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Species control variation in litter decomposition in a pine forest exposed to elevated CO_2

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Abstract

Net primary production and the flux of dry matter and nutrients from vegetation to soils has increased following four years of exposure to elevated CO_2 in a southern pine forest in NC, USA. This has increased the demand for nutrients to support enhanced rates of NPP and altered the conditions for litter decomposition on the forest floor. We quantified the chemistry and decomposition dynamics of leaf litter produced by five of the most abundant tree species in this ecosystem during the third and fourth growing seasons under elevated CO_2. The objectives of this study were to determine (i) if there were systemic or species-specific changes in leaf litter chemistry associated with a sustained enhancement of plant growth under elevated CO_2; and (ii) whether the process of litter decomposition was altered by increased inputs of energy and nutrients to the forest floor in the plots under elevated CO_2. Leaf litter chemistry, including various C fractions and N concentration, was virtually unchanged by elevated CO_2. With few exceptions, plant litter produced under elevated CO_2 lost mass or N at the same relative rate as that produced under ambient CO_2. The relationship between initial litter chemistry and decomposition was not altered by elevated CO_2. The greater forest floor mass and nutrient content in the plots under elevated CO_2 had no consistent or long-term effect on litter decomposition. Thus, we found no evidence that plant and microbial processes under elevated CO_2 resulted in systemic changes in mass loss or N dynamics during decomposition. In contrast to the limited effects of elevated CO_2 on litter chemistry and decomposition, there were large differences among species in initial litter chemistry, mass loss and N dynamics during decomposition. If the species composition of this forest community is altered by elevated CO_2, the indirect effect of a change in species composition will exert greater control over the long-term rate of nutrient cycling than the direct effect of elevated CO_2 on litter chemistry and decomposition dynamics alone.

Keywords: decomposition, elevated CO_2, litter, nitrogen, *Pinus taeda*

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Introduction

Litter production, chemistry and decomposition contribute to the quantity of nutrients cycling between vegetation and soils (Schlesinger, 1997). Changes in litter chemistry and decomposition dynamics dominate the literature on ecosystem-feedbacks to elevated CO_2 because of the strong correlations among initial litter chemistry, the rate of litter decomposition and soil nutrient availability (Melillo *et al.*, 1982; Taylor *et al.*, 1989; Reich *et al.*, 1997; Scott & Binkley, 1997; Norby *et al.*, 2001). Soil nutrient availability can control the size of the carbon (C) sink in woody biomass growing under elevated CO_2 (e.g. Oren *et al.*, 2001). The C balance of forest ecosystems is likely to change if the chemistry or decomposition of litter is altered by rapid plant growth under elevated CO_2.

Based on the observation that plant C:N ratios can increase as a result of rapid plant growth under elevated CO_2, Strain & Bazzaz (1983) proposed that elevated CO_2 could affect nutrient cycling. They suggested that the increase in the C:N ratio of plant litter would slow the rate of litter decomposition, increase the quantity of

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N immobilized in litter during decomposition, and decrease plant-N availability. Under this scenario, they hypothesized that a long-term stimulation of plant growth under elevated CO_2 would not occur because insufficient N would be mineralized from organic matter to support rapid rates of plant growth.

Several studies have reviewed the literature on litter chemistry and decomposition under elevated CO_2 (Cotrufo *et al.*, 1998; Norby & Cotrufo, 1998; Coûteaux *et al.*, 1999; Norby *et al.*, 2001). Among diverse taxa and ecosystem types, Norby *et al.* (2001) reported a mean reduction in litter N concentration of 7.1% and a mean increase in litter lignin concentration of 6.5% under elevated CO_2. However, there was no overall effect of these changes in litter chemistry on the rate of mass loss for litter produced under elevated CO_2.

In the majority of studies, CO_2 fumigation lasts from days to a few years and we might expect short-term litter chemistry and decomposition responses to differ from longer-term responses. On the one hand, there could be a direct effect of long-term CO_2 fumigation on litter chemistry. In the absence of exogenous inputs of N, sustained rates of rapid plant growth under elevated CO_2 may only be possible by increasing N-use efficiency (NUE), as N supplies from soil are exceeded and storage pools of N within plant biomass are exhausted (Rastetter *et al.*, 1997; Luo & Reynolds, 1999). An increase in NUE under long-term CO_2 fumigation could increase the C : N ratio of plant litter to a greater extent than might be observed in short-duration studies. Alternatively, long-term CO_2 fumigation could alter the conditions for litter decomposition at the soil surface independent of changes in litter chemistry. Increases in the quantity of organic matter at the soil surface could increase soil moisture and nutrient availability to the decomposer community thereby accelerating the rate of litter decomposition (Swift *et al.*, 1979).

We have studied the nutrient-cycling response of a southern US pine forest to long-term Free-Air CO_2 Enrichment (FACE) located in the Duke Forest (Orange County, North Carolina, USA). During the first four years of CO_2 fumigation, net primary production (NPP) was stimulated by an average of 25% (DeLucia *et al.*, 1999; Finzi *et al.*, 2002). The increase in NPP has increased the demand for N by vegetation (Finzi *et al.*, 2002), increased the mass and the moisture content of the forest floor (Schlesinger & Lichter, 2001; Schafer *et al.*, 2002), the production of fine roots (Matamala & Schlesinger, 2000) and the rate of C cycling by microbes (Hamilton *et al.*, 2002). The objectives of this study were to determine (i) if there were systemic or species-specific changes in leaf litter chemistry associated with a sustained enhancement of plant growth under elevated CO_2; and (ii) whether the process of litter decomposition was altered by increased inputs of energy and nutrients to the forest floor in the plots under elevated CO_2. We present data on the chemistry, decomposition and N dynamics of leaf litter collected during the third and fourth growing seasons under elevated CO_2.

Methods and materials

Site description

This FACE experiment is located in the Duke Forest, Orange County, NC, and is composed of six 30-m diameter plots. Three experimental plots are fumigated with CO_2 to maintain the atmospheric CO_2 concentration $200\,\mu L\,L^{-1}$ above ambient (i.e. $565\,\mu L\,L^{-1}$). Three control plots are fumigated with ambient air only ($365\,\mu L\,L^{-1}$). The experiment began 27 August 1996 and is continuous. Additional details on the application of FACE to this ecosystem are found in Hendrey *et al.* (1999).

The forest is derived from 3-year-old-loblolly pine (*Pinus taeda* L.) seedlings that were planted in 1983 in a 2.4×2.4-m spacing. In 1996, the pine trees were approximately 14 m tall and accounted for 98% of the basal area of the stand. Since planting, a deciduous understorey layer has recruited from nearby hardwood forests. The most abundant understorey tree species include sweet gum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), red bud (*Cercis canadensis*), and flowering dogwood (*Cornus florida*). The 32-ha site contains an elevation gradient of 15-m between the highest and lowest points, but topographic relief is $\leq 1°$ throughout. Soils are classified as being from the Enon Series (fine, mixed, active, thermic Ultic Hapludalfs). Enon soils are derived from mafic bedrock and are slightly acidic (0.1 M $CaCl_2$ pH = 5.75) and have well-developed soil horizons with mixed clay mineralogy. Additional site details are found in Schlesinger & Lichter (2001) and Finzi *et al.* (2001).

Leaf collection and chemistry

The longevity of loblolly pine foliage in the Piedmont of NC is 19 months (Zhang & Allen, 1996) so that at any time there are needles of two different ages on a single branch – those produced in the current year ('new') and those produced in the previous year ('old'). During September of 1999 and 2000 – the third and fourth growing seasons under FACE – we collected samples of old needles produced in the previous year at three heights within the canopy; the bottom 25%, the middle 50%, and the top 25% of the crown. We focus on the old needles as they senesce in the autumn of the same year in which we collected leaf litter, and they represent the needle cohort from which N is retranslocated prior to senescence. We collected needle samples in the center of each plot by

climbing a canopy-access tower. At each height we sampled a single branch on three or four trees and collected five fascicles from each flush of the old cohort along a primary branch. We calculated the average concentration of N throughout the loblolly pine canopy by averaging the N concentration of each needle samples collected in the bottom, middle, and top of the canopy.

We collected green foliage from the four understorey hardwood species listed above in August of 1999 and 2000. At this point in the growing season, the leaves are fully expanded and mature so that our measures of leaf chemistry avoid the unusually high nutrient concentration of rapidly expanding, young leaves (Chapin & Kedrowski, 1983). Each species occurs in each of the six FACE plots with the exception of red bud that is absent in one of the ambient CO_2 plots. We sampled three leaves from each of 10–20 different trees of each species within each plot. The leaves of each species within a ring were combined into a single bag, oven dried at 65 °C for four days, ground, and analyzed for chemical constituents.

Once a week, between October 15 and November 15 of 1998, 1999, and 2000, we collected recently fallen leaves from the top of the forest floor. We distinguished freshly fallen litter from older litter based on foliage color (brightly or lightly colored litter was considered fresh) and friability (friable litter was considered old). This litter was used in the two-year-leaf-litter-decomposition study (see below) and to characterize the C and N chemistry of freshly abscised plant litter.

We measured the N concentration of green leaves and leaf litter in a sulfuric acid – copper sulfate Kjeldahl digestion followed by colorimetric analysis on an automated ion analyzer (Lachat Quick Chem FIA + 8000 Series, Zellweger Analytics, Milwaukee, WI, USA).

We measured the concentration of C in litter by combustion in an elemental analyzer (NA2500, Carlo Erba Instruments, Milan, Italy). We measured the concentration of total non-structural carbohydrates (TNC; starch, glucose, sucrose, and fructose) in litter colorimetrically using a modification of the Dubois *et al.* (1956) method, as described by Finzi *et al.* (2001). In brief, ground samples were extracted three times with a methanol: chloroform: water (12 : 5 : 3 v/v) solution. We added perchloric acid and determined the quantity of solubilized sugars and starch colorimetrically using the phenol-sulfuric acid method (Dubois *et al.*, 1956).

We measured the lignin concentration in litter using a modified version of an acetyl-bromide extraction procedure (Ilyama & Wallis, 1990). The complete details of this procedure are presented in Finzi *et al.* (2001). In brief, we extracted ground samples in water, ethanol, acetone, and diethyl ether. Following overnight drying at 70 °C, we added acetyl bromide and acetic acid to each sample and measured the concentration of lignin in the acetyl bromide-acetic acid extraction at 280 nm on a spectrophotometer (Hitachi U-2000, Hitachi Instruments Inc., San Diego, CA, USA). We used a National Bureau of Standards Pine sample as our reference material (% Lignin = 21.8, Hobbie & Vitousek, 2000).

To avoid confounding N retranslocation with the retranslocation of C-based compounds during senescence, we calculated the percent of N retranslocated from green leaves prior to senescence on a mass-per-unit-area basis (Staaf, 1982). Retranslocation efficiency was calculated as 100 multiplied by the quotient of the difference in the green leaf and leaf litter N concentration and the green leaf N concentration.

Decomposition

Decomposition was followed for two years from November 1998 to November 2000 in a reciprocal-transplant field study. Leaf litter produced under ambient CO_2 was decomposed in its source plot under ambient CO_2 and in a paired, elevated – CO_2 plot (see below). Similarly, leaf litter produced under elevated CO_2 was decomposed in its source plot under elevated CO_2 and in a paired, ambient-CO_2 plot. For clarity of presentation, we adopt a notation where $[CO_2]_{grown,\ decomp.}$ denotes the CO_2 treatment under which leaves were grown and then decomposed as in, for example, $[CO_2]_{a,e}$ that denotes litter produced under ambient CO_2 and decomposed under elevated CO_2.

Variations in soil N availability have been correlated with changes in the rate of leaf litter decomposition and N immobilization – mineralization dynamics during the process of decomposition (Kelley & Henderson, 1978; Downs *et al.*, 1996). The paired transplant plots were based on the between-plot variation in the annual rate of net N mineralization (Fig. 1). Among the six plots that comprise this FACE facility, annual rates of net mineralization vary > 3-fold from 12 to 43 kg N ha^{-1} yr^{-1} (Finzi *et al.*, 2002). However, annual rates of net N mineralization are not significantly different between paired ambient and elevated CO_2 plots 1 & 2, 6 & 4, and 5 & 3 (Fig. 1). Thus litter produced under ambient or elevated CO_2 within each of these pairings was transplanted to the other plot. For statistical analysis we assigned each of the paired plots to one of three blocks. We assigned plots 1 & 2 to block 1, plots 6 & 4 to block 2, and plots 5 & 3 to block 3.

All of the litter collected from the surface of the forest floor in the Autumn of 1998 was kept in separate bags for each species in each of the three treatment and control plots. This material was used to fill litterbags with a 2.0-g sample of loblolly pine, sweet gum, dogwood, red maple,

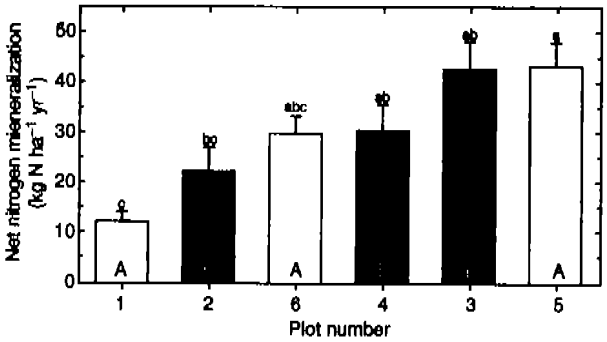

Fig. 1 The annual rate of net N mineralization measured from June 1997 through May 1998. Open bars indicate plots under ambient CO_2 and filled bars indicate plots under elevated CO_2. The differences among FACE plots is significant at $P < 0.001$. Superscript letters indicated significant differences between FACE plots. Data from Finzi *et al.* (2002).

or red bud leaf litter. The litterbags were 10 cm × 10 cm with 1-mm mesh openings on top and 0.1-mm openings on the bottom. We placed the litterbags on the forest floor beneath the freshly fallen litter and we collected them from the field following 6, 12, and 24 months of decomposition. We constructed a total of 72 litterbags per species for this decomposition experiment, the 72 litterbags representing 2 litter types × 2 sites of decomposition × 3 replicate plots per CO_2 treatment × 3 harvest dates × 2 replicate litterbags deployed per harvest. The remaining litter that was not used to fill the litterbags was dried in an oven at 70 °C for three days to determine the oven-dried mass of the litter. This oven-dry mass data were used to correct the initial mass of the air-dried litter deployed in the decomposition experiment.

At each sampling period, we measured the mass and concentrations of C, N, TNC and lignin remaining in the decomposing litter. The handling and the chemical analysis of the litter from the decomposition study was identical to that described in the previous section on foliar chemistry. At each harvest date, we calculated the fraction of the initial mass and N remaining as the difference between the mass or N content of the litter initially present in the litterbag and the mass or N content of the remaining litter in the litterbag divided by the amount that was initially present.

Statistical analysis

We analyzed the data on foliar chemistry (i.e. green leaf chemistry, leaf litter chemistry, and retranslocation efficiency) using nested ANOVA (Underwood, 1997). The CO_2 treatments (2 levels) and Species (5 levels) are independent, fixed effects. The 6 replicate plots are a randomly sampled factor nested in each CO_2 treatment because the 3 replicate plots were randomly assigned a CO_2 treatment. However, the plots nested in each level of CO_2 are independent of species because each level of species is present in each plot. There are a total of 30 degrees-of-freedom to allocate in this statistical model (2 CO_2 levels × 3 replicates × 5 species). We analyzed the two years of data separately.

We tested the main effect of elevated CO_2 on foliar chemistry with the plots nested within CO_2 treatment term as the error-term. We tested for significant differences among species in foliar chemistry using the species × plot nested with CO_2 treatment as the error term. We used the same error term to test the significance of the CO_2 × species interaction (Underwood, 1997). When the CO_2 × species interaction term was significant, we performed 1-way ANOVA to determine which species responded significantly to elevated CO_2.

The decomposition study was designed as a reciprocal transplant study. However, the non-random allocation of the transplanted litterbags prevented us from conducting a factorial analysis of the litter decomposition data with litter chemistry, site of decomposition, and species effects. Thus, we divided our data analysis into two separate analyses of variance. In the first analysis, we used two-way ANOVA and tested for differences in mass loss and N remaining as a function of the effect of elevated CO_2 on litter chemistry (i.e. $[CO_2]_{a,a}$ and $[CO_2]_{a,e}$ vs. $[CO_2]_{e,e}$ and $[CO_2]_{e,a}$) and species. To account for variation in soil N availability among the paired-litter-transplant plots, in the second analysis, we used a randomized block design to test for the effects of site of decomposition and species on mass loss and N remaining (i.e. $[CO_2]_{a,a}$ and $[CO_2]_{e,a}$ vs. $[CO_2]_{e,e}$ and $[CO_2]_{a,e}$). Prior analysis indicated a significant effect of harvest date on mass and N loss during decomposition (Finzi *et al.*, 2001), and we analyzed the mass loss and N remaining data in each analysis separately.

We used stepwise linear regression analysis to determine which initial litter chemical parameters regulated the rate of mass loss and N dynamics during decomposition (SAS, 1990). Initial litter chemical parameters included C, N, TNC and lignin concentrations in addition to the C:N and lignin:N ratio. The initial litter chemistry data used in this analysis were published in Finzi *et al.* (2001). They are reprinted in Table 1. The details of the statistical analysis are available in Finzi *et al.* (2001).

Results

Leaf chemistry

The effect of elevated CO_2 on green leaf and leaf litter concentrations of N was not statistically significant

Table 1 The C fractions and N concentration of the leaf litter of five different species growing under ambient (A) and elevated (E) CO_2 in 1998

	% Total non-structural											
	% Carbon		% Lignin		carbohydrates		N (mg g^{-1})		C : N		Lignin : N	
Species	A	E	A	E	A	E	A	E	A	E	A	E
Red bud	^{b}45.6	45.1	^{b}22.3	20.8	^{ab}10.3	10.1	^{a}11.3	11.4	^{c}40.4	39.6	^{c}19.7	18.2
	(0.4)	(0.2)	(0.8)	(0.8)	(0.2)	(1.3)	(0.1)	(1.5)	(0.8)	(5.8)	(0.9)	(1.8)
Dogwood	^{c}42.5	42.8	^{d}10.8	8.1	^{a}10.9	13.0	^{b}9.6	7.1	^{bc}**44.3**	**60.3***	^{d}11.2	11.4
	(0.4)	(0.8)	(1.1)	(0.3)	(0.8)	(1.0)	(1.4)	(0.4)	(7.6)	(2.1)	(2.1)	(0.2)
Red maple	^{b}46.0	46.1	^{c}15.3	15.5	^{b}8.6	9.9	^{bc}7.4	7.0	^{b}62.2	65.9	^{c}20.7	22.1
	(0.2)	(0.3)	(0.5)	(0.1)	(0.3)	(0.7)	(0.5)	(0.6)	(3.4)	(5.0)	(1.4)	(1.6)
Sweet gum	^{b}44.5	45.3	^{b}**19.3**	**21.0***	^{a}11.2	11.8	^{bc}7.1	6.4	^{b}62.7	70.8	^{b}27.2	**32.8***
	(1.0)	(0.6)	(0.1)	(0.6)	(0.9)	(0.8)	(0.5)	(0.3)	(5.5)	(3.9)	(1.7)	(0.9)
Loblolly pine	^{a}49.7	49.5	^{a}23.6	22.5	^{a}11.6	12.9	^{c}4.9	5.0	^{a}101.4	99.0	^{a}48.2	45.2
	(0.2)	(0.4)	(0.7)	(0.4)	(0.4)	(0.1)	(0.3)	(0.1)	(6.9)	(2.1)	(1.7)	(1.6)

Values with different superscript symbols on the right-hand side of a column indicate a significant within-species treatment effect of elevated CO_2 at * = $P < 0.05$ (in bold). Different superscript letters on the left-hand side of a column indicate significant differences among species. Data are from Finzi *et al.* (2001).

Table 2 *F*-statistics and *P*-values from nested ANOVAS showing the effects of species identity and elevated CO_2 on green leaf and leaf litter C and N chemistry and the efficiency of N retranslocation

		Year			
		1999		2000	
Chemistry	Source of variation	*F*	*P*	*F*	*P*
% N green leaves	CO_2	0.57	0.49	2.15	0.22
	Species	**114.64**	**< 0.0001**	**115.60**	**< 0.0001**
	CO_2 × species	**3.95**	**< 0.05**	0.48	0.75
% N leaf litter	CO_2	0.70	0.45	**4.56**	**0.10**
	Species	**37.97**	**< 0.0001**	**48.80**	**< 0.0001**
	CO_2 × species	0.93	0.47	0.46	0.77
Retranslocation efficiency	CO_2	0.55	0.47	0.01	0.96
	Species	**27.35**	**< 0.001**	**7.94**	**< 0.001**
	CO_2 × species	**4.61**	**< 0.05**	0.50	0.74
% C leaf litter	CO_2	0.66	0.46	0.92	0.39
	Species	**64.01**	**< 0.0001**	**151.24**	**< 0.0001**
	CO_2 × species	1.55	0.24	**3.69**	**< 0.05**
% lignin leaf litter	CO_2	1.04	0.37	0.50	0.52
	Species	**159.36**	**< 0.0001**	**33.77**	**< 0.0001**
	CO_2 × species	0.96	0.46	0.44	0.78
% TNC leaf litter	CO_2	0.02	0.90	0.84	0.41
	Species	**6.91**	**< 0.01**	**25.24**	**< 0.0001**
	CO_2 × species	0.19	0.94	0.63	0.66

P-values < 0.10 are in bold.

during the third and fourth growing seasons (Table 2). The CO_2 × species interaction was statistically significant for green leaf N concentration only in 1999 (Table 2). One-way ANOVA indicated that the concentration of N in red maple leaves was marginally ($P < 0.10$) lower under elevated CO_2 than ambient CO_2 (Table 3). There were large, statistically significant differences among species in the concentrations of N in green leaves and leaf litter (Table 2). Green leaf and litter N concentrations were lowest in loblolly pine and highest in red bud with other species intermediate (Table 3).

In general, elevated CO_2 did not affect the efficiency of N retranslocation prior to leaf senescence (Table 2). However, the CO_2 × species interaction was significant in 1999, when the efficiency of red maple retranslocation was lower and that of dogwood higher under elevated CO_2 than ambient CO_2 (Table 3). In 2000, there was no detectable effect of elevated CO_2 on retranslocation efficiency. Retranslocation efficiency varied significantly among species in both years (Table 2). In general, red maple retranslocated significantly more N than sweet gum or dogwood, with the other species intermediate between these two (Table 3).

The concentrations of C, lignin and TNC in leaf litter were unaffected by elevated CO_2 during both years (Table 2). The CO_2 × species interaction was significant only for % C in 2000 and no other C fraction or year (Table 2). One-way ANOVA demonstrated significantly higher concentrations of C in dogwood and sweet gum litter produced under elevated CO_2 than ambient CO_2 (Table 4). There were large interspecific differences among species in the concentration of C, lignin and TNC in both years (Table 2). The C concentration of leaf litter was highest in loblolly pine and lowest in dogwood with other species intermediate between these two (Table 4). In general, lignin concentrations were highest in red bud, sweet gum and loblolly pine and lowest in dogwood. Total non-structural carbohydrates (TNC) concentrations were highest in loblolly pine and lowest in red maple and sweet gum.

Table 3 The concentration of N in green leaves and leaf litter and the retranslocation efficiency of N during the third and fourth growing seasons under ambient ('A') and elevated ('E') CO_2 (mean ± 1 SE)

		Green (mg g^{-1})		Litter (mg g^{-1})		Retranslocation* (%)	
Year	Species	A	E	A	E	A	E
1999	Loblolly pine	^{b}9.76 (0.57)	10.31 (0.22)	^{c}3.83 (0.24)	4.01 (0.32)	^{bc}53.6 (1.4)	53.5 (3.7)
	Dogwood	^{a}15.42 (0.30)	17.07 (1.31)	^{b}7.05 (0.70)	6.19 (0.76)	^{ab}**55.9** (2.6)	**68.4**† (1.1)
	Red bud	–	–	^{a}10.41 (0.52)	9.08 (2.17)	–	–
	Red maple	^{a}**16.24** (0.69)	**14.75**† (0.37)	^{c}4.53 (0.13)	4.62 (0.14)	^{a}**69.3** (0.8)	**63.7**** (0.6)
	Sweet gum	^{a}16.10 (1.74)	15.06 (1.36)	^{bc}5.99 (0.46)	5.07 (0.40)	^{c}44.5 (4.3)	45.7 (2.6)
2000	Loblolly pine	^{c}9.30 (0.39)	9.02 (0.34)	^{d}3.73 (0.61)	3.56 (0.42)	^{a}62.0 (4.8)	59.7 (5.3)
	Dogwood	^{b}17.10 (0.20)	16.16 (0.62)	^{b}8.95 (0.26)	7.71 (0.51)	^{b}39.1 (5.6)	46.5 (5.8)
	Red bud	^{a}23.63 (1.84)	21.42 (2.56)	^{a}11.30 (0.44)	9.58 (1.51)	^{b}44.1 (0.9)	45.0 (8.8)
	Red maple	^{b}15.98 (0.53)	15.53 (0.22)	^{cd}5.41 (0.52)	4.83 (0.40)	^{a}64.3 (4.4)	63.9 (2.2)
	Sweet gum	^{b}18.58 (0.59)	16.87 (0.60)	^{c}5.98 (0.48)	5.05 (0.34)	^{ab}57.6 (1.5)	52.7 (4.9)

*N-retranslocation efficiency was calculated on a per unit area basis rather than on a mass basis. See Methods and materials for explanation. Values with different superscript symbols on the right-hand side of a column indicate a significant within-species treatment effect of elevated CO_2 at $^{\dagger} = P < 0.10$, $^{**} = P < 0.01$. Different superscript letters on the left-hand side of a column indicate significant differences among species. Significant CO_2 effects are in bold.

Table 4 The concentration of different C fractions in leaf litter produced during the third (1999) and fourth (2000) growing seasons under ambient ('A') and elevated ('E') CO_2 (mean ± 1 SE)

		Carbon (%)		Lignin (%)		Total non-structural carbohydrates (%)	
Year	Species	A	E	A	E	A	E
1999	Loblolly pine	^{a}50.99	50.93	^{a}20.20	21.52	^{a}10.42	10.93
		(0.20)	(0.22)	(0.22)	(0.75)	(0.67)	(0.46)
	Dogwood	^{c}46.26	45.15	^{d}8.12	8.04	^{a}10.53	10.46
		(0.54)	(0.53)	(0.34)	(0.24)	(0.06)	(0.24)
	Red bud	^{bc}46.68	46.37	^{a}20.56	20.54	^{b}9.30	8.90
		(0.14)	(0.59)	(0.96)	(1.76)	(1.01)	(0.27)
	Red maple	^{b}46.84	47.30	^{c}11.05	12.04	^{b}8.77	8.85
		(0.24)	(0.09)	(0.15)	(0.43)	(0.31)	(0.68)
	Sweet gum	^{bc}46.27	46.67	^{b}13.89	13.24	^{b}8.68	8.76
		(0.21)	(0.40)	(0.54)	(0.50)	(0.24)	(0.69)
2000	Loblolly pine	^{a}51.61	51.60	^{b}16.86	17.56	^{a}13.08	12.61
		(0.30)	(0.31)	(0.22)	(0.41)	(0.48)	(0.26)
	Dogwood	^{c}**45.86**	**46.54***	^{c}9.97	10.15	^{ab}10.58	10.73
		(0.10)	(0.17)	(0.75)	(1.65)	(0.16)	(0.71)
	Red bud	^{b}47.86	47.92	^{ab}18.55	19.03	^{bc}9.23	9.30
		(0.27)	(0.70)	(0.14)	(1.03)	(0.05)	(0.78)
	Red maple	^{b}48.05	47.39	^{c}13.44	12.65	^{c}8.13	8.89
		(0.14)	(0.43)	(1.23)	(0.41)	(0.19)	(0.78)
	Sweet gum	^{c}**45.85**	**46.93****	^{a}19.85	21.76	^{c}8.38	9.31
		(0.12)	(0.13)	(1.93)	(0.70)	(0.70)	(0.26)

Within a particular C fraction, columns with different superscript symbols are significantly different at * = $P < 0.05$, ** = $P < 0.01$. Different superscript letters on the left-hand side of a column indicate significant differences among species. Significant CO_2 effects are in bold.

Decomposition

There was a marginally significant effect of elevated CO_2 on litter chemistry that affected the fraction of initial mass remaining after six months of decomposition (Table 5). Leaf litter produced under elevated CO_2 had more mass remaining (66%) than litter produced under ambient CO_2 (64%). Apart from this sample date, however, there was no effect of litter chemistry on the rate of mass loss (Table 5). In contrast, the rate of mass loss varied significantly among species at each harvest date (Table 5). By the end of 24 months, the fraction of initial material remaining was highest in loblolly pine (~40%) and lowest in dogwood (~18%, Fig. 2). There was no significant interaction between litter chemistry and species on the rate of mass loss.

In general, elevated CO_2 did not affect litter chemistry in a manner that altered the fraction of the initial N mass remaining during decomposition (Table 5). The notable exception was during the second harvest when there was a marginally significantly litter chemistry × species interaction in the fraction of the initial N remaining (Table 5). One-way ANOVA indicated a significantly slower rate of N loss from red maple litter produced under elevated CO_2 than under ambient CO_2 following 12 months of decomposition (Fig. 2). In contrast, there were large, statistically significant differences among species in the fraction of initial N remaining at each harvest (Table 5, Fig. 2).

The analysis of the site-of-decomposition data demonstrated a significant effect of the block on the rate of mass loss after 24 months of decomposition (Table 5). There was significantly greater mass remaining (34%) in leaf litter in block 3, the block with the highest rate of net N mineralization, than in blocks 2 and 1 (each with 29% of initial mass remaining), the blocks with intermediate and low rates of N mineralization (Fig. 1). In contrast to this one harvest date, there was no effect of the site of decomposition, block, or their interaction on the mass or the N remaining in leaf litter (Table 5). Species differed significantly from one another in the fraction of initial mass and N remaining at each harvest date (Table 5) reflecting the strong interspecific variation in litter chemistry among species (Table 1). There were no significant interactions between species and block or site of decomposition in mass loss and N remaining on any harvest date.

Table 5 *F*-statistics and *P*-values from ANOVA showing the effects of CO_2-induced variations in litter chemistry, site-of-decomposition, and species effects on the fraction of initial mass and N remaining in leaf litter following 6, 12, and 24 months of decomposition in the field

	Harvest					
	6 months		12 months		24 months	
Source of variation	*F*	*P*	*F*	*P*	*F*	*P*
Effects of litter chemistry						
Mass remaining						
CO_2	**3.26**	**0.07**	0.01	0.97	0.01	0.92
Species	**96.27**	**< 0.0001**	**36.36**	**< 0.0001**	**32.49**	**< 0.0001**
CO_2 × species	1.22	0.31	1.02	0.40	2.01	0.11
N remaining						
CO_2	1.36	0.25	1.96	0.16	0.15	0.69
Species	2.88	**< 0.05**	**24.66**	**< 0.0001**	**17.26**	**< 0.0001**
CO_2 × species	1.33	0.26	**2.18**	**0.08**	1.39	0.24
Site-of-decomposition effects						
Mass remaining						
Block	1.64	0.20	0.93	0.39	3.64	**< 0.05**
Site	0.35	0.56	0.01	0.96	0.58	0.44
Block × site	0.17	0.84	0.27	0.77	1.52	0.22
Species	**82.40**	**< 0.0001**	**37.05**	**< 0.0001**	**29.03**	**< 0.0001**
Block × species	0.76	0.64	1.09	0.38	1.10	0.37
Site × species	0.63	0.64	1.31	0.27	0.17	0.96
Block × site × species	0.30	0.96	1.28	0.27	0.38	0.93
N remaining						
Block	0.18	0.83	1.60	0.21	1.39	0.25
Site	0.38	0.54	0.24	0.62	0.10	0.76
Block × site	0.67	0.52	0.54	0.58	0.04	0.96
Species	2.68	< 0.05	22.37	< 0.0001	16.23	< 0.0001
Block × species	1.43	0.19	1.34	0.24	1.14	0.35
Site × species	0.99	0.42	0.37	0.83	0.27	0.89
Block × site × species	0.88	0.53	0.65	0.74	0.47	0.87

Significant effects are highlighted in bold.

Stepwise linear regression analysis was used to elucidate the factors affecting mass loss and N dynamics in leaf litter during the 24-month decomposition study (Table 6). During the first six months of decomposition both initial nutrient concentrations and C-fractions were correlated with mass loss and N dynamics. By the end of 24 months, only the initial lignin concentration of plant litter was highly correlated with mass loss and N dynamics. No litter chemistry parameter was correlated with the fraction of initial N remaining in leaf litter following 12 months of decomposition (Table 6). In general, mass loss dynamics were highly correlated with initial chemistry at each harvest, whereas N dynamics were poorly predicted by initial chemistry until the final harvest (Table 6). The relationship between initial chemistry and mass or N dynamics was not altered by litter type or site of decomposition (data analysis not shown). The relationship between initial litter chemistry and the fraction of initial mass and N remaining was only related to the differences in initial litter chemistry among species (Fig. 3).

Discussion

In this ecosystem leaf litter chemistry was virtually unchanged by plant growth under elevated CO_2 (Tables 2 and 3). With few exceptions, plant litter produced under elevated CO_2 lost mass and N at the same rate as that produced under ambient CO_2 (Fig. 2). Thus, the relationship between initial litter chemistry and decomposition dynamics was not altered by elevated CO_2 (Table 6). Several studies have reviewed the literature on litter chemistry and decomposition under elevated CO_2 (Cotrufo *et al.*, 1998; Norby & Cotrufo, 1998; Coûteaux *et al.*, 1999; Norby *et al.*, 2001). From these reviews, it is clear that on average elevated CO_2 has a small impact on

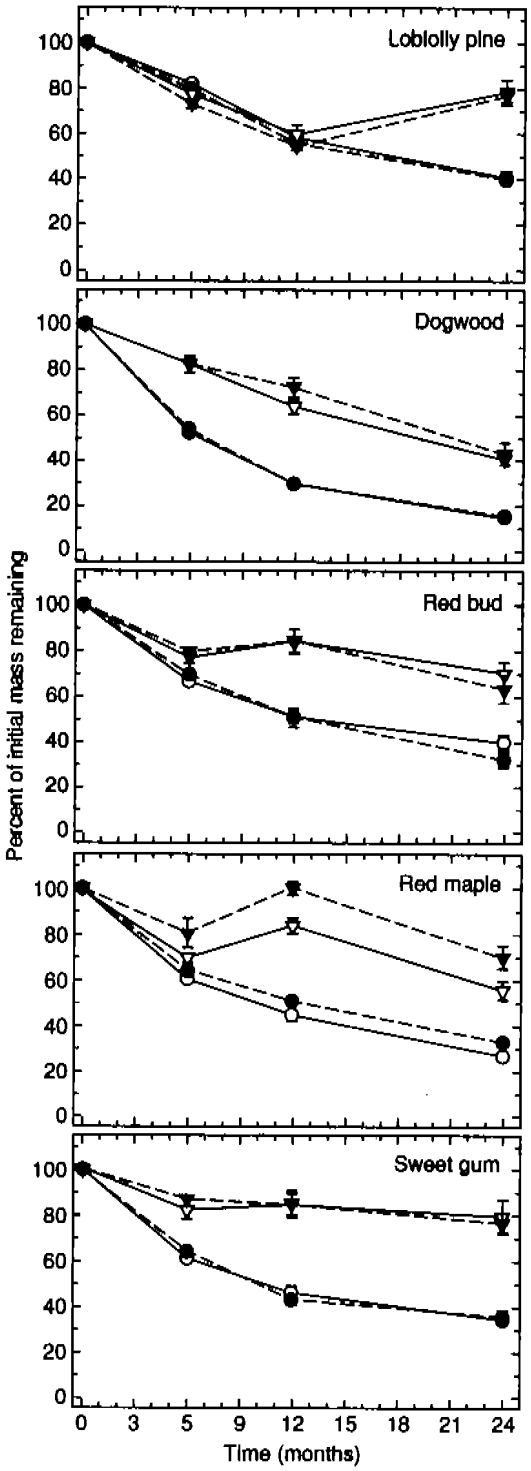

Fig. 2 The effect of litter type on the fraction of initial mass (circles) and N remaining (triangles) remaining in the leaf litter of five different species during two years of decomposition in the field. Each value is the mean ± 1 SE. Open symbols are for litter produced under ambient CO_2 and filled symbols are for litter produced under elevated CO_2.

litter chemistry, typically a small reduction in litter N concentration and an increase in lignin concentrations. However, these small changes in litter chemistry have no impact on the rate of litter decomposition (Norby *et al.*, 2001). Our results are consistent with these reviews in that litter chemistry and decomposition were largely unchanged as a consequence of four years of enhanced forest productivity under elevated CO_2 (Hamilton *et al.*, 2002).

Rapid plant growth under elevated CO_2 has significantly increased the input of C and N to soils, including the forest floor, in this ecosystem (Schlesinger & Lichter, 2001). Soil CO_2 efflux from the surface of the forest floor is 30% higher under elevated CO_2 than ambient CO_2 (Hamilton *et al.*, 2002). Higher rates of litter production contribute to the higher CO_2 efflux from the plots under elevated CO_2 (Finzi *et al.*, 2002). The results of this study suggest that the consistency of the chemistry of litter inputs under elevated CO_2 also contributes to the greater CO_2 efflux because the specific rate of litter decomposition (i.e. g mass lost per g originally present) is unchanged at the same time that the forest floor is aggrading in mass under elevated CO_2.

High rates of NPP under elevated CO_2 have increased forest floor moisture content (Schafer *et al.*, 2002) and the metabolism of C by the microbial community (Hamilton *et al.*, 2002). An increase in moisture availability has a direct, positive effect on decomposer activity and an increase in C availability may decrease the energetic limitation to the decomposition of more recalcitrant components in leaf litter (Swift *et al.*, 1979). Consequently, we hypothesized a higher specific rate of leaf litter decomposition in the plots under elevated CO_2 than ambient CO_2. Analysis of the litter transplant study shows no evidence for an effect of the site of decomposition on the rate of mass loss or N dynamics (Table 5). Thus, the degree of change in the biotic and abiotic environment in the forest floor was insufficient to alter the process of decomposition during the first two years of leaf litter decomposition.

Increasing soil nutrient availability can modulate the production of extracellular enzymes by the microbial community and the rate of decomposition (e.g. Prescott *et al.*, 1992; Hobbie & Vitousek, 2000). By transplanting litter to specific, paired plots, our litter transplant experiment was designed to test for the effects of N supply on the rate of litter decomposition. The variation in the annual rate of net N mineralization is >3-fold across the six plots that comprise this FACE facility (Fig. 1). There is a large increase in NPP along this gradient in the annual rate of net N mineralization (Finzi *et al.*, 2002). However, we found only limited evidence that soil N availability regulated the rate of mass loss or N dynamics during decomposition; the rate of mass loss

Table 6 Stepwise linear regression analysis of the initial litter chemical parameters controlling the fraction of the initial mass and N remaining in litterbags following two years of decomposition in the field

	6 months			12 months			24 months		
Decomposition component	Initial chemistry	Partial Rsq.	Pr. > F	Initial chemistry	Partial Rsq.	Pr. > F	Initial chemistry	Partial Rsq.	Pr. > F
Mass remaining	N	0.82	< 0.0001	Lignin	0.71	< 0.0001	Lignin	0.77	< 0.0001
	Lignin	0.05	0.0053	C	0.10	0.0014			
				L:N	0.03	0.0348			
N Remaining	C:N	0.11	0.0839	NS			Lignin	0.54	< 0.0001

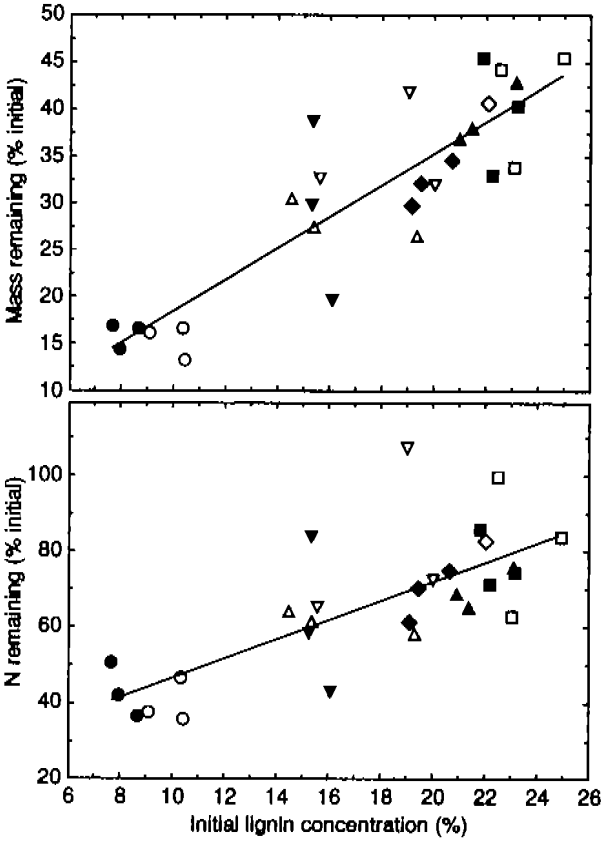

Fig. 3 The relationship between the concentration of lignin in leaf litter and the fraction of initial mass and N remaining following 24-months of decomposition in the field. Open symbols are for litter produced under ambient CO_2 and filled symbols are for litter produced under elevated CO_2. The different symbol shapes correspond to different species according to: circle = dogwood; up-triangle = red bud; down-triangle = red maple; diamond = sweet gum; and square = loblolly pine. The data do not support separate regression lines for the different litter types.

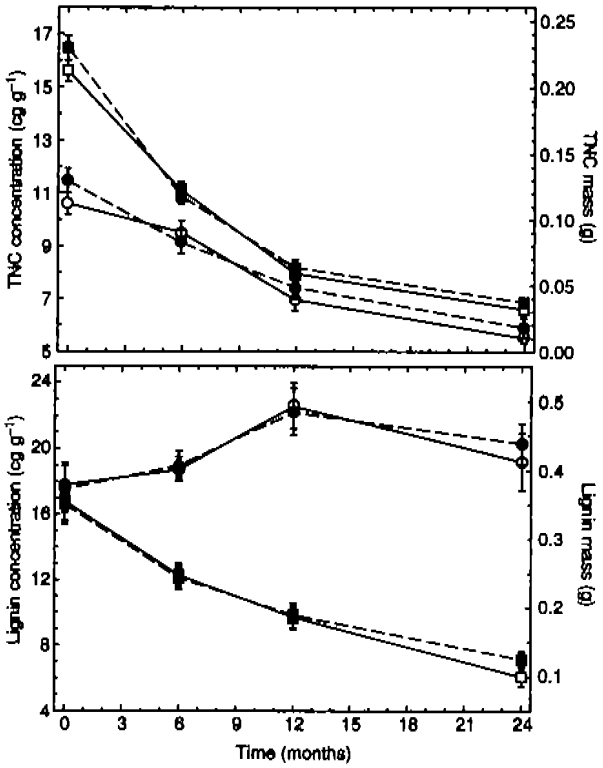

Fig. 4 The effect of the site of decomposition on the fraction of initial TNC and lignin remaining (circles) and the total mass of TNC and lignin remaining (squares) in the leaf litter during two years of decomposition in the field. The data are averaged across the five different species. Error bars represent the standard error of the mean. Open symbols are for litter decomposing under ambient CO_2 and filled symbols are for litter decomposing under elevated CO_2.

in block 3, the block with the highest rate of net mineralization, was significantly slower than that in blocks 1 and 2, the blocks with lower rates of net mineralization. However, the difference in mass loss was quite small (34% of initial remaining in block 3 vs. 29% in blocks 1 and 2), suggesting that variation in soil N supply played only a small role in controlling decomposition. Moreover, there was no effect of the block on the loss of N from litter during decomposition (Table 5). Thus, while the rate of net N mineralization is an important component of the productivity response to elevated CO_2, soil N availability did not exert significant control over

litter decomposition. Our results are consistent with other studies that have not found a significant relationship between soil nutrient supply and the rate of leaf litter decomposition (e.g. Downs *et al.*, 1996; Prescott *et al.*, 1992).

Elevated CO_2 has repressed the activity of phenol oxidase and peroxidase, extracellular enzymes responsible for the degradation of lignin and humus, and increased the activity of several different hydrolase enzymes responsible for the degradation of polysaccharides, in the forest floor of this ecosystem (R.L. Sinsabaugh, personal communication). Based on these data, we hypothesized that the rate of lignin decomposition would be lower in the litter decomposing in the plots under elevated CO_2 while the rate of TNC decomposition would be higher. We found little evidence suggesting that the shift in enzyme activity altered the decomposition of these C fractions. Both the concentration and quantity of TNC decreased during decomposition (Fig. 4), most likely due to the leaching and microbial consumption of labile C fractions during the initial phase of decomposition (McClaugherty *et al.*, 1985; Couteaux *et al.*, 1998). In neither case was the decrease significantly different between CO_2 treatments (Fig. 4). While the concentration of lignin increased during decomposition, the total quantity of lignin decreased over time demonstrating microbial consumption of this C fraction despite the large energetic costs of its metabolism and the availability of other more labile C substrates. Similar to the TNC results, there was no effect of elevated CO_2 on the concentration or quantity of lignin remaining in leaf litter at any point during the 24 months of decomposition.

In contrast to the limited effects of elevated CO_2 on decomposition, there were large differences among species in initial litter chemistry, mass loss and N dynamics during decomposition (Table 2, Fig. 2). These results imply that changes in the species composition of this forest community under elevated CO_2 will have a much larger effect on the long-term rate of nutrient cycling than changes in atmospheric CO_2 alone. Interspecific variation in litter chemistry is often larger than the response of a single species to CO_2 enrichment (e.g. Franck *et al.*, 1997; Dukes & Field, 2000; Korner, 2001; Norby *et al.*, 2001). These results highlight the importance of linking the long-term demographic process of forest succession with ecosystem processes (Peet, 1992; Field, 1999; Korner, 2001).

In a given climatic region, the chemical control over litter decomposition will depend on the mix of species present in an ecosystem and the C and nutrient chemistry of the litter produced (Finzi & Canham, 1998; Berg *et al.*, 2000; Knops *et al.*, 2001). Several studies suggest a two-stage model for litter decomposition where litter nutrient concentrations control mass loss initially with a progressively larger control exerted by recalcitrant C fractions as plant material decomposes (Kelley & Henderson, 1978; Taylor *et al.*, 1989; Berg *et al.*, 2000). Stepwise linear regression analysis of our data for initial litter chemistry and decomposition suggests that a two-stage model describes decomposition and nutrient dynamics in this forest. The fraction of initial dry mass remaining in litterbags after six months of decomposition was highly correlated with the initial N concentration of leaf litter (Table 6). By the end of 24 months of decomposition in the field, the initial lignin concentration was the best predictor of mass and N remaining (Table 6). Notably, elevated CO_2 did not alter the relationship between litter chemistry and decomposition (Fig. 3).

Conclusion

Strain & Bazzaz (1983) proposed a negative-feedback model for soil nutrient availability under elevated CO_2. They argued that rapid plant growth under elevated CO_2 could increase the C:N ratio of plant litter thereby slowing the rate of litter decomposition, increasing N immobilization and decreasing plant-N availability. Support for their hypothesis has been mixed. Some studies support increased N immobilization (e.g. Diaz *et al.*, 1993; Berntson & Bazzaz, 1997) while other studies support increased net mineralization under elevated CO_2 (e.g. Zak *et al.*, 1993; Berntson & Bazzaz, 1997). Our results and those of several recently published analyses do not support the litter chemistry and decomposition portions of the negative feedback hypothesis as applied to tree species exposed to elevated CO_2 (Norby & Cotrufo 1998; Norby *et al.*, 2001; Finzi *et al.*, 2001; King *et al.*, 2001). However, our results do not preclude a feedback effect of litter production and constant decomposition under elevated CO_2 on N cycling. The measured increase in the mass of aboveground litter inputs (Finzi *et al.*, 2002) should widen the C:N ratio of the forest floor and increase the immobilization of N in litter by the microbial community. Over time however, the rate of net N mineralization should increase as the larger mass of the decomposing organic matter in the forest floor reaches a C:N ratio where gross N mineralization exceeds gross N immobilization.

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