

Marlene Tyner is an intern in the Science Undergraduate Laboratory Internship Program at Oak Ridge National Laboratory, researching how climate change effects on decomposition are mediated by species composition. Her paper entitled "Climate Change Effects on Species Composition Mediates Decomposition in an Old-Field Ecosystem" was based on this research. Ms. Tyner received her undergraduate degree in ecology and evolutionary biology at the University of Michigan in Ann Arbor, and she is a member of the Society of Biological Students. Her hometown is Royal Oak, Michigan, and she enjoys hiking, reading, music, movies, mushrooms, China, and shoes.

Aimée Classen is a staff scientist at Oak Ridge National Laboratory, in the Environmental Sciences Division, and an Assistant Research Professor in the Ecology and Evolutionary Biology Department at the University of Tennessee. She received a B.A. in biology from Smith College, and a Ph.D. in biological sciences from Northern Arizona University. Her research in the Classen lab focuses on the interactions and feedbacks among communities of plants, herbivores, and ecosystem processes with an emphasis on the impacts of global change. Recent projects include understanding: how multiple climate change stressors might alter ecosystem function in terrestrial and aquatic ecosystems; how genes may be linked to ecosystem function; and how arthropods may impact ecosystem structure and function.

CLIMATE CHANGE EFFECTS ON SPECIES COMPOSITION MEDIATES DECOMPOSITION IN AN OLD-FIELD ECOSYSTEM

MARLENE L. TYNER AND AIMÉE T. CLASSEN

ABSTRACT

Decomposition of leaf litter collected from an old-field community grown under a combination of elevated atmospheric CO₂ concentrations (+300ppm) and elevated surface temperature (+ 3.2°C) was examined in ambient conditions over 8 months in two separate experiments. In the first experiment, we examined the main effects and interactions of CO₂ and warming on litter quality and subsequent mass loss rates. Multi-species litter bags were constructed with litter collected from chambers with ambient CO₂ and ambient temperatures (ACAT), elevated CO₂ and elevated temperature (ECET), ambient CO₂ and elevated temperature (ACET), and elevated CO₂ and ambient temperature (ECAT). Litter collected from 6 species in each chamber was represented in decomposition bags in equal proportions. There were no differences in initial litter percent carbon (C) or nitrogen (N) among treatments. After 8 months, litter collected from ACET chambers lost over 20% more mass than litter collected from ECET or ACAT chambers, although biological differences were small. In the second experiment, we examined the indirect effect climate change may have on plant community composition, litter inputs, and subsequent mass loss rates. Litter bags were made from the same chambers mentioned above, but the amount of litter in the bag from each species was proportional to peak standing biomass of that species within the treatment. Initial litter in ECAT bags had up to 4% less C and 29% less N than ECET and ACET bags. Mass loss from ACET bags was 48% higher than mass loss from ECAT bags and 37% higher than mass loss from ACAT bags after 8 months of decomposition. These differences may have been driven by the higher proportion of litter from *Lespedeza*, a N-fixer, in the natural ACET bags. Taken together, these data suggest that climate change will have a larger effect on decomposition by causing shifts in plant communities than it will by altering litter quality.

INTRODUCTION

Global changes in atmospheric CO₂ concentration, temperature, and moisture will have important consequences for the functioning of ecosystems [1]. Climatic warming will occur in response to rising atmospheric greenhouse gas concentrations, and elevated CO₂ can alter or compensate for many of the responses of plants and ecosystems to temperature, thus the effects of warming and CO₂ on ecosystem responses should be studied together [2]. Previous research has focused on how single factors such as changes in CO₂ concentrations [e.g. 1] or changes in temperature [e.g. 3] may alter ecosystem functions such as decomposition, but the interactions of climate change drivers have been less studied [4-5]. Interactions among climate drivers may increase or decrease the effect single factors have on ecosystem function, thus understanding how they shape ecosystem responses is important if we are to make good

predictions about how ecosystems will respond to climatic change in the future.

Decomposition is the process that links decaying organic material to living organisms by transforming nutrients from organic to inorganic forms [6]. Decomposition is responsible for recycling nutrients, including carbon, in ecosystems and can be an important indicator of changes in plant available nutrients [6]. Ecosystem decomposition and nutrient release rates can be altered when the quality of litter inputs into ecosystem changes [7-8]. Litter quality inputs could be altered by changing the litter chemistry and inputs of existing plants or it can happen when the community of plants in an ecosystem changes [4]. Much research has focused on how increases in atmospheric CO₂ concentrations may alter initial litter quality and thus decomposition rates [e.g., 1] or how climate may alter decomposition rates [e.g., 9]. It is possible that changes in climate will also alter the community of species in an ecosystem and

the change in species litter inputs will be greater than the change in litter chemistry due to elevated CO₂. Additionally, until recently, research has focused on manipulating single climate change factors such as the effects of elevated CO₂ or elevated temperature on ecosystem processes [e.g., 1, 3]. These factors, however, will not occur independently and are likely to alter ecosystem processes differently, perhaps mediating some of the effects [10]. This project investigated how climate change drivers (elevated CO₂ and temperature) and their interactions effected decomposition rates either directly by altering litter quality or indirectly by altering the community of species present, which would then alter the quality of litter input to the ecosystem.

An open-top chamber experiment was utilized that contained a constructed old-field ecosystem with plant species that included C3 and C4 grasses, forbs, and legumes. Two experiments were constructed that investigated the direct (litter quality) and indirect (changes in species composition) effects of elevated CO₂ and temperature on decomposition rates in an adjacent old-field ecosystem. The first experiment examined the main effects and interactions of CO₂ and warming on litter quality and subsequent mass loss rates. The second experiment examined the indirect effect climate change may have on plant community composition, litter inputs, and subsequent mass loss rates. Changes in atmospheric CO₂ and temperature appear to have a greater effect on decomposition rates by changing the species composition in the chambers than by causing a change in litter chemistry.

MATERIALS AND METHODS

Site Description

This experiment was conducted on the Oak Ridge National Laboratory National Ecological Research Park (NERP) in Oak Ridge, Tennessee, USA. Agricultural use of the site was abandoned in 1943 and the soil at the site is classified as Captina silt loam [11]. The Oldfield Community Climate and Atmospheric Manipulation (OCCAM) project was established in 2002. Five research plots in three blocks (n = 3) were trenched to 75cm to create 4-m diameter plots. Plots were trenched down the center and all the trenches were lined 4 mil PVC film and backfilled with soil to provide a moisture and thermal barrier. Vegetation remaining in the plots was killed with herbicide and removed.

Seedlings of seven plant species, *Plantago lanceolata*, *Dactylis glomerata*, *Lespedeza cuneata*, *Trifolium pratense*, *Solidago canadensis*, *Andropogon virginicus*, and *Festuca pratense*, were grown in a green house and planted in each plot in July 2002 and April 2003. These plants include a C3, C4, and N-fixing grasses, forbs, and shrubs (Table 1).

Open-top chambers (OTCs) with rain-out shelters were constructed on three of the four treatments in each block, the fourth was left unchambered as a control. There was a significant chamber effect, thus unchambered plots were not sampled for this experiment. OTCs were 2.2m high and 4m in diameter, constructed of aluminum frames and covered with clear PVC panels. The bottom half of the PVC panel is a plenum with the inner wall perforated with 2.5cm holes. A fan pushed ambient air through an evaporative cooler and

Treatment (bag designation)	Plantago C3 dicot	Andropogon C4 bunchgrass	Solidago perennial forb	Dactylis C3 bunchgrass	Lespedeza N-fixing shrub
ECAT	0.03	0.44	0.07	0.98	0.48
ACAT	0.01	0.35	0.04	0.88	0.72
ECET	0.04	0.03	0.06	0.57	0.80
ACET	0.08	0.42	0.18	0.35	0.97
Standard	0.40	0.40	0.40	0.40	0.40

Table 1. Leaf litter mass (g) placed in decomposition bags in the field. Litter mass was determined from peak standing biomass of plants in the open-top chamber experiment. Treatments are designated as following: EC = Elevated CO₂, AC = Ambient CO₂, ET= Elevated Temperature, AC = Ambient Temperature, Standard = Standard Amount of litter in each bag.

in-line heating coils into the plenum distributing it around the plot. Heaters and coolers regulated chamber temperature while pure CO₂ was introduced into the plenum of elevated CO₂ plots to achieve daytime CO₂ enrichment of 300 ppm over ambient air. Treatments began in May 2003. Elevated [CO₂] treatments have averaged 338ppm above outside ambient [CO₂], and elevated temperatures averaged 3.2°C above outside ambient temperatures. These values are consistent with IPCC projections of climate change in the southeastern US within the next 100 years. Treatments are designated as: ECAT, ACAT, ECET, ACET, where EC = Elevated CO₂, AC = Ambient CO₂, ET= Elevated Temperature, AC = Ambient Temperature.

Irrigation treatments began in June 2003 and mimicked long-term mean weekly precipitation records from a local weather station in Oak Ridge, TN. Rainwater was collected and added weekly to dry (2mm) and wet (25mm) plots.

Experimental Design

At the end of the growing season in 2005, leaf litter material was collected from species in each plot. Litter was brought back to the laboratory, air-dried, and each species was homogenized within each plot. Insufficient leaf material was available to use litter from wet and dry treatments, so wet and dry treatments were combined. Also, *Trifolium* was not present in significant amounts in 2005 and thus was not included in the experiment. Using peak biomass data from each species in each of the plots in 2005 (Engle et al. unpublished data), decomposition bags were constructed that reflected the proportion of plant material entering the ecosystem in each of the treatments (hereafter 'natural' bags). Decomposition bags were also constructed that contained a standard amount of leaf material collected in each plot (hereafter 'standard' bags). These bag types represent the different possible effects treatments (elevated temperature and CO₂) may have on decomposition; direct via tissue quality changes, indirect via species composition changes. Each decomposition bag contained approximately 2g of leaf material (Table 1).

Leaf litter decomposition bags (15.5cm x 15.5cm) were constructed of a double layer of 3-mm nylon mesh on the side facing up and a single layer of 1.3mm plastic window screening on the side in contact with the soil surface. The larger mesh size on top enabled litter microarthropods to access the bags, while the smaller mesh

on the bottom reduced litter loss due to fractionation. Bags were stitched together on three sides with polyester thread and closed with stainless steel staples. For each chamber, two replicates of natural and standard bags were constructed with three removal dates. In total, 144 bags were placed in an oldfield adjacent to the experimental plots (12 plots x 2 bag types x 2 replicates x 3 removal dates = 144). The adjacent old-field contained species that were similar to those found within the experimental plots. The experimental chambers were not used for this experiment, as insufficient space in the plots for the decomposition bags and their placement would have compromised the experiment.

Decomposition bags were deployed in May of 2005 and collected in July 2005, September 2005, and January 2006. Litter bags were secured to the soil surface using metal stakes and their locations flagged for easy collection. Upon collection, decomposition bags were brought back to the laboratory in individual paper bags, air dried, and sorted to remove debris that might have entered the bag after deployment. Air-dried samples were oven dried at 70°C, weighed, and ground using a Pica ball-mill grinder (Cianflone Scientific Instruments Corporation, Pittsburg, PA) to a fine powder. Subsamples were analyzed for total C and N using a Costech CHN analyzer (Milan, Italy). Samples were ashed in a muffle furnace at 550°C for 6 hours and data are presented on an ash-free oven-dry mass basis.

Data Analysis

All statistical analyses were conducted using JMP 4 statistical software with significance defined as $P \leq 0.05$ (SAS Institute, 2001, Pacific Grove, CA). Natural and standard decomposition bag data were analyzed separately. Initial litter chemistry data were analyzed using ANOVA with the independent variable chamber type (ECAT, ACAT, ECET, ACET). For decomposition data, full factorial, fixed effects ANOVAs were conducted to test the independent variables of chamber type (ECAT, ACAT, ECET, ACET) and sample removal date (July, September, January) with interactions on mass loss. A student-t test was used to test for differences among treatment means. Proportional data were transformed using the arcsine square root transformation. All data are shown as non-transformed means in figures and tables. Where appropriate, data are shown on an ash-free, oven-dry mass basis.

RESULTS

Initial litter %C, %N, and C:N values were not different among treatments in standard decomposition bags (Table 2). Initial litter chemistry in natural decomposition bags differed significantly among treatments (Table 2). % C values were 4.5% higher ($F_{3,11} = 5.48$, $P = 0.02$) and %N were 41% higher ($F_{3,11} = 4.19$, $P < 0.05$) in ACET and ECET chambers than the ECAT chambers (Table 2). C:N ($F_{3,11} = 4.87$, $P = 0.03$) values were significantly lower in ACET and ECET chambers relative to ECAT chambers (Table 2).

Chamber type ($F_{11,3} = 3.53$, $P = 0.03$) and removal date ($F_{11,2} = 301.41$, $P < 0.001$) each had a significant effect on standard decomposition bag mass loss, but there were no interactions (Table 3,

Bag Type	Standard			Natural		
	%C	%N	C:N	%C	%N	C:N
ECAT	44.01	1.05	41.91	44.27 ^a	0.99 ^a	44.72 ^a
ACAT	44.72	1.10	40.65	45.10 ^{ab}	1.22 ^{ab}	36.97 ^{ab}
ECET	45.00	1.05	42.86	45.77 ^b	1.40 ^b	32.69 ^b
ACET	45.08	1.19	37.88	45.95 ^b	1.40 ^b	32.82 ^b

Table 2. Initial litter chemistry for decomposition bags in each treatment (n=3). Litter was placed in decomposition bags in the percentages found in open-top chambers. Natural bags reflect natural percentages of plants found in the field, while standard bags have a standard amount of each species. Treatments are designated as following: EC = Elevated CO₂, AC = Ambient CO₂, ET = Elevated Temperature, AC = Ambient Temperature. Letters denote significant differences ($P \leq 0.05$) within columns.

Model	Standard			Natural		
	df	P-value	F-value	df	P-value	F-value
Model	11	< 0.001*	55.94	11	< 0.001*	33.30
Effect						
Chamber	3	< 0.03*	3.54	3	< 0.004*	5.92
Removal date	2	< 0.001*	301.41	2	< 0.001*	170.15
Chamber x Removal date	6	0.92	0.32	6	0.27	1.38

Table 3. Probability values and F statistics generated using ANOVA of leaf litter % mass remaining over three collection dates for standard and natural decomposition bags. Chamber refers to the source of the litter. Stars (*) indicate significant differences ($P \leq 0.05$).

Figure 1). ACET showed the highest rates of mass loss followed by ECAT, ECET, and ACAT. ACET mass loss rates were significantly higher than ECET and ACAT rates ($P < 0.05$, Table 3, Figure 1). ECET bags contained 26% more mass than ACAT bags after 8 months of decomposition (Figure 1).

Chamber type ($F_{11,3} = 5.92$, $P < 0.004$) and removal date ($F_{11,2} = 170.15$, $P < 0.001$) also had a significant effect on natural decomposition bag mass loss, and again there were no interactions (Table 3, Figure 1). Once again, ACET lost more mass than the other treatments followed by ECET, ACAT, and ECAT. ECET showed significantly higher mass loss rates than ECAT and ACAT. ECAT showed significantly slower mass loss rates than ACET and ACET (Figure 1). After 8 months of decomposition, 94% more mass remained in ECAT bags than ACET bags (Figure 1).

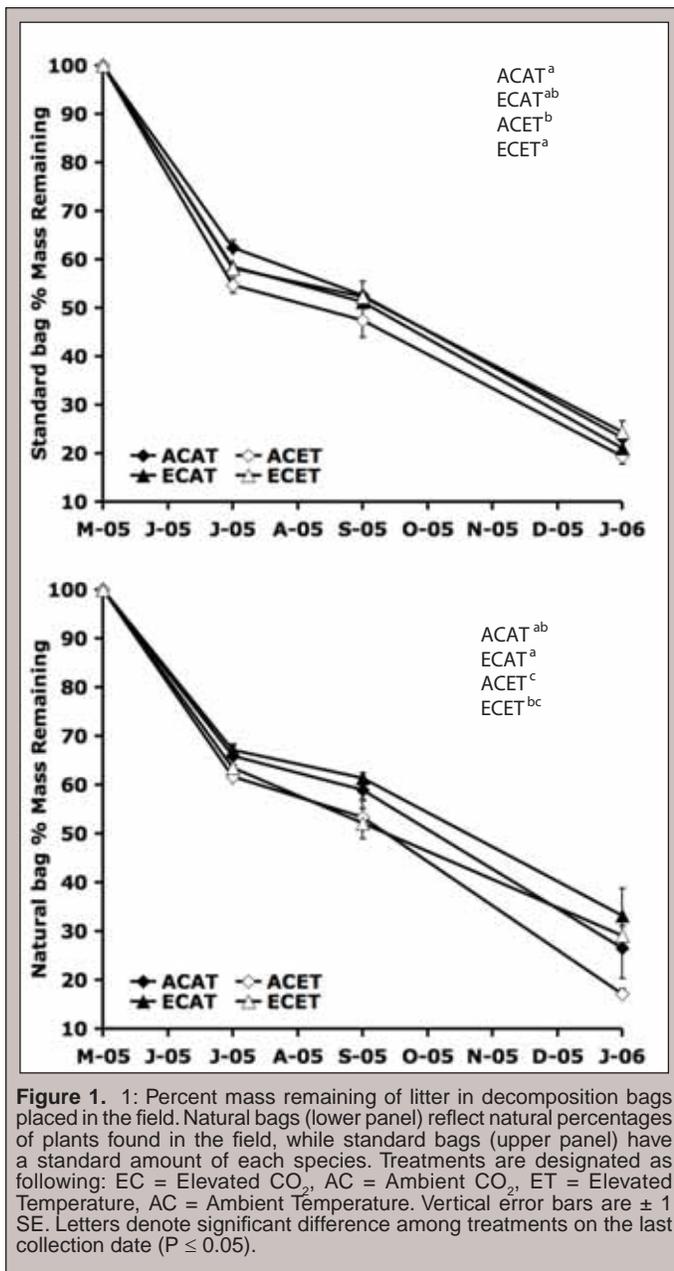


Figure 1. 1: Percent mass remaining of litter in decomposition bags placed in the field. Natural bags (lower panel) reflect natural percentages of plants found in the field, while standard bags (upper panel) have a standard amount of each species. Treatments are designated as following: EC = Elevated CO₂, AC = Ambient CO₂, ET = Elevated Temperature, AC = Ambient Temperature. Vertical error bars are ± 1 SE. Letters denote significant difference among treatments on the last collection date (P ≤ 0.05).

DISCUSSION

This project resulted in two significant findings: 1) Although initial litter %C and %N did not differ among treatments in standard decomposition bags, litter from ACET chambers lost over 20% more mass than litter collected from ECET or ACAT chambers. This result, while statistically significant, is likely to have little biological significance. 2) Differences in plant communities under different climate treatments resulted in changes in initial litter quality. Initial litter in ECAT bags had up to 4% less C and 29% less N than ECET and ACET bags. Mass loss from ACET bags was 48% higher than mass loss from ECAT bags. *Lespedeza*, a N-fixing shrub, was found in a higher proportion in ACET and ECET chambers and, therefore made up the largest proportion of ACET and ECET decomposition bags. The increase in nitrogen in these bags may be

driving their increase in mass loss over time. These results will be discussed in turn below.

Elevated CO₂ and temperature have a limited direct effect on litter chemistry and decomposition

Elevated CO₂ and temperature have limited direct effects on litter chemical quality and mass loss in this experiment. Initial litter %N and %C did not differ among treatments. Although ACET lost more mass than litter collected from other chambers, the biological difference is small and unlikely to change nutrient cycling rates, at least during the first 8 months of the decomposition process. These results support other studies showing minimal effects of elevated CO₂ on litter chemistry [12-13] and decomposition [1]. These studies suggest that other impacts of global change on decomposition, such as changes in species composition, may have a larger impact on litter mass loss and litter nutrient dynamics in ecosystems than small changes in litter chemistry [1].

Elevated CO₂ and temperature mediate decomposition via their impacts on plant community composition

Previous research has documented that changes in plant species composition in communities will occur with rising atmospheric CO₂ concentrations and temperature [4]. This shift in plant community composition may lead to changes in mass loss and nutrient cycling if nutrient rich or nutrient poor species become more abundant in the community. For example, if changes in climate lead to an increase in N-fixers in an N-limited ecosystem, then decomposition and nutrient availability may increase with an increase in N-rich plant material [8]. Alternatively, N-fixers could become less abundant, leading to a decrease in the quality of litter inputs at a community-level and an overall decrease in community litter decomposition and nutrient cycling rates [7]. The current study found that treatments that resulted in a greater abundance of N-fixers also had higher rates of decomposition after 8 months (Figure 1). *Lespedeza*, a N-fixing shrub, was found in higher proportion in the ACET and ECET chambers compared to ACAT and ECAT. It is possible that elevated temperature created a more favorable climate for *Lespedeza* to establish in, thus leading to an increase in N inputs and decomposition rates of litter in these plots.

CONCLUSION

The results of this study corroborate those of other studies demonstrating that the indirect effect of climate change on species composition has a larger impact on decomposition than the direct effect of climate on initial litter chemical quality [9]. However, it is important to remember that resource availability, such as site nitrogen availability, and the large amount of variation found within natural ecosystems substantially broadens the range and timing of climate effects on nutrient processes [7]. When establishing experiments and developing hypotheses about climate impacts on ecosystems, researchers should be as cognizant of how the existing community may shift as they are about how the existing plants will respond to a single climate change factor.

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