect on community-level decomposition, given the depression of *V. microstachys* decomposition observed previously (Franck and others 1997).

A number of experiments in California grasslands showed changes in N cycling that were likely caused by increased fluxes of C to soil (Hungate 1996, 1997a; Hu and others 2001)—changes that reflected altered N availability to plants and to decomposer microorganisms (Hu and others 2001). Thus, the effects of elevated [CO_2] on decomposition via increased C input to soil can interact with the availability of other nutrients.

Soil Moisture

As atmospheric [CO_2] rises, changes in the water-use efficiency (WUE) of plants may also affect the environment in which litter decomposes. The WUE of plants increases under elevated [CO_2], which can lead to temporary increases in soil moisture in some ecosystems, including California grasslands (Bremer and others 1996; Field and others 1997; Fredeen and others 1997). In the Jasper Ridge CO_2 Experiment, differences in soil moisture were most pronounced on sandstone soils and late in the growing season. Given the initial position of root and shoot litter, CO_2-driven changes in the availability of soil moisture are likely to affect root decomposition more strongly than shoot decomposition. Dukes and Field (2000) did not observe any differences in the decomposition of buried litter among microcosms that received a factorial combination of two concentrations of CO_2 and two levels of fertilization, despite significant differences in soil moisture associated with fertilization.

Elevated [CO_2] is likely to cause the greatest changes in soil moisture in years when plants have time to deplete most of the available soil moisture between saturating rains. In years with frequent rains, soil moisture is unlikely to limit plant growth or decomposition until late in the growing season. Given the magnitude of the observed differences in soil moisture (Field and others 1997; Fredeen and others 1997; Dukes and Field 2000), the patterns of precipitation necessary for these differences to be important, the fraction of litter likely to be exposed to differences in soil moisture, and past experimental results that have shown no difference in decomposition rates among treatments (Dukes and Field 2000), it seems unlikely that CO_2-driven increases in water availability will consistently cause important direct changes in ecosystem-level litter decomposition rates. However, increases in soil moisture may have more important effects on the turnover of SOM. Hungate and others (1997a) observed increased N mineralization in sandstone and serpentine grasslands exposed to elevated CO_2 and argued that increased soil moisture best explained these changes. This result suggests that CO_2-driven changes in soil moisture can accelerate SOM turnover.

Soil Microbiota

Changes in the decomposer community in response to elevated CO_2 could also alter litter decomposition. Two previous studies at Jasper Ridge have documented changes in the biomass and activity of soil microorganisms. Rillig and others (1999a) found that elevated CO_2 increased the abundance of mycorrhizal fungi on the sandstone grassland but not on the serpentine soils; by contrast, CO_2 increased fine-root biomass in serpentine soils but not in sandstone soils. These results suggest a tradeoff between C allocation to fine roots and fine-root mutualists. We know of no studies that have assessed the differences in litter quality between fine roots and mycorrhizal hyphae; however, given the obvious chemical differences—for example, chitin versus cellulose—it seems likely that these differences are large. Furthermore, arbuscular mycorrhizae are known to produce glomalin, an extremely recalcitrant protein implicated in long-term soil organic formation and soil structure (Wright and Upadhyaya 1998; Rillig and others 1999b). Thus, shifts in allocation between fine roots and mycorrhizal hyphae could influence ecosystem-scale decomposition rates, even if total C allocation belowground remained unchanged.

Hungate and others (2000) found that elevated CO_2 altered the composition of the nematode community on both types of grasslands, and increased the abundance of root-feeding nematodes in the serpentine soils, a finding consistent with the observation of increased root biomass there (Rillig and others 1999a). Additionally, elevated CO_2 increased the biomass of protozoa and metabolically active fungi, increased total rates of bacterial metabolism, and altered patterns of bacterial substrate use as indicated by the BIOLOG assay (Garland and Mills 1991). However, many components of the microbial community remained unchanged by elevated CO_2 in this study, and the changes that were observed were apparent only during the early part of the growing season (Hungate and others 2000). We suspect that, for the most part, the changes observed in the microbial community were responses to changes in the quantity, quality, and timing of plant litter inputs.

RELATIVE IMPORTANCE OF THE DIFFERENT MECHANISMS: RESULTS OF A SIMPLE CALCULATION

Which of the various mechanisms in Figure 1 are of greatest importance in California grasslands? To gain a better understanding of the relative importance of the diverse effects of elevated [CO_2] on decomposition, we used the results from two litter decomposition experiments (Franck and others 1997; Dukes and Field 2000) in a simple sensitivity analysis. We multiplied the decomposition rates of root and shoot litter by the fractions of litter allo-

Table 2. Potential Importance of CO_2 Effects on Litter Decomposition in California Annual Grasslands

		Variable Manipulated			
Parameter	Control Values	Litter Quality Response	Species Composition	R:S Allocation	Placement
Mass loss from roots[a] (%)	70.2	89.3 (hi), 64.0 (lo)	84.6 (hi), 49.8 (lo)	70.2	70.2
Mass loss from shoots[a] (%)	79.3	89.6 (hi), 73.4 (lo)	90.6 (hi), 64.6 (lo)	79.3	79.3
R:S ratio[b]	0.579	0.579	0.579	0.94 (hi), 0.35 (lo)	0.579
Placement factor (roots)	1	1	1	1	1
Placement factor (shoots)[c,d]	0.86	0.86	0.86	0.86	1 (hi), 0.54 (lo)
Environment factor[c,e]	1	1	1	1	1
Simulated mass loss	68.8	81.4–63.3	80.2–53.3	69.1–68.6	76.0–52.9
Range (%)	—	18.1	26.9	0.5	23.1

Experimentally derived values were used to estimate the amount of potential variation in mass loss rates based on variation in four properties: (a) the CO_2 response of an individual species, (b) the species composition of the grassland, (c) allocation to roots and shoots in the grassland, and (d) the location in which the litter decomposed. Mass loss values for roots and shoots were weighted by the percentage of mass made up by those plant parts and multiplied by scalars that accounted for litter placement and environmental conditions under elevated CO_2. The range between low and high "simulated mass loss" values indicates the potential sensitivity of ecosystem-level decomposition to the different variables.

[a] *Values are from unfertilized treatments of Franck and others (1997). Control value is average for four species grown at ambient and elevated CO_2. Direct effect values are for* L. multiflorum *grown at ambient (lo) and elevated (hi) CO_2. Species effect values are for* V. microstachys *(hi) and* A. fatua *(lo) grown in ambient air.*

[b] *Values are from Joel (2000). Control value is average of ratios for four species grown at ambient and elevated CO_2. Allocation effect values are from* L. multiflorum *grown at elevated CO_2 (hi) and* V. microstachys *grown in ambient air (lo), both in unfertilized soil. See also Franck and others (1997).*

[c] *Values derived from the results of Dukes and Field (2000)*

[d] *Control value is the proportion of litter lost from litterbags on the soil surface divided by the proportion of litter lost from buried bags. The "lo" placement effect value is the proportion of litter lost from bags suspended above the soil surface divided by the proportion of litter lost from buried litterbags.*

[e] *Because this variable did not alter decomposition in the cited experiment, we have assumed that it has no effect.*

cated to those parts, and then by scalars that accounted for placement of the different plant parts in different physical environments. We multiplied the resulting values by scalars that account for differences in physical and biotic aspects of the decomposition environment under ambient and elevated $[CO_2]$. Values for root and shoot litter were then added to obtain the expected proportion of mass lost from a sample of the specified litter in the specified environment.

We used average values from the two decomposition experiments as "control" values for the variables and scalars, and then determined the potential range of response to different factors by replacing single control values with experimentally observed extremes. By using the calculation to independently determine mass loss rates at high and low extremes for each variable and examining the difference between these rates, we developed a rough measure of the potential sensitivity of decomposition to each variable. Because $[CO_2]$ in the location where decomposition occurred did not measurably alter decomposition rates in Dukes and Field (2000), this value was held constant (at 1) in all analyses. We leave it in Table 2 simply to highlight the lack of importance of this mechanism.

The results of our calculation suggest that short-term decomposition rates in California grasslands are most sensitive to changes in litter quality that accompany shifts in species composition (Table 2). However, because the response of litter quality to elevated $[CO_2]$ is positive in some species and negative in others (Franck and others 1997), this effect may partially cancel out on the ecosystem level. Changes in litter placement and changes in the litter quality of individual species also have the potential to cause important changes in decomposition rates. We emphasize that we do not expect changes in $[CO_2]$ to alter ecosystem-level decomposition rates as drastically as we have assumed in this calculation. The calculation is simply an attempt to identify mechanisms that could be important in the initial stages of decomposition.

CONCLUSIONS

Results from experiments in California's annual grasslands suggest that there are several mechanisms through which rising atmospheric $[CO_2]$ could cause biologically important effects on de-

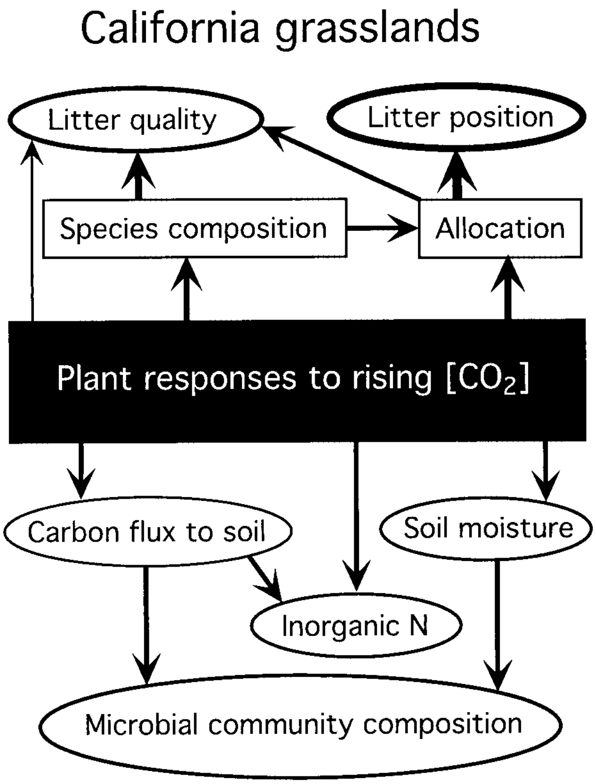

Figure 7. Conceptual diagram of mechanisms through which responses of plants to rising [CO_2] might alter litter decomposition rates in California grasslands. Circled properties directly affect decomposition. Thickness of lines indicates our opinion of the relative strengths of the mechanisms altering decomposition.

composition (Figure 7). First, changes in the aboveground allocation patterns of grasses and late-flowering annuals are likely to slow decomposition rates by increasing the proportion of litter that is (a) more recalcitrant and (b) suspended above the soil surface. Second, further changes in litter quality and allocation patterns are likely to occur as the result of CO_2-driven changes in species dominance. Changes in litter chemistry will feed back to the C cycle both directly, by altering rates of C mineralization, and indirectly, by altering nutrient cycling.

Relatively few researchers working outside of Jasper Ridge have studied how CO_2-driven changes in allocation and species dominance might influence decomposition rates. Changes in biomass allocation are uncommon among woody species (Curtis and Wang 1998) and are inconsistently observed among nonagricultural herbaceous species (or communities) in unfertilized settings (for example, see van Ginkel and others 1996; Cotrufo and Gorissen 1997; Leadley and others 1999; Owensby and others 1999; Bernacchi and others 2000), although allocation patterns beyond root:shoot partitioning are rarely measured. Unfortunately, allocation measurements of herbaceous species are often made early in the ontogeny of the plants, limiting the utility of the observations for predictions of litter placement and quality. Species composition changes have been observed in several systems (for example, see Leadley and others 1999; Owensby and others 1999; Smith and others 2000). Clearly, CO_2-driven species shifts are a potentially important mechanism for changes in litter quality. However, the consequences for litter decomposition of changes in species composition have rarely been examined in the context of elevated [CO_2] research (but see Kemp and others 1994). Given the inconsistency of direct CO_2 effects on litter quality (Norby and others 2001), it seems likely that changes in species composition will have greater consequence in many systems, through effects on both biomass allocation and litter quality. The relative importance of different mechanisms will vary by system; for instance, in systems dominated by a single species, small changes in litter quality of that species might influence decomposition more than any changes in biomass allocation or the abundance of subordinate species. Environmental conditions may also dictate which mechanisms are important; for instance, in herbaceous systems where snowfall pushes standing litter to the ground, changes in above ground allocation patterns may have little impact on decomposition rates.

Plant physiological responses to rising [CO_2] will affect the below ground environment and may consequently affect decomposition. Changes in the availability of C and soil moisture could directly affect the activities of decomposers, or they could affect the composition and size of the microbial community. In many systems, soil respiration and microbial respiration increase in response to elevated [CO_2], suggesting that C inputs to soil increase as [CO_2] rises and that the microbial community metabolizes this C (Zak and others 2000). In some systems, an increase in the turnover or decomposability of fine roots may provide the microbial community with additional C (Zak and others 2000). Carbon dioxide–driven increases in soil moisture (Bremer and others 1996; Niklaus and others 1998) may also impact SOM decomposition (and possibly root litter decomposition) in several systems. In California grassland, the direct effects of changes in soil moisture are unlikely to cause substantial increases in litter decomposition rates, but they are likely to accelerate SOM turnover and nutrient cycling (Hungate and others 1997a). Increased inputs of labile C to soil may slow the decomposition of older SOM. Changes in the microbial community in response to elevated [CO_2] can also have implications for decomposition and soil organic matter stabilization. For example, CO_2 could alter ecosystem-level decomposition by increasing the abundance of a group of microorganisms responsible for the synthesis of compounds involved in SOM stabilization (for example, mycorrhizae and glomalin, fungi and chitin), an effect analogous to CO_2 altering decomposition by changing the relative abundances of plant species that differ in litter quality.

Because the two types of grassland at Jasper Ridge differ in species composition, we anticipate that they will also differ in their response to elevated [CO_2]. In single-year experiments, we would expect the response of decomposition in the sandstone grasslands to depend on changes in allocation (and thus litter quality) of the dominant grass species. In the serpentine grassland, the initial response might depend on changes in allocation patterns of late-season annuals, which can make up a large proportion of the community's total biomass. Over a longer and more relevant time scale, responses of both grasslands are likely to be controlled by changes in species dominance in these systems, which will affect the quality and position of litter (Figure 7). In sandstone grasslands, increases in the dominance of late-season annuals or legumes could substantially alter ecosystem-level decomposition rates. Such changes in species composition may be driven by the rise in [CO_2], climate change, N deposition, or other factors.

Recent research has identified several potentially important mechanisms linking the increase in atmospheric [CO_2] to the decomposition process. It seems possible that the most important mechanisms in one ecosystem may be trivial in the next and vice versa. Identification of the critical mechanisms in diverse regions will improve our effectiveness in studying and predicting the effects of increasing atmospheric [CO_2] on decomposition rates.

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