

Richard J. Norby · M. Francesca Cotrufo
Philip Ineson · Elizabeth G. O'Neill
Josep G. Canadell

Elevated CO₂, litter chemistry, and decomposition: a synthesis

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Abstract The results of published and unpublished experiments investigating the impacts of elevated [CO₂] on the chemistry of leaf litter and decomposition of plant tissues are summarized. The data do not support the hypothesis that changes in leaf litter chemistry often associated with growing plants under elevated [CO₂] have an impact on decomposition processes. A meta-analysis of data from naturally senesced leaves in field experiments showed that the nitrogen (N) concentration in leaf litter was 7.1% lower in elevated [CO₂] compared to that in ambient [CO₂]. This statistically significant difference was: (1) usually not significant in individual experiments, (2) much less than that often observed in green leaves, and (3) less in leaves with an N concentration indicative of complete N resorption. Under ideal conditions, the efficiency with which N is resorbed during leaf senescence was found not to be altered by CO₂ enrichment, but other environmental influences on resorption inevitably increase the variability in litter N concentration. Nevertheless, the small but consistent decline in leaf litter N concentration in many experiments, coupled with a 6.5% increase in lignin concentration, would be predicted to result in a slower decomposition rate in CO₂-enriched litter. However, across the assembled data base, neither mass loss nor respiration rates from litter

produced in elevated [CO₂] showed any consistent pattern or differences from litter grown in ambient [CO₂]. The effects of [CO₂] on litter chemistry or decomposition were usually smallest under experimental conditions similar to natural field conditions, including open-field exposure, plants free-rooted in the ground, and complete senescence. It is concluded that any changes in decomposition rates resulting from exposure of plants to elevated [CO₂] are small when compared to other potential impacts of elevated [CO₂] on carbon and N cycling. Reasons for experimental differences are considered, and recommendations for the design and execution of decomposition experiments using materials from CO₂-enrichment experiments are outlined.

Keywords Decomposition · Elevated atmospheric CO₂ · Lignin · Litter quality · Meta-analysis · Nitrogen

Introduction

There is ongoing debate about whether the increasing atmospheric concentration of CO₂ is resulting in increases in net terrestrial ecosystem carbon (C) storage (Melillo et al. 1996). The average annual rate of increase of CO₂ is 1.8 ppm, with a predicted doubling of pre-industrial concentrations by the end of the 21st century (Houghton et al. 1996). Despite an increasing number of studies on soil processes (see Canadell et al. 1996), little is known about the overall impact of elevated atmospheric CO₂ on net ecosystem C storage (Amthor and Koch 1996). The suggestion that the rise in CO₂ will lead to increases in plant biomass, and hence terrestrial C storage, is an oversimplification, since belowground C storage dominates in some terrestrial ecosystems (Anderson 1992).

C storage in ecosystems (i.e., net ecosystem productivity, NEP) is the difference between net primary productivity (NPP) and ecosystem heterotrophic respiration, both of which could change as atmospheric CO₂ concentrations ([CO₂]) increase. Two general issues of concern are whether increases in NPP in response to rising CO₂

R.J. Norby (✉) · E.G. O'Neill
Environmental Sciences Division,
Oak Ridge National Laboratory, Bldg. 1059,
PO Box 2008, Oak Ridge, TN 37831-6422 USA
e-mail: rjn@ornl.gov
Tel.: +1-865-5765261, Fax: +1-865-5769939

M.F. Cotrufo
Facoltà di Scienze Ambientali, II Università di Napoli,
via Arena 22, 81100 Caserta, Italy

P. Ineson
Department of Biology, University of York,
PO Box 373, York, YO10 5YW UK

J.G. Canadell
GCTE International Project Office,
CSIRO Wildlife and Ecology, PO Box 284,
Canberra ACT, 2601, Australia

will be sustained if negative feedbacks through the N cycle occur, and whether decomposition rates will change if atmospheric $[\text{CO}_2]$ affects the chemistry of the substrates for decomposition. Both of these issues depend in part on whether the chemistry of plant-derived detrital material (litter) is different under elevated CO_2 .

Changes in plant tissue chemistry may have important long-term ecosystem consequences. The rate at which litter decomposes has been related to its initial N concentration, lignin concentration, C:N ratio, and lignin:N ratio (Melillo et al. 1982). Decomposition rate, relative to the rate of litter production, is a determinant of ecosystem C sequestration. Decomposition is also a controller of N availability (see review by Marris et al. 1983). Long-term ecosystem responses to elevated CO_2 may ultimately depend on N availability to plants and on the ability of plants to use N more efficiently under conditions of increased atmospheric CO_2 . The extent to which the C:N ratio of plant tissues can change is one of the key biogeochemical determinants regulating the amount of C that can be sequestered from the atmosphere into vegetation (Rastetter et al. 1992).

The possibility that CO_2 enrichment will alter the chemistry of litter such that decomposition is slowed and N availability reduced was first proposed by Strain and Bazzaz (1983). At that time there was evidence suggesting that the foliar N concentration was lower in CO_2 -enriched plants, so it was reasonable to assume that the N concentration in leaf litter would also be lower and its decomposition rate reduced. This, in turn, would result in lower N availability in the soil, providing a negative feedback to photosynthesis and plant growth. This scenario, called the "litter quality" hypothesis, has been frequently invoked to suggest that the increases in growth of plants observed in short-term experiments under elevated CO_2 could not be sustained.

Since the litter quality hypothesis was first proposed, a number of studies have evaluated the effect of elevated CO_2 on litter chemistry or decomposition. The premise that green leaf tissue [N] is lower in elevated CO_2 has been widely supported. Several compilations of the literature have reported declines in foliar [N] in tree species averaging 21% (McGuire et al. 1995), 16% (Curtis and Wang 1998), 14% (Cotrufo et al. 1998a), or 13% (Norby et al. 1999). Much of this decline is related to an increased dry matter content of leaves rather than reduced total N content (Curtis 1996; Norby et al. 1999), but it is the N concentration (or C:N ratio) rather than total N content that is the more important expression of litter chemistry with regard to decomposition. The question remains, however, whether the [N] of leaves accurately predicts the [N] of litter or, indeed, its subsequent decomposition rate. Experimental results have been mixed, with some studies indicating a lower [N] in leaf litter in response to CO_2 enrichment (reduced litter quality) (Cotrufo et al. 1994; Jongen et al. 1995; Van Ginkel et al. 1996), and others indicating no effect of CO_2 (Gahrooei 1998; Hirschel et al. 1997; O'Neill and Norby 1996; Randlett et al. 1996). These different responses

may be due to specific aspects of experimental design (e.g., nitrogen nutrition, light quality), the state of senescence of the plant materials used (O'Neill and Norby 1996), or factors influencing the process of senescence (Arp et al. 1997; Norby et al. 2000).

The relationship between N in green leaves and N in litter is controlled by the process of resorption, which involves the breakdown of proteins during leaf senescence and amino acid translocation in the phloem to perennial tissue. Nitrogen resorption is a proximate controller of leaf litter [N], so any consideration of CO_2 effects on litter chemistry should explicitly consider CO_2 effects on resorption (Norby et al. 2000). Although there is wide variation among species in resorption efficiency, or the fraction of green leaf N that is resorbed during senescence (Chapin and Kedrowski 1983), most ecosystem models set resorption efficiency as a constant, typically 50%, which is the average value across many species (Aerts 1996; Chapin and Kedrowski 1983).

Changes in litter chemistry can be seen as a physiological response to elevated CO_2 , amenable to short-term experimental observation and with potentially important long-term implications (Norby et al. 1986). Experimental data on decomposition responses during short-term (several years at most) manipulations, however, are very difficult to extrapolate through time, and ecosystem models are the best way to represent responses over realistic time scales (Thornley and Cannell 2000). Nevertheless, it is instructive to compare the predicted responses of decomposition to CO_2 enrichment to actual experimental results. In so doing, we can better define the important research questions and refine the methods to be used in a new generation of longer-term studies. The experimental evidence on the decomposition of plant tissues grown in elevated $[\text{CO}_2]$ has been mixed, probably depending not only on plant culture and litter chemistry (Cotrufo et al. 1994; Van Ginkel et al. 1996), but also on the biological complexity of laboratory systems (Coûteaux et al. 1991; Schläppli and Körner 1997), and the length of the decomposition study (Ball and Drake 1997).

A limited comparative analysis of elevated $[\text{CO}_2]$ on litter chemistry and decomposition processes was performed by O'Neill and Norby (1996), with the recognition that certain aspects of experimental design and methods may compromise experimental outcome. Since the publication of that analysis, a considerable number of further investigations have been performed and reported, and both published and unpublished data have been collated for the synthesis presented here. Preliminary conclusions from this synthesis have been presented (Norby and Cotrufo 1998), but the full data set and statistical analyses from which these conclusions were drawn have yet to be published; that is the purpose of the current review. Here we have used meta-analysis techniques (Curtis and Wang 1998; Gurevitch and Hedges 1993) to investigate the effects of elevated CO_2 on litter chemistry and decomposition, based on all relevant available data on the subject. We also reconsider the analysis presented by Arp et al. (1997) on the effect of $[\text{CO}_2]$ on N

resorption to help explain some inconsistencies in the data sets. Finally, we use these analysis as a basis for discussion of issues of experimental design and protocol, with a view toward future studies of decomposition and global change.

Materials and methods

Sources of data

The synthesis originated from a workshop, "Litter Quality and Decomposition under Elevated CO₂" held in Capri, Italy, September 1998, under the auspices of Global Change and Terrestrial Ecosystems project (GCTE) and the European COST network (Norby and Cotrufo 1998). Data on litter chemistry and decomposition of plant tissue grown in elevated and ambient CO₂ concentrations were gathered from participants of that workshop and from other published and pre-publication sources. The litter chemistry data base (Table 1) comprised observations of naturally senesced leaves of plants exposed to elevated CO₂ (typically 600–700 ppm) in the field or in field chambers. Data from plants grown in growth chambers with artificial lighting were excluded because of the possible artifacts of unbalanced nutrition or abnormal senescence. Also excluded were data from non-senescent green leaves. The measures of litter chemistry were N concentration (mg g⁻¹) and lignin concentration (mg g⁻¹), with the number of replications and standard deviations included when available. The decomposition data base (Table 1) was less restrictive and included a wide range of plant tissue from different types of CO₂-enrichment regimes and different protocols for measuring decomposition. The measures of decomposition were percentage mass loss over time and the respiration rate of decomposing litter.

Categorical variables

Categorical variables describing characteristics of the source material, exposure protocol, and measurement protocol were defined, and observations were grouped into classes within these categories. The procedures for exposing the plants to elevated [CO₂] included open-top field chambers (OTC), solardomes (SD), growth cabinets (GC), or open-field exposure. The open-field class included free-air CO₂ enrichment (FACE), screen-aided CO₂ control (SACC), and natural CO₂ springs (CS) (Table 1). The exposure protocol was also classified by whether the plants were in pots or soil boxes or free-rooted in the ground. The source material was classified as originating either from woody or herbaceous plants, and the plant part was leaf, wood, whole shoots, or roots. Leaves and herbaceous shoot tissue were classified as to whether they had senesced naturally, were standing dead, or were harvested prior to senescence; roots and twigs were always classified as harvested material. Other categories described whether the plant tissue used in decomposition experiments was intact, cut into pieces, or ground, whether it was air-dried or oven-dried; and whether the decomposition experiment was conducted in the laboratory or field.

Statistical analysis

The meta-data on leaf litter N and lignin concentrations and mass loss during decomposition were analyzed using MetaWin 2.0 software (Rosenberg et al. 2000). The procedure is analogous to the partitioning of variance in a classic ANOVA, enabling partitioning of variances in the comparisons of groups to within-class and between-class homogeneity (see Curtis and Wang 1998). The effect size for each observation was calculated as the natural log of the response ratio (lnRR) (Hedges et al. 1999), where the response ratio is the mean in elevated [CO₂] divided by the mean in ambient

[CO₂]. The mean effect size of a group is the weighted mean of individual effect sizes, using the reciprocal of the standard deviation as the weight. Observations in which there was no standard deviation reported (as when $n=1$) were included conservatively by assigning them the minimum weight calculated from other observations in the data set, following the approach of Medlyn et al. (2001) and P.S. Curtis (personal communication). A mixed model was used, whereby it is assumed that studies within a class share a common mean effect, but there is also random variation among studies in a class, in addition to sampling variation (Gurevitch and Hedges 1993; Rosenberg et al. 2000). The significance of the difference between class means was analyzed by the Q_B statistic, assuming a χ^2 distribution. The mean effect size of a class was considered significant when the 95% confidence interval of the response ratio (after back conversion from the lnRR statistic) did not overlap 1.

The effect of [CO₂] on resorption of N from senescing leaves was analyzed with a data set assembled from CO₂-enrichment experiments that reported both [N] in green leaves and [N] in leaf litter after senescence. Resorption efficiency was calculated as the difference in green leaf and litter [N] divided by green leaf [N]. In most cases resorption efficiency was not explicitly measured in the original studies, and it was calculated from mean values, which precluded any estimate of variance. Only data from unfertilized, free-rooted trees and grasses that were grown in the open air or in field chambers were included in this analysis.

Results

N concentration in leaf litter

N concentrations in naturally senesced leaves were reduced when the plants were grown in elevated concentrations of atmospheric CO₂ in field experiments (Fig. 1a). The median of 67 experimental observations of N concentrations in leaf litter was 9.8 mg g⁻¹ in ambient CO₂ (range 2.9–31.0 mg g⁻¹) and 9.2 mg g⁻¹ in elevated CO₂ (range 2.4–23.1 mg g⁻¹). Meta-analysis of this data set indicated a significant effect of CO₂ on litter [N] (Fig. 2). Based on analysis of the lnRR statistic, [N] was 7.1% lower in CO₂-enriched litter. There were no significant differences in response between woody and herbaceous plants, whether plants were free-rooted in the ground or in pots or soil boxes, or whether they were fertilized. There was, however, an effect ($P=0.053$) of exposure protocol (Fig. 2). The effect of CO₂ on litter [N] was largest in SD experiments, and there was no significant effect in plants exposed in the open (SACC, FACE, and CO₂ springs). The CO₂ effect also was larger ($P=0.049$) when the control litter [N] was greater than 10 mg g⁻¹, the level that Killingbeck (1996) sets as indicative of incomplete resorption. The slope of the regression of lnRR on [N] was statistically significant ($P=0.012$), indicating an increasing effect of [CO₂] with increasing [N].

Nitrogen resorption

The average resorption efficiency from 20 observations in experiments with both grasses and tree species was 49% in ambient CO₂ and 48% in high CO₂ (not signifi-

Table 1 Sources of observations of effects of [CO₂] on litter chemistry and decomposition. Experimental systems in which plants were exposed to elevated [CO₂] were open-top chambers (OTC), growth chambers including mesocosms in greenhouses (GC), screen-aided CO₂ control (SACC), natural CO₂ springs (CS),

soldardomes (SD), and free-air CO₂ enrichment (FACE). Observations were included in one or more data bases: leaf litter nitrogen and lignin concentration (N and L), decomposition measured as mass loss (M), and CO₂ efflux from decomposing litter (R)

Reference	Species	Plant part	Exposure system	Data bases			
Herbaceous plants							
Arnone and Hirschel (1997)	<i>Carex curvula</i>	leaf	OTC	N	L	M	
Ball and Drake (1997)	<i>Spartina patens</i>	leaf	OTC	N	L		R
Ball and Drake (1998)	<i>Scirpus olneyi</i>	leaf	OTC	N	L		R
Curtis et al. (1989)	<i>Scirpus olneyi</i>	leaf	OTC	N			
Dukes and Field (2000)	C ₃ grassland mixture	leaf	OTC	N	L	M	
Franck et al. (1997)	<i>Avena fatua</i>	shoot, root	OTC			M	
Franck et al. (1997)	<i>Bromus hordaceus</i>	shoot, root	OTC			M	
Franck et al. (1997)	<i>Lolium multiflorum</i>	shoot, root	OTC			M	
Franck et al. (1997)	<i>Vulpia microstachys</i>	shoot, root	OTC			M	
Gorissen and Cotrufo (2000)	<i>Lolium perenne</i>	leaf	GC			M	
Gorissen and Cotrufo (2000)	<i>Agrostis capillaris</i>	leaf	GC			M	
Gorissen and Cotrufo (2000)	<i>Festuca ovina</i>	leaf	GC			M	
Henning et al. (1996)	<i>Glycine max</i>	leaf	OTC				R
Henning et al. (1996)	<i>Sorghum bicolor</i>	leaf	OTC				R
Hirshel et al. (1997)	<i>Carex curvula</i>	leaf	OTC	N	L	M	
Hirshel et al. (1997)	Graminoid mixture	leaf	SACC	N	L	M	
Hirshel et al. (1997)	<i>Carex flacca</i>	leaf	SACC	N	L	M	
Hungate et al. (1997)	Serpentine mixture	leaf	OTC	N			
Hungate et al. (1997)	Sandstone mixture	leaf	OTC	N			
Kemp et al. (1994)	<i>Andropogon gerardii</i>	leaf	OTC	N	L	M	
Kemp et al. (1994)	<i>Sorghastrum nutans</i>	leaf	OTC	N	L	M	
Kemp et al. (1994)	<i>Poa pratensis</i>	leaf	OTC	N	L	M	
Kratz et al. (1995)	<i>Festuca pratensis</i>	leaf	GC			M	
Lutze et al. (2000)	<i>Danthonia richardonii</i>	leaf, root	GC				R
Matamala (unpublished)	<i>Spartina patens</i>	root	OTC			M	
Robinson et al. (1997)	<i>Festuca vivipara</i>	shoot, root	GC			M	
Ross et al. (1996)	Grass/clover turves	shoot	GC				R
Sowerby et al. (2000)	<i>Holcus lanatus</i>	leaf	CS	N			
Sowerby et al. (2000)	<i>Pennisetum clandestinum</i>	leaf	CS	N			
Torbert et al. (1998)	Sorghum/soybean	leaf	OTC				R
Van Ginkel et al. (1996)	<i>Lolium perenne</i>	root	GC			M	
Van Ginkel and Gorissen (1998)	<i>Lolium perenne</i>	root	GC				R
Van Vuuren et al. (2000)	<i>Triticum aestivum</i>	root	GC			M	R
Woody plants							
Cotrufo and Ineson (1996)	<i>Betula pendula</i>	leaf	SD	N	L	M	
Cotrufo and Ineson (2000)	<i>Fagus sylvatica</i>	wood	OTC			M	
Cotrufo and Ineson (2000)	<i>Quercus pubescens</i>	wood	CS			M	
Cotrufo (1994)	<i>Picea sitchensis</i>	leaf	SD			M	
Cotrufo et al. (1994)	<i>Fraxinus excelsior</i>	leaf	SD	N	L	M	R
Cotrufo et al. (1994)	<i>Betula pubescens</i>	leaf	SD	N	L	M	R
Cotrufo et al. (1994)	<i>Acer pseudoplatanus</i>	leaf	SD	N	L	M	R
Cotrufo et al. (1994)	<i>Picea sitchensis</i>	leaf	SD			M	R
Cotrufo et al. (1998b)	<i>Fraxinus excelsior</i>	leaf	SD	N	L	M	
Cotrufo et al. (1998b)	<i>Acer pseudoplatanus</i>	leaf	SD	N	L	M	
Cotrufo et al. (1999)	<i>Quercus pubescens</i>	leaf	CS	N	L	M	
Coûteaux et al. (1991, 1996)	<i>Castanea sativa</i>	leaf	GC			M	R
De Angelis et al. (2000)	<i>Quercus ilex</i>	leaf	OTC	N	L	M	
De Angelis et al. (2000)	<i>Phillyrea angustifolia</i>	leaf	OTC	N	L	M	
De Angelis et al. (2000)	<i>Pistacia lentiscus</i>	leaf	OTC	N	L	M	
Edwards N.T. (unpublished)	<i>Quercus alba</i>	wood	OTC			M	
El-Kohen et al. (1992)	<i>Castanea staiva</i>	leaf	OTC	N			
Finzi et al. (2001)	<i>Pinus taeda</i>	leaf	FACE	N	L	M	
Finzi et al. (2001)	<i>Cornus florida</i>	leaf	FACE	N	L	M	
Finzi et al. (2001)	<i>Cercis canadensis</i>	leaf	FACE	N	L	M	
Finzi et al. (2001)	<i>Acer rubrum</i>	leaf	FACE	N	L	M	
Finzi et al. (2001)	<i>Liquidambar styraciflua</i>	leaf	FACE	N	L	M	
Gahrooee (1998)	<i>Quercus cerris</i>	leaf	CS	N	L		R
Gahrooee (1998)	<i>Quercus pubescens</i>	leaf	CS	N	L		R
Gifford and Drake (unpublished)	<i>Quercus geminata</i>	leaf	OTC			M	
Gifford and Drake (unpublished)	<i>Quercus myrtifolia</i>	leaf	OTC			M	

Table 1 (continued)

Reference	Species	Plant part	Exposure system	Data bases		
Hättenschwiler et al. (1999)	<i>Fagus sylvatica</i>	leaf	OTC	N	L	M
Hättenschwiler et al. (1999)	<i>Picea abies</i>	shoot	GC			M
Hirshel et al. (1997)	<i>Elettaria cardamomum</i>	leaf	GC	N	L	M
Hirshel et al. (1997)	<i>Ficus benjamina</i>	leaf	GC	N	L	M
Hirshel et al. (1997)	<i>Cecropia peltata</i>	leaf	GC	N	L	M
Ineson et al. (1999)	<i>Rubus chamaemorus</i>	leaf	SD			M
Johnson et al. (2000)	<i>Pinus ponderosa</i>	leaf	OTC	N		M
Matamala (unpublished)	<i>Pinus taeda</i>	root	FACE			M
Norby (unpublished)	<i>Liquidambar styraciflua</i>	leaf	FACE	N		
Norby (1996)	<i>Quercus alba</i>	leaf	OTC	N	L	
Norby et al. (1995)	<i>Liriodendron tulipifera</i>	leaf	OTC	N	L	
Norby et al. (2000)	<i>Acer rubrum</i>	leaf	OTC	N		
Norby et al. (2000)	<i>Acer saccharum</i>	leaf	OTC	N		
Nussbaumer et al. (1997)	<i>Ctenanthe lubbersiana</i>	leaf	GC			R
O'Neill and Norby (1996)	<i>Liriodendron tulipifera</i>	leaf	OTC			M
O'Neill and Norby (unpublished)	<i>Liriodendron tulipifera</i>	leaf	OTC			M
O'Neill and Norby (unpublished)	<i>Quercus alba</i>	leaf	OTC			M
Randlett et al. (1996)	<i>Populus × euramericana</i>	leaf	OTC	N		
Rey and Jarvis (1998)	<i>Betula pendula</i>	leaf	OTC	N	L	
Strand et al. (1999)	<i>Quercus rubra</i>	leaf	OTC	N		
Strand et al. (1999)	<i>Betula papyrifera</i>	leaf	OTC	N		
Vogel et al. (1997)	<i>Alnus glutinosa</i>	leaf	OTC	N		

cantly different by paired *t*-test), and most of the plotted data fall very close to the 1-to-1 line (Fig. 3).

Lignin concentration in leaf litter

The N concentration decreased in litter with CO₂ enrichment, whereas the lignin concentration tended to increase (Fig. 1b). The median of 46 experimental observations of lignin concentrations in leaf litter was 138 mg g⁻¹ in ambient CO₂ (range 23–253 mg g⁻¹) and 149 mg g⁻¹ in elevated CO₂ (range 26–287 mg g⁻¹). Meta-analysis of the lignin data (lnRR statistic) indicated a significant effect of CO₂ treatment, with a 6.5% increase in elevated CO₂ (Fig. 4). There was a significant difference in response to CO₂ between woody and herbaceous species (*P*=0.019), with CO₂ enrichment increasing lignin concentration in woody plants but not in herbaceous species (Fig. 4). The lignin concentration of leaf litter was not affected by [CO₂] in plants planted in the ground or exposed in OTCs or in the open, but it increased in plants grown in pots or soil boxes or exposed in SDs. There was a confounding of effects among these categories: most of the observations in SDs were of woody plants growing in soil boxes or pots. There was no effect of [CO₂] in litter in which [N] was less than 10 mg g⁻¹ (Fig. 4).

Mass loss of litter from ambient and elevated CO₂

The percentage mass losses of litter produced at ambient or elevated CO₂ across all the studies varied enormously (Fig. 5a). The wide range from 0.85 to 97.6% mass loss

was not surprising given the large number of materials and experimental conditions being compared. Meta-analysis indicated that there was no significant effect of [CO₂] on mass loss during decomposition (Fig. 6). The only categorical variable with a significant effect was exposure protocol (*P*=0.007). CO₂ enrichment significantly reduced decomposition (mass loss) when the plant tissue was grown in SDs but had no effect when the plants were exposed in other experimental facilities (Fig. 6). There were also significant CO₂ effects on the decomposition of tissues from woody plants and from leaves, but the differences between classes of the plant type or plant part categories were not significant. Again, there was a confounding of the woody plant and leaf classes with the SD class, and when the SD data were not included, the response ratios of mass loss for the woody plant and leaf classes were not significantly different from 1. There were no other classes for which the response ratio was significantly different from 1.

Litter decomposition – CO₂ release

There were many fewer observations of respiration rates of decomposing litters than of mass loss, and the data were reported in different units in different experiments so only the response ratios can be compared. There was no consistent effect of CO₂ enrichment (Fig. 5b). There were not enough observations with error terms to permit meta-analysis.

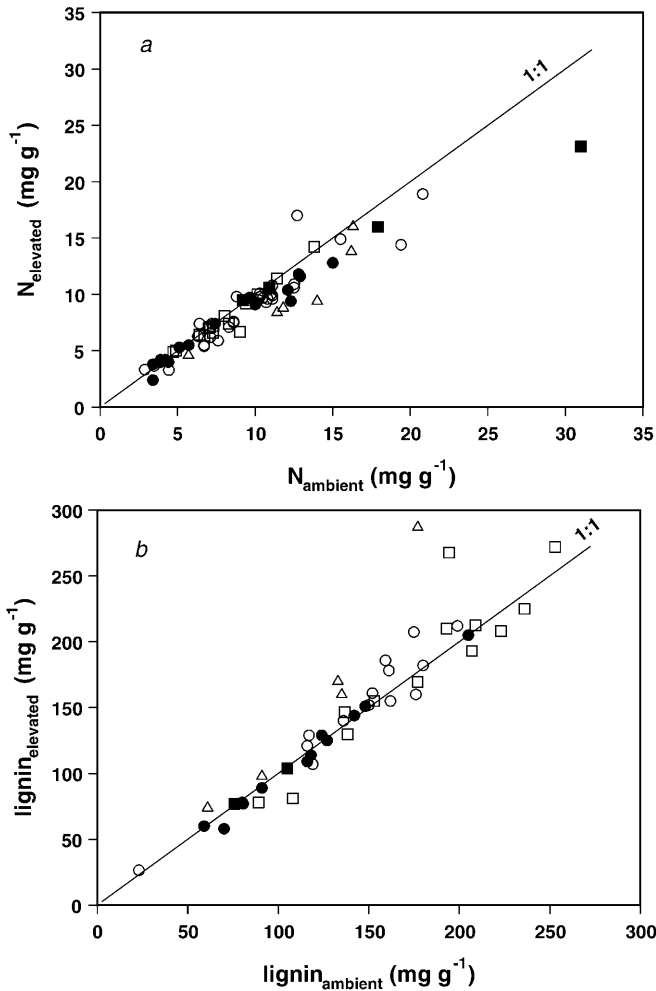


Fig. 1a, b Litter chemistry of naturally senesced and abscised leaves of plants grown in field exposure systems with an elevated atmospheric CO₂ concentration compared to equivalent plants grown in ambient CO₂. **a** Nitrogen concentration; **b** lignin concentration. The line indicates the 1:1 relationship. (Open symbols Herbaceous plants, filled symbols woody plants.) (○, ● Plants exposed to elevated CO₂ in open-top chambers, □, ■ exposed in open-field systems [free-air CO₂ enrichment (FACE), screen-aided CO₂ control (SACC), CO₂ springs], △ exposed in solardomes.) Sources of data are shown in Table 1

Discussion

Litter N concentration

Previous compilations of the data on the effect of elevated [CO₂] on initial leaf litter N concentration have led to conflicting conclusions (Cotrufo et al. 1998a; Coûteaux et al. 1999; O'Neill and Norby 1996). Although some individual experiments have documented statistically significant declines in [N] in CO₂-enriched leaf litter (e.g., Cotrufo and Ineson 1996; Cotrufo et al. 1994), very few experiments with plants rooted in the ground have done so, and O'Neill and Norby (1996) concluded that the responses of litter chemistry of plants grown in pots or in growth chambers may be artifactual. In fact, because

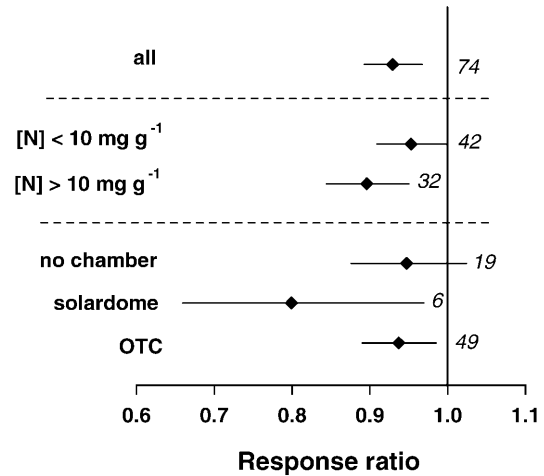


Fig. 2 Response ratio of leaf litter N concentration to elevated CO₂. The data shown are the weighted mean response ratio and 95% confidence interval for classes of different categorical variables. The number to the right of the confidence interval is the number of observations. If the confidence interval includes a response ratio of 1, there was no significant effect of [CO₂]

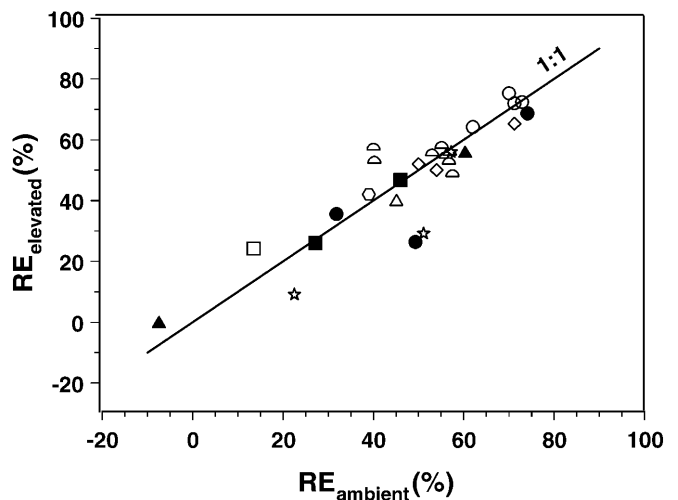


Fig. 3 The effect of CO₂ enrichment on resorption efficiency (RE) in leaves of woody (open symbols) and herbaceous (solid symbols) plants. All of the data are from unfertilized plants grown in field chambers with unconstrained root systems. Sources of data: solid circle Curtis et al. (1989), *Scirpus olneyi* and *Spartina patens* (pure and mixed communities); solid square Hungate et al. (1997), annual grasses on serpentine and sandstone soils; solid triangle Owensby et al. (1993) and Kemp et al. (1994), *Poa pratensis* and *Andropogon gerardii*; open square Curtis et al. (1995) and Randlett et al. (1996), *Populus deltoides* × *P. nigra*; open circle Norby et al. (1999), *Acer rubrum* and *A. saccharum* in ambient and elevated temperature; open triangle up Norby et al. (1999), *Quercus alba*; open rhombus Rey and Jarvis (1998), *Betula pendula*; open star Kubiske and Pregitzer (1996) and Strand et al. (1999), *Betula papyrifera* (sun and shade) and *Quercus rubra*; open triangle down Johnson et al. (2001), *Liquidambar styraciflua*; open hexagon Vogel et al. (1997), *Alnus glutinosa*; open half circle Finzi et al. (2001), *Pinus taeda*, *Liquidambar styraciflua*, *Acer rubrum*, *Cercis canadensis*, and *Cornus florida*

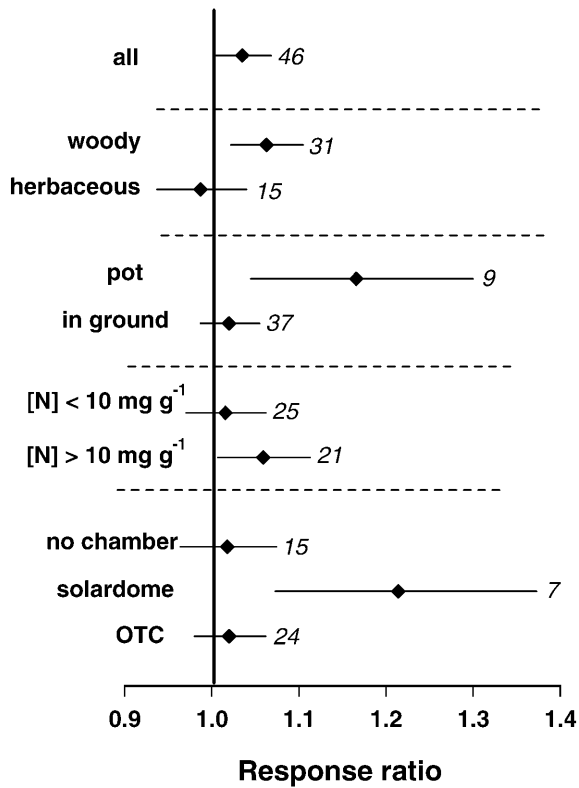


Fig. 4 Response ratio of leaf litter lignin concentration, presented as in Fig. 2

most individual experiments with field-grown plants failed to detect statistically significant effects of $[\text{CO}_2]$ on litter chemistry, the consensus opinion among researchers participating in the Capri workshop was that there is no compelling evidence supporting the hypothesis that litter $[\text{N}]$ will be lower in a high- CO_2 world (Norby and Cotrufo 1998).

The data compilation reported here is the first to be comprehensive, while excluding data that may not be representative of the responses of plants in the field. In most of the individual experiments included in the data base there was no statistically significant effect of CO_2 on litter $[\text{N}]$. Nevertheless, mean litter $[\text{N}]$ usually declined a small amount, and when the data sets were combined in a meta-analysis framework a significant effect was revealed. The 0.6 mg g^{-1} decline in $[\text{N}]$ is much less than the 3.0 mg g^{-1} decline reported from the data set compiled by Côtéaux et al. (1999), which included green leaves, stems, and roots in addition to leaf litter. The decline just in leaf litter $[\text{N}]$ (1.6 mg g^{-1}) in their analysis was also much higher than that of our analysis. It is difficult to determine what was coded as litter in the Côtéaux et al. analysis, but it is clear that the data set included leaf material that did not senesce under field conditions or was picked off the plant before senescence was complete (e.g., Norby et al. 1986).

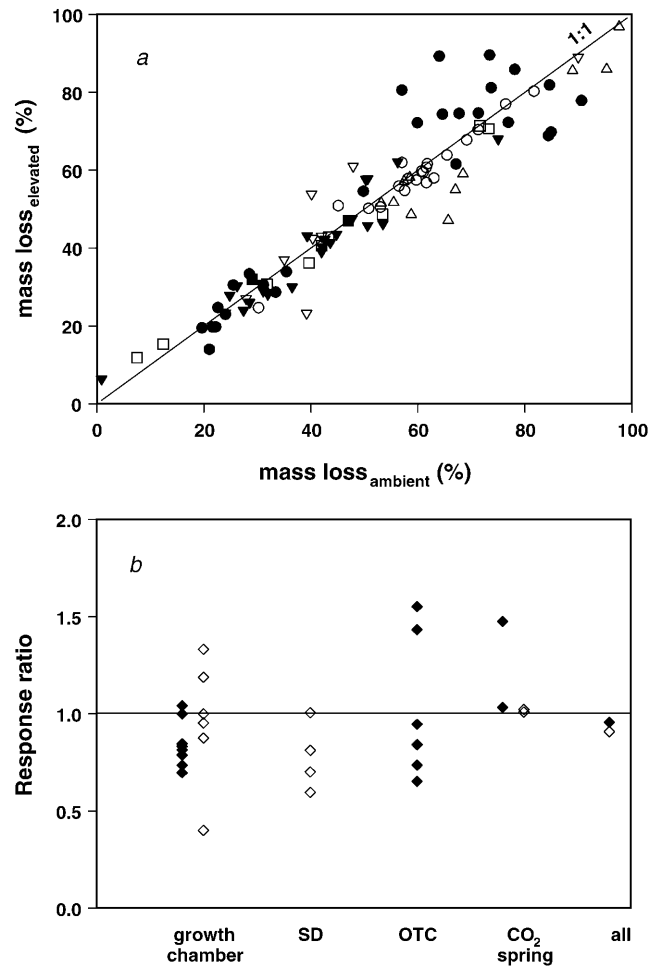


Fig. 5a, b Effect of CO_2 concentration during growth on subsequent decomposition of plant tissue. **a** Relative mass loss of decomposing tissue after growth in ambient versus elevated CO_2 . The line indicates the 1:1 relationship. (Open symbols Herbaceous plants, filled symbols woody plants.) (○, ● Plants exposed to elevated CO_2 in open-top chambers, □, ■ exposed in open-field systems (FACE, SACC, CO_2 springs), △ exposed in solardomes, ▼ exposed in growth chambers. Sources of data are shown in Table 1. **b** Response ratio to growth $[\text{CO}_2]$ of CO_2 release from decomposing litters

Nitrogen resorption

An unstated assumption of the “litter quality” hypothesis of Strain and Bazzaz (1983) is that the reduction in $[\text{N}]$ commonly observed in the leaves of CO_2 -enriched plants would result in litters with associated reduced $[\text{N}]$ and reduced decomposition. The 7.1% decline in leaf litter $[\text{N}]$ caused by CO_2 enrichment in our analysis is less than the decline reported for green leaves of plants in elevated CO_2 , which for trees averages from 10 to 21%. The lower end of this range is from field-grown trees exposed to elevated CO_2 for more than 2 years (Norby et al. 1999), whereas the higher end includes data from many short-term studies with tree seedlings in fertilized potting soil (McGuire et al. 1995).

If plants grown in elevated CO_2 have the same resorption efficiency as plants in current ambient CO_2 , then

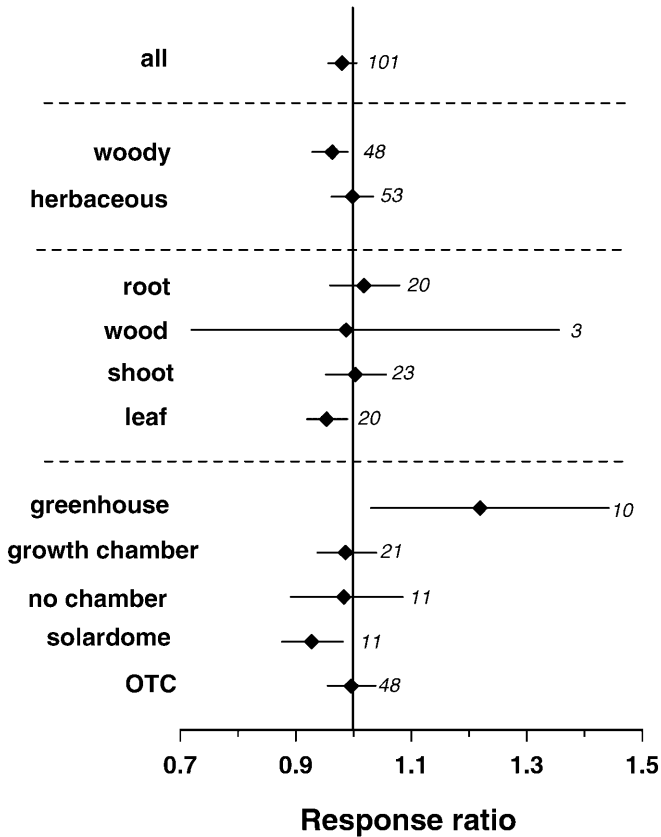


Fig. 6 Response ratio of mass loss during decomposition, presented as in Fig. 2

any CO_2 effect on foliar [N] should be reflected in the litter, as assumed in the “litter quality” hypothesis. The discrepancy between the CO_2 effect on green leaves (from the literature) and the effect on litter reported here might indicate that resorption is less efficient in elevated $[\text{CO}_2]$. Elevated CO_2 could influence resorption by changing the ratio of soluble to structural N in a leaf (Arp et al. 1997), which is thought to be an important controller of resorption (Pugnaire and Chapin 1993). Arp et al. (1997) concluded that the resorption efficiency was reduced in elevated CO_2 , based on their summary of studies in which there were data on both green and senescent plant tissue. Resorption efficiency in ambient CO_2 averaged 40% (range: 7–74%) but was reduced to 26% in high CO_2 . However, only one of the studies included in their analysis was a field study (Curtis et al. 1989), and there were several apparent artifacts in the other growth chamber studies that could have influenced N resorption (discussed in Norby et al. 2000). With more field data now available, we could conduct a similar analysis to that of Arp et al. (1997), but based only on studies with unfertilized plants free-rooted in the field or field chambers. This new analysis (Fig. 2) indicates that resorption efficiency should be similar in ambient and high CO_2 , and that CO_2 effects on green leaf [N] should be reflected in leaf litter.

Why then have most individual field CO_2 -enrichment experiments failed to detect an effect on litter [N]? The analysis of resorption in *Acer rubrum* and *A. saccharum* (Norby et al. 2000) provides some clues. There are several sources of variation in the resorption process that inevitably increase the variance in litter [N] data compared to the variance in green leaves. Resorption involves changes not just in N, but in dry matter as well, and the resulting N concentration in litter is determined by changes in both N content and dry matter content. N concentrations of both green leaf and litter of the *Acer* species were lower in elevated CO_2 , but this was explained completely by increased dry matter content – there were no differences in N content. This analysis was based on the [N] of individual, pre-selected leaves. Most analyses of litter quality, however, are based on bulk collections of all of the litter produced by a plant or group of plants – clearly a more ecologically relevant perspective. Resorption efficiency is variable from leaf to leaf, especially if unpredictable events such as herbivory, storms, water stress, or early frost cause leaves to fall before the resorption process is complete.

Killingbeck (1996) argued that environmental influences that prevent the fulfillment of potential resorption are the major cause of year-to-year variation in litter [N]. When [N] is greater than 10 mg g^{-1} , resorption was probably incomplete (Killingbeck 1996). In this synthesis of litter chemistry, the effects of CO_2 were greater when [N] was higher and indicative of incomplete resorption. Incomplete resorption could result from an artifact of growth chamber conditions (e.g., Norby et al. 1986), premature abscission by herbivores (B.G. Drake, personal communication), or unusual climatic events. In the first year of the experiment with the *Acer* species, the onset of leaf senescence was delayed in trees grown in elevated temperatures in open-top field chambers (OTC) (Norby et al. 2000). When an early frost occurred, the still green leaves were killed, and they eventually abscised with significantly higher [N] than the leaves of trees in ambient temperature, which had completed resorption prior to the frost. The effects of elevated $[\text{CO}_2]$ on autumn phenology are less consistent than those of temperature, but this example of interrupted resorption illustrates an important – and largely unpredictable – influence on litter [N]. Ecosystem models that assume resorption efficiency to be constant as CO_2 rises and set litter [N] as a constant fraction of green leaf [N] (e.g., Comins and McMurtrie 1993) are consistent with experimental studies, but the necessary simplifications will miss much of the complexity of the real (and future) world.

Litter lignin concentration

Initial lignin concentrations in fresh, naturally senesced leaf litter was 6.5% (11 mg g^{-1}) higher in response to elevated $[\text{CO}_2]$, and the effect on lignin concentration occurred only in leaves of woody species. Although the response of the lignin-to-N ratio could not be calculated

from the separate means of lignin and N, the small increase in lignin coupled with a small decrease in [N] implies a somewhat larger increase in lignin-to-N ratio, a commonly used index of leaf litter decomposability (Melillo et al. 1982). The responses of N and lignin concentrations to elevated $[\text{CO}_2]$ were not greatly influenced by experimental conditions (e.g., type of field exposure or fertilizer addition) as long as the data set was restricted to observations of naturally senesced leaf litter that developed under field conditions.

Decomposition

The central role of both N and lignin in controlling litter decomposition rates (Fog 1988; Melillo et al. 1982; Taylor et al. 1989) suggests that any changes in these determinants of litter quality could lead to subsequent alterations in litter decomposition rates. For example, a reduction in [N] (with associated increase in C:N ratio) of litter within a species would be expected to result in a decrease in the rate of litter decomposition, regardless of the atmospheric CO_2 concentration (Cotrufo et al. 1995). Lignin is particularly important in the later stages of decomposition, regulating litter mass loss rates (Berg and Staaf 1980; Berg et al. 1987). The degradation of lignin is accomplished by a limited group of soil micro-organisms, and it is known that high N levels may suppress lignin degradation rates through effects on these organisms (Berg and Ekbohm 1991). The reader is referred to the reviews of Fog (1988) and Cotrufo et al. (1998a) for a detailed description of these interactions, but it is clear that any decreases in litter [N] occurring under elevated $[\text{CO}_2]$ may well lead to an increase in lignin degradation in the final stages of decomposition. The overall, long-term outcome is, therefore, difficult to predict (Cotrufo et al. 1998a), but in a field study in which leaf litter was decomposed to nearly total mass loss, a reduction in decomposition rate attributable to elevated $[\text{CO}_2]$ was still evident at these very late stages (Cotrufo and Ineson 1996).

The decrease in initial litter [N] and increase in initial lignin concentration revealed in this synthesis would predict a slower decomposition rate. However, the experimental results show no single clear response, or even direction of response. This is especially noteworthy given that the data base may be biased toward showing a decomposition response because material from experiments in which leaf litter chemistry was found not to have changed may not have been used in subsequent decomposition experiments. The median values across all decomposition studies in the data base were 50.8% mass loss of ambient-derived tissue and 50.9% mass loss for CO_2 -enriched material. The compilation of data on CO_2 release from decomposing litter also showed no consistent effect of $[\text{CO}_2]$. The experimental conditions in which plants were grown, however, influenced subsequent decomposition rates. The effects of elevated CO_2 on N and lignin concentrations were largest in plants ex-

posed in SDs, so it is perhaps not surprising that this material also showed the largest CO_2 effect on decomposition.

Longer-term influences on decomposition

If the overall conclusion from this synthesis is correct, namely that there is no consistent evidence for a negative effect of growth in elevated $[\text{CO}_2]$ on subsequent rates of litter mass loss, then what information is still needed? It is essential that the *long-term* decomposition responses be assessed since many questions remain concerning the extrapolation of short-term studies to long-term effects (Cotrufo et al. 1998a; Thornley and Cannell 2000). Undetected or biologically insignificant differences in initial litter chemistry (including constituents in addition to N and lignin) may propagate or amplify over the long term. Studies conducted over the course of months to a few years have been useful, but they fail to capture long-term dynamics, particularly with regard to lignin degradation, humification, and the ultimate fate of litter-derived C. Incubations are required that follow the course of decomposition over a decade, and even longer in the case of coniferous material and acidic soils, where litter accumulates and decomposes very slowly. The experiment of Latter et al. (1998) involving litter bag incubations over 23 years suggested that initial high rates of decomposition may lead to a residue with a higher fraction of stabilized material. Lower initial decomposition rates resulting from lower initial [N] may allow lignin to be more readily degraded in later stages; this is a crucial aspect when net ecosystem C storage is being modeled.

From both a statistical and predictive viewpoint much information can be gained from examining inter-annual and inter-site variability in litter chemistry within species. Indications so far from a few species suggest that any response to elevated $[\text{CO}_2]$ is minimal compared to variability from year to year, soil to soil, and site to site. Berg et al. (1993) report changes in [N] in Scots pine needle litter over a 17-year study with annual variation of the order of 23%. Presumably, such changes are due to year-to-year variation in plant growth, resorption and soil N mineralization rates caused by inter-annual variations in climate. The direct effects of temperature and moisture on the decomposition process are well documented, yet little work has been done on the interactive effects of either of these factors with elevated CO_2 , and still less on interactions between CO_2 and atmospheric pollutants such as ozone. For example, while CO_2 enrichment alone may have only small effects on litter chemistry, physical damage from ozone exposure, combined with increased C fixation might result in more highly lignified litter (Boerner and Rebbeck 1995).

Although an attempt has been made in the current synthesis to compare materials grown, and sometimes decomposed under both ambient and elevated $[\text{CO}_2]$, no studies have measured decomposition rates in soils that developed under elevated $[\text{CO}_2]$. For example, new de-

composer communities might emerge after years of CO₂ enrichment. Equilibration of ecosystems to higher [CO₂] could result in soils with different moisture or physical conditions that would influence decomposition rates. In most studies it has been impractical to decompose litter in situ under elevated [CO₂]; it may well be impossible to do it in soils that developed in a CO₂-enriched atmosphere. The idea of changes in soils due to CO₂ enrichment is one that should be examined further, possibly in ecosystems with rapid turnover times or in ecosystems exposed over time to natural sources of CO₂ enrichment (e.g., CO₂ springs).

This analysis has considered how elevated [CO₂] might alter the decomposition of individual plant tissues, but the potential long-term effects of [CO₂] on plant community composition could have more profound influences on ecosystem-wide decomposition and nutrient cycling (Pastor and Post 1988). If a long-term effect of rising atmospheric [CO₂] or climatic change is a shift in community composition from species with low lignin:N litter to species with high lignin:N litter, the overall effect on litter chemistry and decomposition at the community level could be much larger than the direct effect on an individual plant's litter. Changes in the overall composition of litter could also influence the decomposition of an individual leaf which is intimately connected with the litter and soil surrounding it (Chadwick et al. 1998). The input of N to the system, as well as the timing and rates of immobilization versus mineralization may change nutrient cycling rates and serve as either a positive or a negative feedback on the system's response to elevated [CO₂].

Recommendations for standardizing measures of litter quality and decomposition in elevated-CO₂ studies

Synthesis of the effects of elevated CO₂ or other global change factors on decomposition across a wide range of species and environmental conditions would be facilitated if experimental and analytical methods were standardized. For example, standardized assessment of initial litter chemistry is critical, with, as a minimum, lignin and N concentrations as well as labile C being needed. Comparison litter data should also be obtained from plants of the same species grown under non-experimental conditions in their natural habitat (O'Neill and Norby 1996). This may help to establish whether the litter chemistry of experimental controls are being compromised through experimental artifacts. Lack of such information does not necessarily invalidate relative responses to treatment (unless of course, the impact of the artifact is influenced by treatment) but does make it difficult to judge whether the response can be extrapolated to the real world.

Litter should be obtained from plants grown in the ground under natural conditions of water, light, and temperature (unless these conditions are part of the experimental manipulation). Litter produced under artificial

culture conditions, while valid for use in some studies, results in data that are difficult to interpret when synthesis is attempted. Likewise, it is critical that foliar litter be naturally abscised and representative of a typical senescence period. In ecosystems where foliage persists over multiple growing seasons, it is recommended that only foliage that was both produced and abscised under treatment conditions be used. The microbial populations on the surface of plant tissue are important in initiating litter decomposition; hence, the plant material used in litter-bag studies should not be oven-dried, but used fresh or after minimal air-drying. For example, oven-drying at 50°C has been shown to reduce N concentrations and chemically increase lignin concentration in litter compared to air-drying at 25°C (Mafongoya et al. 1997). Likewise, it is recommended that litter should not be ground before measuring decomposition, as is standard for some laboratory methods. The effect of particle size on CO₂ evolution and N mineralization-immobilization appears to differ with litter C-to-N ratios (Handayanto et al. 1997).

Decomposition experiments should be conducted close to the origin of the litter (Bocock et al. 1960; Chadwick et al. 1998). Forest litter should decompose on forest soils, grass on grassland soil and so on, because decomposer communities may differ greatly between systems. Where practical, decomposition as well as litter production should occur under CO₂ treatments, and reciprocal experiments should be done to control for both direct and indirect effects of CO₂ enrichment, although direct effects of [CO₂] can probably be considered insignificant (Ineson and Cotrufo 1997).

With the emergence of large-scale experiments in a number of critical ecosystems, a unique opportunity has arisen for extended investigations into the process of long-term decomposition in a CO₂-enriched world. Appropriate care toward experimental and analytical methods will benefit future syntheses on the effects of atmospheric CO₂ and other global change factors on litter chemistry and decomposition.

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