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EFFECTS OF ELEVATED CO_2 AND HERBIVORE DAMAGE ON LITTER QUALITY IN A SCRUB OAK ECOSYSTEM

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Abstract—Atmospheric CO_2 concentrations have increased dramatically over the last century and continuing increases are expected to have significant, though currently unpredictable, effects on ecosystems. One important process that may be affected by elevated CO_2 is leaf litter decomposition. We investigated the interactions among atmospheric CO_2, herbivory, and litter quality within a scrub oak community at the Kennedy Space Center, Florida. Leaf litter chemistry in 16 plots of open-top chambers was followed for 3 years; eight were exposed to ambient levels of CO_2, and eight were exposed to elevated levels of CO_2 (ambient + 350 ppmV). We focused on three dominant oak species, *Quercus geminata*, *Quercus myrtifolia*, and *Quercus chapmanii*. Condensed tannin concentrations in oak leaf litter were higher under elevated CO_2. Litter chemistry differed among all plant species except for condensed tannins. Phenolic concentrations were lower, whereas lignin concentrations and lignin/nitrogen ratios were higher in herbivore-damaged litter independent of CO_2 concentration. However, changes in litter chemistry from year to year were far larger than effects of CO_2 or insect damage, suggesting that these may have only minor effects on litter decomposition.

Key Words—Elevated CO_2, herbivory, litter quality, *Quercus myrtifolia*, *Quercus chapmanii*, *Quercus geminata*, Kennedy Space Center.

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INTRODUCTION

Increasing atmospheric carbon dioxide (CO_2) is likely to alter ecosystem processes, yet most research to date has focused on the direct effects of CO_2 on plant physiological processes, with less attention to indirect effects on ecosystem processes, including those mediated by plant herbivores. Elevated CO_2 can alter foliar chemistry directly, for example by reducing nitrogen (N) concentrations in green leaves (Lincoln et al., 1993; Agrell et al., 2000; Hall et al., 2005). Elevated CO_2 could also alter leaf chemistry indirectly by affecting the feeding behavior of herbivores, in turn eliciting plant synthesis of chemical defenses. For example, elevated CO_2 can increase foliar concentrations of polyphenols, possibly a response to a CO_2-induced increase in herbivore feeding (Agrell et al., 2000). Changes in plant chemistry affect the quality of herbivore diets and may result in behavioral and physiological changes that influence subsequent herbivory (Lindroth, 1996; Stiling et al., 1999). Whether such changes in foliar chemistry persist in senesced leaves is not clear (Curtis et al., 1989; Coûteaux et al., 1991; Kemp et al., 1994; Finzi et al., 2001) but is important to determine given the importance of litter chemistry for decomposition and nutrient cycling.

The quality of leaf litter is an important determinant of decomposition rates and nutrient dynamics in many systems (Swift et al., 1979). Litter nitrogen, lignin concentrations, and C/N ratios are often good predictors of decay rates within and among species (Cotrufo et al., 1994). Carbon-based compounds such as polyphenols also decrease litter quality and may exert some control on litter decomposition (Hättenschwiler and Vitousek, 2000).

Elevated CO_2 may affect litter quality through several mechanisms including chemical changes in green leaf tissue that persist beyond leaf abscission or changes in patterns of herbivory that influence subsequent chemistry. The quality of green leaf tissue can change as a result of elevated concentrations of atmospheric CO_2 (Lindroth et al., 1995; Hall et al., 2005). Generally, nitrogen concentrations in green leaves decline and C/N ratios increase under elevated CO_2 (Lincoln et al., 1993; Hall et al., 2005). There may also be increases in polyphenolic concentrations in green leaves under elevated CO_2 (Agrell et al., 2000). It is unclear, however, if these changes persist in senesced leaves (Curtis et al., 1989; Coûteaux et al., 1991; Kemp et al., 1994; Finzi et al., 2001). Given the significance of litter chemistry to decomposition processes and nutrient dynamics (Heal et al., 1997), it is important to study the links among elevated CO_2, foliar chemistry, and litter chemistry.

In addition to possible direct effects of elevated CO_2 on litter quality, another potential route by which elevated CO_2 might influence litter quality is through its impact on herbivores. Changes in plant chemistry affect the quality of herbivore diets and may result in behavioral and/or physiological changes that influence subsequent herbivory (Lindroth, 1996; Stiling et al., 1999). For example, to compensate for lower nitrogen concentrations in leaves under elevated CO_2, insect herbivores often increase their consumption rates by 20–80% (Lincoln et al., 1993). However, lepidopteran larvae can exhibit slower growth rates when feeding on elevated CO_2 plants (Fajer et al., 1991) and become more susceptible to pathogens, parasitoids, and predators (Lindroth, 1996; Stiling et al., 1999). At our field site, which hosts the longest continuous study of the effects of elevated CO_2 on insects, herbivore populations decline markedly under elevated CO_2 (Stiling et al., 1999, 2002, 2003; Hall et al., 2005).

Changes in the feeding behavior of herbivores alter ecosystem processes. Consumption of plant tissue by insect herbivores can have direct affects on ecosystem productivity. Herbivores can also influence ecosystem function by changing organic matter added to the soil (Chapman et al., 2003; Frost and Hunter, 2004). These changes may come from herbivore by-products (Stadler et al., 2001; Frost and Hunter, 2004), alteration of the plant community via selective herbivory (Ritchie et al., 1998; de Mazancourt and Loreau, 2000), or by altering the chemical properties of plant litter (Chapman et al., 2003).

Plant foliage responds to herbivore activity in multiple ways including changes in nitrogen concentrations and induction of secondary compounds (Schultz and Baldwin, 1982). If these changes carry over to litter, subsequent decomposition rates and related nutrient transformations may be altered (Melillo et al., 1982; Scott and Binkley, 1997). Chemical alteration of litter quality may also occur when herbivory instigates premature leaf abscission, which effectively limits nutrient resorption and results in litter with higher nutrient concentrations (Kahn and Cornell, 1983).

Given that herbivore damage can influence subsequent foliar and litter quality, declines in herbivore density under elevated CO_2 have the potential to influence decomposition and nutrient dynamics. Therefore, elevated CO_2 has the potential to cause changes in litter quality through direct effects on foliar chemistry and indirect effects mediated by herbivores. In this study, we explore the impacts of CO_2, herbivory and their interactions on scrub oak litter chemistry.

METHODS AND MATERIALS

Study Site. Our study site lies within a two-hectare native scrub oak community located at Kennedy Space Center, Florida. The scrub oak forest is xenomorphic, largely consisting of evergreen or semi-evergreen trees with a mature canopy height of 3 to 5 m. This plant community is fire controlled and was last burned January 1996. Prior to site burning, the plant composition consisted primarily of oak species (76% *Quercus myrtifolia*, 15% *Quercus geminata*, and 7% *Quercus chapmanii*). The remaining 2% of the community included *Serenoa repens* (palmetto), *Myrica serifera* (wax myrtle), *Lyonia* *ferruginea* (rusty lyonia), *Ceratiola ericoides* (Florida rosemary), and *Galactia elliottii* (milk pea). Continuous ground cover and longleaf pine (*Pinus palustris*), wiregrass (*Aristida beyrichiana*), and turkey oak (*Quercus laevis*) are absent. Fire in scrub communities is a stand-replacing disturbance that typically removes all aboveground vegetation. Plant regrowth is rapid and there is little change in species composition. When fire is suppressed, the scrub community transitions into a pioneer xeric hammock, which is defined by the retention of some scrub species and the lack of traditional hammock species. The last burn cycle was in 1996 prior to site set up. Sixteen 3.6-m-diam plots, each enclosed with a clear polyester film open-top chamber 3.4 m in height, were utilized to control CO_2 levels. Chambers were overlaid on an octagonal framework of PVC pipe with a removable access door and frustum to reduce dilution of air within the chamber by outside wind. After burning, all regrowth was cut to ground level in May 1996, and, since that time, the vegetation in eight of the chambers was kept at ambient levels of CO_2 while the other eight chambers were exposed to elevated CO_2 (ambient + 350 ppmV). Carbon dioxide is constantly supplied to the elevated CO_2 chambers. In ambient CO_2 chambers, the airflow is identical to that of the elevated CO_2 chambers. (See Dijkstra et al. (2002) for a detailed description of the site setup.) Three oak species dominate this community and are present in every chamber: *Q. myrtifolia* Willd, *Q. chapmanii* Sargent, and *Q. geminata* Small.

Litter Chemistry. Leaf litter was collected quarterly for 3 yr (2000, 2001, 2002) from litter trays placed inside each chamber. Litter was sorted by species and by herbivore damage type (undamaged, chewed, mined). The oak species are evergreen and abscise leaves throughout the year; samples within a year were combined. This resulted in 144 samples (16 chambers × 3 plant species × 3 damage categories) per year. Chambers (8 per treatment) acted as replicates. Litter samples collected in 2000 were assayed prior to samples collected in 2001 and 2002, which were assayed concurrently. Otherwise, all samples were processed identically. The air-dried litter was ground to a fine powder and stored at $-80°C$ prior to analysis.

Percent dry weight nitrogen and carbon were estimated from leaf powder on a Carlo-Erba NA1500 model C/N analyzer (Milan, Italy). These data also provided estimates of litter C/N ratios. Subsamples of leaf powder were used to assess the effects of elevated CO_2 on litter concentrations of cellulose, hemicellulose, and lignin by sequential neutral detergent/acid detergent digestion on an Ankom fiber analyzer (Abrahamson et al., 2003).

Proanthocyanidins, an estimate of condensed tannin concentration, were assayed using n-butanol/HCL methods described in Rossiter et al. (1988). Total phenolics were estimated with the Folin–Denis assay (Swain, 1980), and gallotannins (hydrolyzable tannins) were estimated with a potassium iodate technique developed by Bate-Smith (1977) and modified by Schultz and

Baldwin (1982). Standards for tannin analysis were generated by multiple sequential washes of a bulk sample by acetone extraction. The small amount of available litter material for some species resulted in a bulk sample that was a mix of all species of litter for each year. All tannin assays produced colorimetric reactions, in proportion to tannin concentration, which were quantified using a BioRad microplate reader.

Statistical Procedures. Data were initially analyzed with the GLM procedure of SAS 8.2. However, the residuals of the ANOVA models failed the test for normality (Kery and Hatfield, 2003). Data were transformed and reanalyzed and again failed the test of normality. Data were finally analyzed with the repeated-measures GENMOD procedure of SAS 8.2 (SAS Institute, 1999) and the log likelihood ratio was maximized. With the development of generalized estimating equations (GEE), GENMOD is a nonparametric alternative for repeated-measures data (Littell et al., 2002), although *post hoc* analyses are not performed. The GENMOD procedure allows the explanatory variables to be selected and changes in the goodness-of-fit statistics are used to evaluate the contribution of each variable to the model. Thus, the importance of each additional variable and interaction can be assessed, allowing a sequence of models to be tested while taking into account main effects as well as interactions. The data presented contain only those effects that made significant contributions to the model.

RESULTS

Except for condensed tannins, all measures of litter chemistry varied among the species of oak (Table 1). The only consistent effect of elevated CO_2 on litter chemistry was higher condensed tannin concentrations under elevated CO_2 ($\chi^2 = 19.34$, $P < 0.001$) (Figure 1). All other effects of elevated CO_2 on

TABLE 1. LITTER CHEMISTRY OF THREE OAK SPECIES AT THE KENNEDY SPACE CENTER, FLORIDA

	Q. myrtifolia	*Q. chapmanii*	*Q. geminata*	*P* value
Condensed tannins	19.41 (0.68)	18.02 (0.81)	18.02 (0.71)	NS
Hydrolyzable tannins	20.46 (0.62)	23.38 (1.01)	19.68 (0.67)	0.001
Total phenolics	23.93 (0.58)	25.53 (1.05)	18.36 (0.57)	<0.001
Nitrogen	0.76 (0.01)	0.81 (0.02)	0.75 (0.02)	0.018
Carbon	48.71 (0.36)	46.97 (0.38)	46.59 (0.39)	<0.001
C/N ratio	66.44 (1.10)	60.58 (1.24)	65.23 (1.14)	0.002
Cellulose	22.62 (0.17)	19.05 (0.21)	25.09 (0.17)	<0.001
Hemicellulose	14.56 (0.19)	13.59 (0.22)	15.07 (0.35)	0.001
Lignin	14.27 (0.29)	10.54 (0.29)	12.47 (0.32)	<0.001
Lignin/nitrogen ratio	19.75 (0.56)	13.79 (0.40)	17.70 (0.55)	<0.001

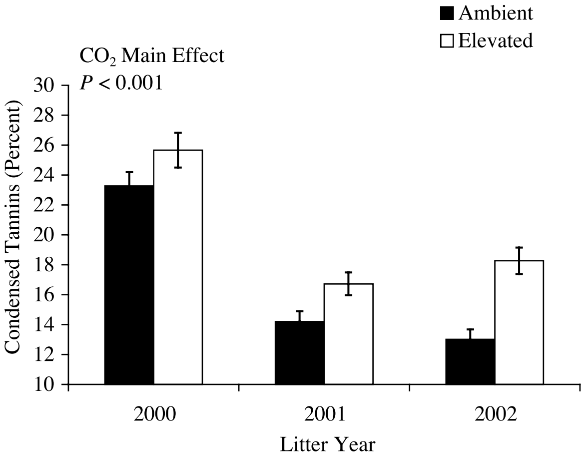

FIG. 1. Condensed tannin concentrations in litter across plant species. Data are the means of 72 samples and bars represent standard errors.

litter chemistry were either not significant (Table 2) or inconsistent among years (Figure 2a–c). The latter was one of our dominant findings—that interannual variation has a profound influence on the effects of elevated CO_2 on litter chemistry. A second result to emerge was that elevated CO_2 has no influence on litter nitrogen concentration or C/N ratio (Table 2). We have previously shown that in living green leaves of these oak species, nitrogen concentrations decrease whereas C/N ratios increase under elevated CO_2 (Hall et al., 2005). Apparently, these changes are lost by the time that leaves senesce.

Phenolic concentrations (condensed tannins, hydrolyzable tannins, total phenolics) were generally lower in chewed and mined litter than in undamaged

TABLE 2. RESULTS OF ANALYSES OF LITTER CHEMISTRY FOR CO_2 AND CO_2 × YEAR INTERACTIONS AT THE KENNEDY SPACE CENTER, FLORIDA

Litter chemistry	CO_2	$CO_2 \times$ year
Condensed tannins	$\chi^2 = 19.34$, $P < 0.001$	NS
Hydrolyzable tannins	NS	$\chi^2 = 20.39$, $P < 0.001$
Total phenolics	NS	NS
Nitrogen	NS	NS
Carbon	NS	NS
C/N ratio	NS	NS
Cellulose	NS	$\chi^2 = 9.54$, $P = 0.023$
Hemicellulose	NS	$\chi^2 = 11.86$, $P = 0.008$
Lignin	NS	NS
Lignin/nitrogen ratio	NS	NS

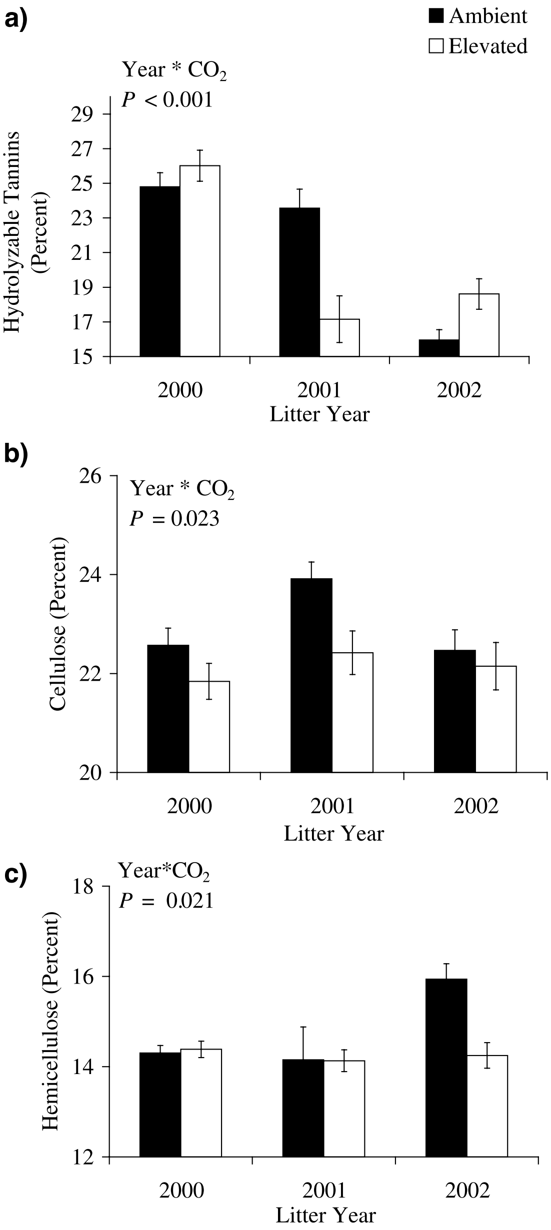

FIG. 2. Differences in litter chemistry between ambient and elevated CO_2 treatments across plant species by growing season. (a) Hydrolyzable tannins, (b) cellulose, (c) hemicellulose. Data are the means of 72 samples and bars represent standard errors.

litter (condensed tannins, $\chi^2 = 22.88$, $P < 0.001$; hydrolyzable tannins, $\chi^2 = 10.07$, $P = 0.006$; total phenolics, $\chi^2 = 15.55$, $P = 0.004$) (Figure 3a–c). However, mining only reduced hydrolyzable tannins and total phenolics in *Q. myrtifolia*

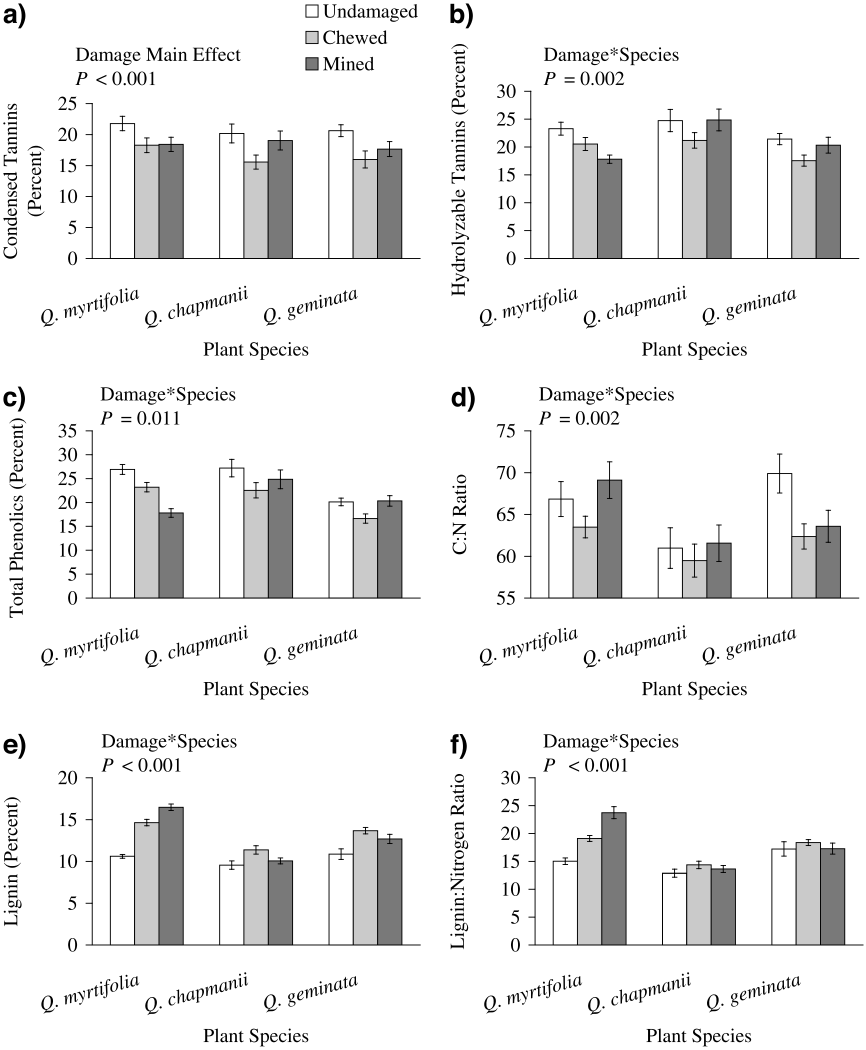

FIG. 3. Differences in litter chemistry among undamaged, chewed, and mined litter by plant species for (a) condensed tannins, (b) hydrolyzable tannins, (c) total phenolics, (d) C/N ratio, (e) lignin, (f) lignin/nitrogen ratio. Data are the means of 48 samples and bars represent standard errors.

(Figure 3b, c), and had no effect for the other species. Effects of damage on litter C/N ratios were inconsistent among the species ($\chi^2 = 20.73$, $P = 0.002$, Figure 3d) suggesting no dominant impact of damage on C/N ratios. Lignin concentrations and lignin/nitrogen ratios were higher in damaged litter from *Q. myrtifolia*, but

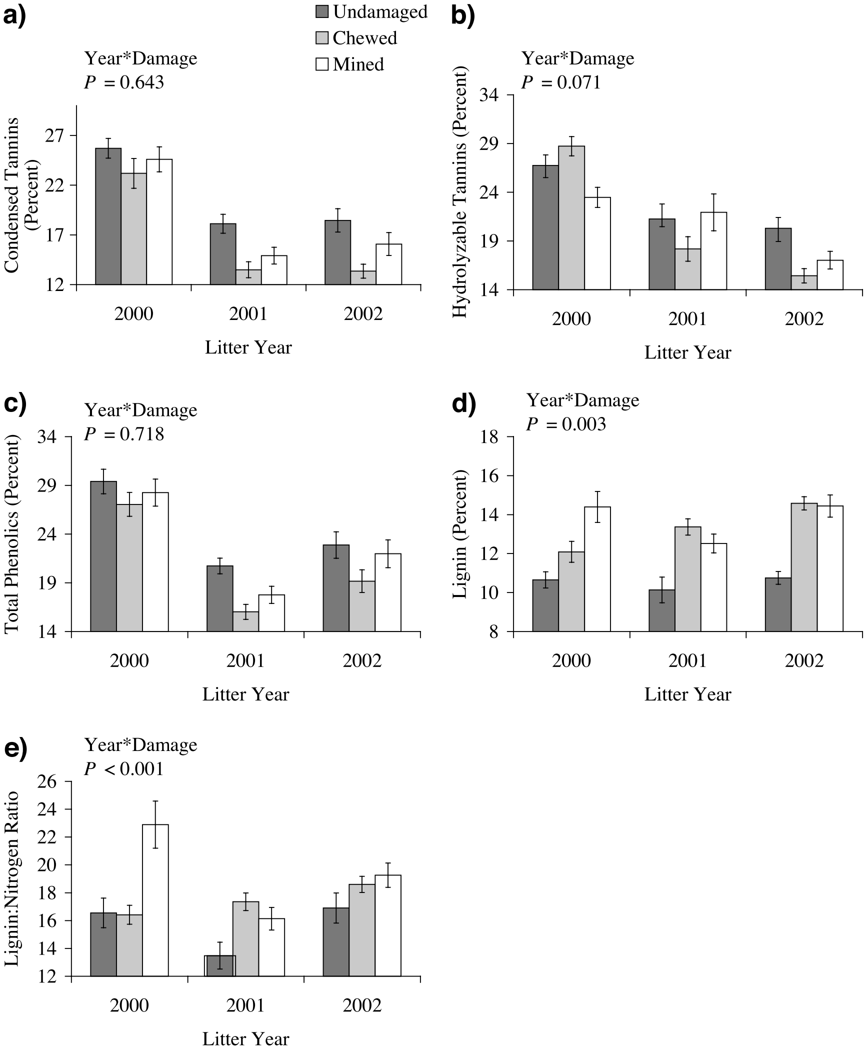

FIG. 4. Differences in litter chemistry of undamaged, chewed, and mined oak litter over time (a) condensed tannins, (b) hydrolyzable tannins, (c) total phenolics, (d) lignin, (e) lignin/nitrogen ratio. Data are the means of 48 samples and bars represent standard errors.

not from the other oak species (Damage × Species, $\chi^2 = 30.35$, $P < 0.001$, and $\chi^2 = 30.06$, $P < 0.001$ for lignin and lignin/nitrogen ratio, respectively, Figure 3e, f). As with the effects of CO_2, effects of damage on litter chemistry were relatively minor when compared to yearly variation from one growing season to the next (Figure 4a–e).

DISCUSSION

Climate and chemical composition of litter determine decomposition rates and nitrogen mineralization (Swift et al., 1979). Components influencing the quality of the litter include concentrations of nitrogen, lignin, and polyphenols. Typically, high concentrations of nitrogen are positively correlated with decomposition rates, whereas high lignin and polyphenolic concentrations are negatively correlated with decomposition rates (Swift et al., 1979). Low litter quality generally decreases decomposition, reducing nitrogen mineralization and soil nitrogen availability (Swift et al., 1979; Melillo et al., 1982). Previous studies of the effect of elevated CO_2 on litter quality have been equivocal. In some studies, increased levels of atmospheric CO_2 affected litter quality for several species (Coûteaux et al., 1991; Cotrufo et al., 1994; Parsons et al., 2004; Henry et al., 2005), whereas others have found no effect of elevated CO_2 on litter quality (Curtis et al., 1989; Finzi et al., 2001). Parsons et al. (2004) found that nitrogen concentrations declined and C/N ratios and condensed tannin concentrations increased under elevated CO_2 in paper birch (*Betula papyrifera*). Likewise, they found that mass loss was lower and decay rates were higher for birch litter from CO_2 environments compared to the control. Henry et al. (2005) found that lignin concentrations increased in grass and forb litter under elevated CO_2; however, they found no differences in total phenolic concentrations or percent nitrogen in the litter from elevated CO_2 environments. They found that the increase in lignin concentrations due to elevated CO_2 did not affect decomposition rates.

In our study, condensed tannin concentrations increased under elevated CO_2 regardless of species, herbivore damage, or growing season. Although the traditional measures of litter quality focus on lignin and nitrogen concentrations, there is growing consensus that polyphenols can have an effect on decomposition processes. Palm and Sanchez (1990) found that soluble polyphenolic concentrations were a better measure for predicting decomposition rates in leguminous litter in the tropics than were lignin or lignin/nitrogen ratios. Polyphenols may affect the rates of decomposition by influencing the composition and activity of the detritivore community (Hättenschwiler and Vitousek, 2000). In addition, polyphenols may alter the availability of nitrogen by binding with proteins and making the litter resistant to some detritivores, thus reducing the rates of nitrogen mineralization (Bernays et al., 1989). In our system, increased condensed tannin concentrations under elevated CO_2 have the potential to affect ecosystem processes by slowing down litter decomposition and nutrient turnover. However, increases in condensed tannins were low (2–5%, Figure 1) and considerably smaller than interannual variation.

Prior work on green leaves in this system established that plant growth under elevated CO_2 reduced foliar nitrogen concentrations and increased C/N ratios by an average of 6 and 7%, respectively, across all three species (Hall et al., 2005). In contrast, secondary metabolites were unaffected in the green leaves (Hall et al., 2005). In this study of litter, however, there was no evidence of lower nitrogen concentrations or higher C/N ratios. Rather, the strongest CO_2 effects were seen in secondary metabolites, particularly condensed tannins (Figures 1 and 2a–c). Thus, differences in green leaf chemistry caused by growth under elevated CO_2 disappeared by the time leaves senesced. Few studies have directly compared foliar and litter chemistry under elevated CO_2. Curtis et al., (1989) found that nitrogen concentrations were lower and C/N ratios higher in green leaves of *Scripus olneyi* under elevated CO_2 but differences did not persist in senesced leaves. Finzi et al., (2001) found no effect of elevated CO_2 on total nonstructural carbohydrates or nitrogen in green leaves or in leaf litter of five tree species. Kemp et al., (1994), on the other hand, found significantly lower nitrogen concentrations in senesced foliage from *Poa pratensis* L. exposed to elevated levels of CO_2 compared to senesced foliage growing in ambient levels of CO_2. Similarly, Coûteaux et al., (1991) found that nitrogen concentrations were lower in leaf litter of chestnut trees grown in elevated CO_2 compared to ambient CO_2. The studies by Kemp et al., (1994) and Coûteaux et al., (1991) did not apply elevated CO_2 continuously to field plants, and this may account for the differences in their results from ours and other studies.

Phenolic concentrations were lower, whereas lignin concentrations and lignin/nitrogen ratios were higher, in litter following herbivore damage. Given that herbivores on oak generally induce increases in foliar phenolics (Schultz and Baldwin, 1982), it seems unlikely that the lower phenolic concentrations in damaged litter resulted directly from herbivore feeding. Rather, insect herbivores may be avoiding high phenolic leaves (Cooper-Driver et al., 1977; Bernays et al., 1989), leading to a preponderance of damage on low phenolic litter. This needs to be explored experimentally by manipulating herbivore abundance. Likewise, the apparent induction of lignification following damage (Figure 3e) requires experimental verification. Chapman et al., (2003) found that two insect herbivores from different feeding guilds (*Matsucoccus acalyptus* and *Dioryctria albovittella*) increased nitrogen concentrations and decreased C/N and lignin/nitrogen ratios in pinyon pine (*Pinus edulis*) litter. Moreover, these herbivore-induced changes resulted in increased litter decomposition rates. However, damaged litter in our study was lower in condensed tannins yet higher in lignin and lignin/nitrogen ratios, changes that should have counteracting effects on decomposition rates. Herbivore-damaged litter may decompose more rapidly due to the decline in phenolic concentrations, particularly condensed tannins, compared to undamaged litter. Conversely, damaged litter may decompose more slowly due to higher concentrations of lignin and higher lignin/nitrogen ratios.

In our study, growing season had the dominant impact on litter chemistry so that yearly variation overwhelmed most effects of CO_2 or herbivore damage. Therefore, relative to the influence of seasonal variables, elevated CO_2 and herbivore activity may be less significant factors in leaf litter decomposition and ecosystem function. Although it is well known that climate and litter chemistry control the dynamics of decomposition (Swift et al., 1979), there has been little research on changes in litter quality based on yearly variation in climate. It is known, however, that the same plant species grown on different sites can vary in its litter chemistry (Vitousek et al., 1994; Scowcroft et al., 2000). Therefore, it is reasonable to expect within-site variation in litter chemistry from year to year due to climatic and other differences among the growing seasons. At our study site, climatic data available for precipitation and temperature did not offer insight to the yearly difference found in litter chemistry. Yearly precipitation, based on mean monthly data, varied only slightly with an average of 240 mm of precipitation recorded for 2000, 242 mm for 2001, and 263 mm for 2002. The average daytime temperature, based on mean monthly data, did not vary among years. The daytime mean temperature within CO_2 chambers was 27°C for all 3 years. The daytime mean temperature outside of chambers was 26°C for 2000 and 2002 and 25°C for 2001. Although precipitation and temperature did not vary among years, variation in monthly precipitation patterns based on timing of precipitation and litter fall may result in differential leaching of soluble compounds from year to year, thus leading to differences in litter chemistry. In addition to temperature and precipitation, differences in macro- and micronutrient supply as well as UV-B levels may affect litter quality (Heal et al., 1997; Horner et al., 1988). Given the magnitude of changes in litter chemistry from one growing season to the next, it is possible that decay rates and nitrogen mineralization will vary over time depending on the cohort of leaves that serve as substrate. Future work on the effects of climate change and herbivory on decomposition and nutrient cycling should occur over several years of study so that annual variation can be taken into account and key abiotic variables that drive variation in litter chemistry can be identified.

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REFERENCES

ABRAHAMSON, W. G., HUNTER, M. D., MELIKA, G., and PRICE, P. W. 2003. Cynipid gall-wasp communities correlate with oak chemistry. *J. Chem. Ecol.* 29:209–223.

AGRELL, J., MCDONALD, E. P., and LINDROTH, R. L. 2000. Effects of CO_2 and light on tree phytochemistry and insect performance. *Oikos* 88:259–272.

BATE-SMITH, E. C. 1977. Astringent tannins of Acer species. *Phytochemistry* 16:1421–1426.

BERNAYS, E. A., COOPER-DRIVER, G., and BILGENER, M. 1989. Herbivores and plant tannins, pp. 263–302, *in* M. Begon, A. H. Fitter, E. D. Ford, and A. MacFadyen (eds.). Advances in Ecological Research. Vol. 19. Academic Press, New York, NY.

CHAPMAN, S. K., HART, S. C., COBB, N. S., WHITHAM, T. G., and KOCH, G. W. 2003. Insect herbivory increases litter quality and decomposition: an extension of the acceleration hypothesis. *Ecology* 84:2867–2876.

COOPER-DRIVER, G., FINCH, S., and SWAIN, T. 1977. Seasonal variation in secondary plant compounds in relation to the palatability of *Pteridium aquilinum*. *Biochem. Syst. Ecol.* 5:177–183.

COTRUFO, M. F., INESON, P., and ROWLAND, A. P. 1994. Decomposition of tree leaf litters grown under elevated CO_2: effect of litter quality. *Plant Soil* 163:121–130.

COÛTEAUX, M.-M., MOUSSEAU, M., CÉLÉRIER, M.-L., and BOTTNER, P. 1991. Increased atmospheric CO_2 and litter quality: decomposition of sweet chestnut leaf litter with animal food webs of different complexities. *Oikos* 61:54–64.

CURTIS, P. S., DRAKE, B. G., and WHIGHAM, D. F. 1989. Nitrogen and carbon dynamics in C_3 and C_4 estuarine marsh plants grown under elevated CO_2 *in situ*. *Oecologia* 78:297–301.

DE MAZANCOURT, C. and LOREAU, M. 2000. Effect of herbivory and plant species replacement on primary production. *Am. Nat.* 155:735–754.

DIJKSTRA, P., HYMUS, G., COLAVITO, D., VIEGLAIS, D. A., CUNDARI, C. M., JOHNSON, D. P., HUNGATE, B. A., HINKLE, C. R., and DRAKE, B. G. 2002. Elevated atmospheric CO_2 stimulates aboveground biomass in a fire-regenerated scrub-oak ecosystem. *Glob. Chang. Biol.* 8:90–103.

FAJER, E. D., BOWERS, M. D., and BAZZAZ, F. A. 1991. The effects of enriched CO_2 atmospheres on the buckeye butterfly, *Junonia coenia*. *Ecology* 72:751–754.

FINZI, A. C., ALLEN, A. S., DELUCIA, E. H., ELLSWORTH, D. S., and SCHLESINGER, W. H. 2001. Forest litter production, chemistry, and decomposition following two years of free-air CO_2 enrichment. *Ecology* 82:470–484.

FROST, C. and HUNTER, M. D. 2004. Insect canopy herbivory and frass deposition affect soil nutrient dynamics and export in oak mesocosms. *Ecology* 85:3335–3347.

HALL, M. C., STILING, P., MOON, D. C., DRAKE, B. G., and HUNTER, M. D. 2005. Effects of elevated CO_2 on foliar quality and herbivore damage in a scrub oak ecosystem. *J. Chem. Ecol.* 31:267–286.

HÄTTENSCHWILER, S. and VITOUSEK, P. M. 2000. The role of polyphenols in terrestrial ecosystem nutrient cycling. *Trends Ecol. Evol.* 15:238–243.

HEAL, O. W., ANDERSON, J. M., and SWIFT, M. J. 1997. Plant litter quality and decomposition: an historical overview, pp. 3–30, *in* G. Cadisch and K. E. Giller (eds.). Driven by Nature: Plant Litter Quality and Decomposition. CAB International, Wallingford.

HENRY, H. A. L., CLELAND, E. E., FIELD, C. B., and VITOUSEK, P. M. 2005. Interactive effects of elevated CO_2, N deposition and climate change on plant litter quality in a California annual grassland. *Oecologia* 142:465–473.

HORNER, J. D., GOSZ, J. R., and CATES, R. G. 1988. The role of carbon-based plant secondary metabolites in decomposition in terrestrial ecosystems. *Am. Nat.* 132:869–883.

KAHN, D. M. and CORNELL, H. V. 1983. Early leaf abscission and folivores: comments and considerations. *Am. Nat.* 122:428–432.

KEMP, P. R., WALDECKER, D. G., OWENSBY, C. E., REYNOLDS, J. F., and VIRGINIA, R. A. 1994.

Effects of elevated CO_2 and nitrogen fertilization pretreatments on decomposition on tallgrass prairie leaf litter. *Plant Soil* 165:115–127.

KERY, M. and HATFIELD, J. S. 2003. Normality of raw data in general linear models: the most widespread myth in statistics. *Bull. Ecol. Soc. Am.* 84:92–94.

LINCOLN, D. E., FAJER, E. D., and JOHNSON, R. H. 1993. Plant–insect herbivore interactions in elevated CO_2 environments. *Trends Ecol. Evol.* 8:64–68.

LINDROTH, R. L. 1996. CO_2-mediated changes in tree chemistry and tree–Lepidoptera interactions, pp. 105–120, *in* G. W. Koch and H. A. Mooney (eds.). Carbon Dioxide and Terrestrial Ecosystems. Academic Press, San Diego, CA.

LINDROTH, R. L., ARTEEL, G. E., and KINNEY, K. K. 1995. Responses of three saturniid species to paper birch grown under enriched CO_2 atmospheres. *Funct. Ecol.* 9:306–311.

LITTELL, R. C., STROUP, W. W., and FREUND, R. J. 2002. SAS for Linear Models. SAS Publishing, Cary, NC.

MELILLO, J. M., ABER, J. D., and MURATORE, J. F. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63:621–626.

PALM, C. A. and SANCHEZ, P. A. 1990. Decomposition and nutrient release patterns of the leaves of three tropical legumes. *Biotropica* 22:330–338.

PARSONS, W. F. J., LINDROTH, R. L., and BOCKHEIM, J. G. 2004. Decomposition of *Betula papyrifera* leaf litter under the independent and interactive effects of elevated CO_2 and O_3. *Glob. Chang. Biol.* 10:1666–1677.

RITCHIE, M. E., TILMAN, D., and KNOPS, J. M. H. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology* 79:165–177.

ROSSITER, M. C., SCHULTZ, J. C., and BALDWIN, I. T. 1988. Relationships among defoliation, red oak phenolics, and gypsy moth growth and reproduction. *Ecology* 69:267–277.

SCHULTZ, J. C. and BALDWIN, I. T. 1982. Oak leaf quality declines in response to defoliation by gypsy moth larvae. *Science* 217:149–151.

SCOTT, N. A. and BINKLEY, D. 1997. Foliage litter quality and annual net N mineralization: Comparison across North American forest sites. *Oecologia* 111:151–159.

SCOWCROFT, P. G., TURNER, D. R., and VITOUSEK, P. M. 2000. Decomposition of *Metrosideros polymorpha* leaf litter along elevational gradients in Hawaii. *Glob. Chang. Biol.* 6:73–85.

STADLER, B., SOLINGER, S., and MICHALZIK, B. 2001. Insect herbivores and the nutrient flow from the canopy to the soil in coniferous and deciduous forests. *Oecologia* 126:104–113.

STILING, P., ROSSI, A. M., HUNGATE, B., DUKSTRA, P., HINKLE, D. R., KNOTT, W. M., and DRAKE, B. III. 1999. Decreased leaf-miner abundance in elevated CO_2: reduced leaf quality and increased parasitoid attack. *Ecol. Appl.* 9:240–244.

STILING, P., CATTELL, M., MOON, D. C., ROSSI, A., HUNGATE, B. A., HYMUS, G., and DRAKE, B. 2002. Elevated atmospheric CO_2 lowers herbivore abundance, but increases leaf abscission rates. *Glob. Chang. Biol.* 8:658–667.

STILING, P., MOON, D. C., HUNTER, M. D., COLSON, J., ROSSI, A. M., HYMUS, G. J., and DRAKE, B. G. 2003. Elevated CO_2 lowers relative and absolute herbivore density across all species of a scrub-oak forest. *Oecologia* 134:82–87.

SWAIN, T. 1980. The importance of flavonoids and related compounds in fern taxonomy and ecology: an overview of the symposium. *Bull. Torrey Bot. Club* 107:113–115.

SWIFT, M. J., HEAL, O. W., and ANDERSON, J. M. 1979. Decomposition in Terrestrial Ecosystems. University of California Press, Berkeley, CA.

VITOUSEK, P. M., TURNER, D. R., PARTON, W. J., and SANFORD, R. L. 1994. Litter decomposition on the Mauna Loa environmental matrix, Hawai'i: patterns, mechanisms, and models. *Ecology* 75:418–429.