Global Change Biology (2009) **15**, 1356–1363, doi: 10.1111/j.1365-2486.2008.01815.x

Litter decomposition in grasslands of Central North America (US Great Plains)

ELIANA E. BONTTI*†, JOSEPH P. DECANT*†, SETH M. MUNSON*†, MARK A. GATHANY*†, AGNIESZKA PRZESZLOWSKA†, MICHELLE L. HADDIX*†‡, STEPHANIE OWENS*, INGRID C. BURKE*†‡, WILLIAM J. PARTON*‡ and MARK E. HARMON§

**Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523, USA, †Department of Forest, Rangeland, and Watershed Stewardship, Colorado State University, Fort Collins, CO 80523, USA, ‡Natural Resources Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, USA, §Department of Forest Sciences, Oregon State University, Corvallis, OR 97331, USA*

Abstract

One of the major concerns about global warming is the potential for an increase in decomposition and soil respiration rates, increasing CO_2 emissions and creating a positive feedback between global warming and soil respiration. This is particularly important in ecosystems with large belowground biomass, such as grasslands where over 90% of the carbon is allocated belowground. A better understanding of the relative influence of climate and litter quality on litter decomposition is needed to predict these changes accurately in grasslands. The Long-Term Intersite Decomposition Experiment Team (LIDET) dataset was used to evaluate the influence of climatic variables (temperature, precipitation, actual evapotranspiration, and climate decomposition index), and litter quality (lignin content, carbon : nitrogen, and lignin : nitrogen ratios) on leaf and root decomposition in the US Great Plains. Wooden dowels were used to provide a homogeneous litter quality to evaluate the relative importance of above and belowground environments on decomposition. Contrary to expectations, temperature did not explain variation in root and leaf decomposition, whereas precipitation partially explained variation in root decomposition. Percent lignin was the best predictor of leaf and root decomposition. It also explained most variation in root decomposition in models which combined litter quality and climatic variables. Despite the lack of relationship between temperature and root decomposition, temperature could indirectly affect root decomposition through decreased litter quality and increased water deficits. These results suggest that carbon flux from root decomposition in grasslands would increase, as result of increasing temperature, only if precipitation is not limiting. However, where precipitation is limiting, increased temperature would decrease root decomposition, thus likely increasing carbon storage in grasslands. Under homogeneous litter quality, belowground decomposition was faster than aboveground and was best predicted by mean annual precipitation, which also suggests that the high moisture in soil accelerates decomposition belowground.

Keywords: climate change, grasslands, Great Plains (USA), litter decomposition, litter quality, precipitation, root and leaf decomposition, temperature

Received 23 May 2008; revised version received 6 October 2008 and accepted 6 October 2008

Introduction

Global warming has the potential to elicit a positive feedback between increased temperature, decomposition, and carbon dioxide (CO_2) emissions, further increasing global temperatures. Ecosystems vary in the

Correspondence: Eliana E. Bontti, Department of Forest, Rangeland, and Watershed Stewardship, Colorado State University, Fort Collins, CO 80523, USA, tel. + 1 970 491 7274, fax + 970 491 2796, e-mail: elianab@cnr.colostate.edu

mechanisms that lead to changes in litter decomposition and soil respiration rates under increased temperatures.

Changes in litter decomposition rates are particularly important in arid and semiarid grasslands because they cover 40% of the earth's land surface (White *et al*., 2000), store most of the carbon belowground (Vandermaarel & Titlyanova, 1989; Lauenroth & Sala, 1992; Milchunas & Lauenroth, 2001), and have characteristically slow decomposition rates (Gill & Burke, 2002).

Altered decomposition rates in these ecosystems could affect the global carbon cycle. Thus, a better understanding of long-term effects of climate and litter quality on litter decomposition in grasslands is needed to predict litter decomposition accurately under global climate change.

One of the challenges in understanding litter decomposition in grasslands is to determine the relative importance of climatic variables on decomposition. The relative importance of precipitation and temperature as predictors of decomposition is likely to vary across regions. Mean annual precipitation (MAP) and mean annual temperature (MAT) explained leaf decomposition in Canadian ecosystems (Moore *et al*., 1999). In the US Great Plains, given the water limitations, MAP explained a higher proportion of decomposition variability, compared with MAT or soil texture (Epstein *et al*., 2002). Other studies showed that climate variables integrating temperature and rainfall explained decomposition better across broad spatial scales (Lang & Forman, 1978; Meentemeyer, 1978; Gholz *et al*., 2000; Liski *et al*., 2003). However, it is still unknown which climate variables best explain decomposition on continental and regional scales, such as grasslands in the US Great Plains.

The second factor that adds to the complexity of litter decomposition in grasslands is litter quality. Initial litter quality (i.e. lignin content – %L, carbon to nitrogen ratio – C : N, and lignin to nitrogen ratio – L : N) influences rates of decomposition, particularly root decomposition (Silver & Miya, 2001).

The complexity of the decomposition processes stem from interactions between climate and litter quality, which makes it difficult to evaluate the relative importance of each factor on litter decomposition. Climate affects litter quality by influencing plant community composition and decomposers activity. In the US Great Plains, aboveground litter quality is inversely related to rainfall (Murphy *et al*., 2002), such that litters in the highest precipitation areas have the lowest quality, potentially decomposing at a slow rate, and leading to carbon storage (Aber & Melillo, 1982). However, it is unclear whether higher precipitation would also accelerate decomposition, even of low quality litter.

The third important aspect of litter decomposition in grasslands is the relative contribution of leaves and roots, as well as the potential for climatic and litter quality variables to differentially affect them. Most past studies have focused on decomposition of aboveground litter and little is known about climatic and litter quality controls on decomposition of belowground root biomass. Because grasslands have root : shoot ratios greater than other ecosystems (Mokany *et al*., 2006), it is also important to consider differences between leaf and root decomposition in grasslands to avoid underestimation of total ecosystem decomposition. The goal of this study was to determine how climate and litter quality affect both aboveground (leaf) and belowground (root) decomposition in dry and wet grasslands after long-term incubations.

The influence of simple (i.e. MAP, MAT) and complex climatic variables (i.e. AET), as well as litter quality on leaf and root litter decomposition was investigated by using a cross-site and long-term litter decomposition experiment (LIDET, 1995). Moreover, the use of homogenous litter across sites allowed the evaluation of differences in patterns between above- and belowground decomposition.

Materials and methods

The data used in this study was from a 10-year (start in 1989) reciprocal litterbag study including leaf and root litter of different ecosystems from 27 plant species across 28 sites in North and Central America (LIDET, 1995). The grassland sites spanned a large variation in MAP, but the experimental design did not include sites with intermediate MAP for grasslands. Analysis of initial litter quality effects on decomposition therefore grouped sites into xeric and mesic grasslands (climatic data, latitude, and longitude in Gholz *et al*., 2000). Three xeric grassland sites with MAP of 254.5–440.4 mm included: Sevilleta National Wildlife Refuge, Jornada Experimental Range, and Central Plains Experimental Range. Three mesic grassland sites with MAP of 791.2–822.8 mm were Cedar Creek Natural History Area, Konza Prairie Research Natural Area, and Kellogg Biological Station.

LIDET (1995) and Gholz *et al*. (2000) described the experiment in detail. The original design of the experiment included 10 types of 'standard' litters that were incubated at each site to compare the decomposition of a specific range of litter quality across different biomes. The standard set of species included three functional types of fine roots (<2 mm, graminoid, hardwood, and conifer), six species of leaf litter (initial L : N ranged 5–78), and wooden dowels. This design did not include most of the native grassland species of the US Great

Table 1 Initial chemical composition of plant litters used in the Long-Term Intersite Decomposition Experiment Team (LIDET) study (mean ± SE)

Species	% Carbon	% Lignin	% Nitrogen
Leaf			
Acer saccharinum	49.8 ± 1.1	15.9 ± 0.4	0.81 ± 0.02
Drypetes glauca	47.8 ± 0.5	10.9 ± 1.0	1.97 ± 0.03
Pinus resinosa	53.4 ± 0.9	19.2 ± 4.6	0.59 ± 0.05
Quercus prinus	51.5 ± 0.7	23.5 ± 0.8	1.03 ± 0.04
Thuja plicata	51.1 ± 0.8	26.7 ± 3.7	0.62 ± 0.04
Triticum aestivum	47.3 ± 0.8	16.2 ± 0.9	0.38 ± 0.05
Root			
Andropogon gerardii	37.0 ± 1.3	10.5 ± 0.9	0.63 ± 0.04
Drypetes glauca	48.2 ± 0.7	16.1 ± 1.2	0.76 ± 0.06
Pinus elliottii	49.4 ± 0.4	34.9 ± 2.2	0.82 ± .05
Dowel			
Gonystlylus bancannus	50.0 ± 0.1	25.0 ± 2.2	0.32 ± 0.01

Sample size varied and was between 3 and 8, except for the dowel which only had two samples for %C and %N.

Plains, but allowed for comparison of the same litter quality (Table 1) among grasslands characterized by different climatic conditions. The species of which leaf litter was analyzed were *Acer saccharum* Marsh., *Drypetes glauca* Vahl, *Pinus resinosa* Ait., *Quercus prinus* L., *Thuja plicata* Donn ex D. Don, *Triticum aestivum* L. Root litter data were gathered from *Andropogon gerardii* Vitman, *D. glauca* Vahl, and *Pinus elliottii* Englem. (Table 1). Hereafter the terms leaf and root decomposition refer to plant species, whereas both above- and belowground decomposition refer only to dowel decomposition (dowels are described below).

Litter was incubated in 20 cm × 20 cm litter bags. Leaf litter bags contained 10 g of litter with a top mesh of 1 mm and a bottom of 55 μm mesh DACRON cloth to reduce fragmentation losses. Root litter bags were made entirely of 55 ím mesh DACRON cloth and contained 5–7 g of fine roots (<2 mm diameter).

Leaf bags were placed flat on the top of the existing litter layer while root bags were buried 10–20 cm with the top edge of the bag parallel with the surface of the mineral soil. Litter bags for all grassland sites were collected each year for 10 years.

Wooden dowels (*Gonystylus bancanus* (Miq.) Kurz, GOBA) were used as a homogeneous substrate to control for litter quality in the comparison of above- vs. belowground decomposition Harmon (personal communication). The wood of this species was considered not resistant to decay and was rated as perishable (LIDET, 1995). The dowels were 1.3 cm in diameter and 61 cm in length and they were positioned vertically, with half of the wood aboveground and half of it belowground. Different quality above- and belowground substrates were assessed by comparing leaves and root of *D. glauca* (DRGL) and *Pinus* spp., the only groups represented in grasslands by both leaves and roots in the initial experimental design.

Co-investigators from each LTER site provided environmental data for each site, most of which were multiyear averages over the study period (1990–2000) from nearby standard meteorological stations. Simple (MAP and MAT) and complex [AET and climatic decomposition index (CDI)] climatic variables were assessed for their ability to predict decomposition rates. The CDI (referred to as DEFAC in previous papers) is a more complex climate variable from the CENTURY model (Parton *et al.*, 1994) that was shown to control the turnover rate of litter biomass and soil organic matter pools. Monthly CDI (CDI_i) was calculated as a function of mean monthly air temperature (T_i), precipitation (PPT_i), and potential evapotranspiration rate (PET_i) using Eqns (1)–(3):

$$\mathrm{CDI}_i = F_t(T_i) \times F_{\mathrm{w}}(\mathrm{PPT}_i, \mathrm{PET}_i), \quad (1)$$

$$F_t(T_i) = 0.56 + 0.45 \times \mathrm{ATAN}[0.097 \times (T_i - 15.4)], \quad (2)$$

$$F_{\mathrm{w}}(\mathrm{PPT}_i, \mathrm{PET}_i) = \frac{1.0}{1.0 + 30 \times \exp(-8.5 \times \mathrm{PPT}_i/\mathrm{PET}_i)}, \quad (3)$$

where $F_t(T_i)$ and $F_{\mathrm{w}}(\mathrm{PPT}_i, \mathrm{PET}_i)$ are the effects of temperature and water stress on decomposition for the month *i*th. Del Grosso *et al.* (2005) derived the temperature function for decomposition (where ATAN is an arctangent function) and showed that it predicts decomposition rates better than other functions. PET_i was calculated as a function of the monthly average daily maximum temperature and minimum air temperature and latitude of the site using an equation developed by the Food and Agriculture Organization (FAO) (Allen *et al.*, 1998). The FAO PET equation includes the impact of solar radiation (calculated from latitude and time of year), air temperature, and relative humidity on PET (diurnal range of temperature is correlated to relative humidity). The mean annual value of CDI for each of the sites was the average of the CDI_i.

Decomposition rates of leaves, roots, and dowels were calculated from percent ash-free remaining material for the six grassland sites by using the negative exponential decay constant (*k*) derived from the model of Olson (1963):

$$y = \mathrm{e}^{-kt}. \quad (4)$$

where y is the fraction of mass remaining at a given time, t (years). Averages were used from the replicates available at each site, for each species and for each time point for the analyses.

Statistical analyses

Simple linear regression analyses (SAS Institute Inc., 1989) between each climatic variable and *k* were used to evaluate the relative importance of single (MAP and MAT) and complex (AET and CDI) climatic variables on decomposition. Separate analyses were performed for root and leaf decomposition, and each regression included all the sites and species together.

Simple linear regression analyses between *k* of leaves and roots with C : N, L : N, and %L were used to determine the best litter quality index for decomposition rates. These analyses were performed twice, first for xeric and mesic sites separately, and second, pooling all sites. The purpose was to assess potential differences in the relationship between *k* and litter quality that might be influenced by the precipitation regime of the sites. The *k* values were log-transformed when they did not meet the assumptions for regression analyses.

To evaluate the relative importance of climate and initial litter quality, an Akaike Information Criterion (AIC_c) approach was utilized. Different combinations of two variables (one climatic and one quality variable) were included in several mixed model regressions to estimate AIC_c (for small samples). We then used AIC_c to determine strength of evidence in the data to support competing models explaining decomposition rates (*k*) (Proc Mixed, SAS Institute Inc., 1989). Comparisons of the relative importance were assessed for the best quality variable and the best climatic variable to explain litter decomposition upon identifying the best model to predict decomposition. This comparison was made through partial regressions, and using the partial sum of squares and the *F* values as a measure of the relative importance of each variable in the model.

A mixed model regression (Proc Mixed, SAS Institute Inc., 1989) was used to test leaf vs. root decomposition and above vs. belowground decomposition through separate analyses of *DRGL*, *Pinus* spp. (leaf vs. root), and dowels (above vs. belowground), respectively. Each species or genus was analyzed separately. The same model was used to test the relationship between dowel decomposition and climatic variables including above- and belowground dowel decomposition in separate analyses.

Results

Rates of litter decomposition exhibited differences based on climate, litter quality, and the place of litter incubation (i.e. above- or belowground). When all sites were considered together, the ash free percentage mass remaining after 10 years varied from 15% to 50% for leaves, 5% to 82% for roots, and 60% to 80% for dowels. In xeric sites the *k* values ranged from 0.02 for aboveground dowels to 0.35 for pine leaves, which represented mean residence times from 54 to 7 years, respectively. The *k* values for mesic grasslands ranged from 0.03 for aboveground dowels to 0.5 for DRGL leaves, indicating mean residence times from 30 to 2 years, respectively.

Climate variables

Variability in leaf litter decomposition rates was not explained by climatic variables despite a wide range in MAP (250–820 mm) and MAT (5–15 °C) (data not shown). In contrast, root decomposition variability was explained by MAP, followed by the complex variables AET and CDI in order of importance (Table 2).

Initial litter quality

Initial %L was negatively related to and explained more variation in leaf litter decomposition than other litter quality indices in xeric and mesic sites separately and all sites together (Fig. 1 and Table 3). The very narrow range of C : N ratio for roots (ex. 59–63) prevented these values from being evaluated. Initial litter quality (L : N and %L) appeared to be more important for root decomposition than leaf decomposition based on the proportion of variance explained (R^2 in Fig. 2). Low leaf litter quality exhibited higher *k* values in xeric sites compared with mesic sites, whereas *k* values of high quality litter were greater at mesic sites (Fig. 1). Root *k* values were consistently higher in mesic sites across all species ($P < 0.0001$) compared with xeric sites (Fig. 2). Decomposition rates also decreased as the amount of

Table 2 Regressions of climatic variables with decomposition rates (*k*) for root litter in six grasslands included in the Long-Term Intersite Decomposition Experiment Team (LIDET) experiment ($n = 6$)

Parameter	Linear regression	R^2	*P*
Climatic variables			
MAP	$k = 0.080 + 0.002(\text{MAP})$	0.86	<0.01
MAT	$k = 0.244 - 0.006(\text{MAT})$	0.22	0.34
AET	$k = 0.075 + 0.002(\text{AET})$	0.81	0.01
CDI*	$k = 0.085 + 0.441(\text{CDI})$	0.83	0.01

Analyses include all sites together (mesic and xeric sites).
*CDI decomposition factor described in 'Materials and methods'.

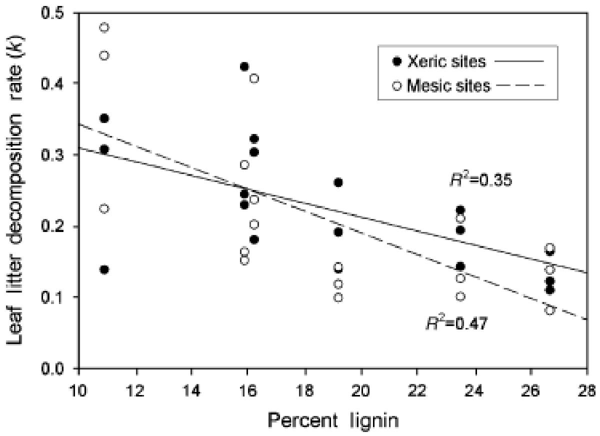

Fig. 1 Relationship between percent lignin and leaf decomposition rate (*k*) by species in six grasslands included in the Long-Term Intersite Decomposition Experiment Team (LIDET) experiment. Regression analyses were performed for xeric sites and mesic sites separately ($P<0.001$ in xeric as well as in mesic sites).

Table 3 Regressions of litter quality with decomposition rate (*k*) for leaf and root (leaf: $n=36$, root: $n=18$) in six grasslands included in the Long-Term Intersite Decomposition Experiment Team (LIDET) experiment

Parameter	Linear regression	R^2	*P*
Leaf			
C : N	$\ln k=-1.501-0.002(\mathrm{C:N})$	0.01	0.47
%L	$\ln k=-0.574-0.056(\%\mathrm{L})$	0.42	<0.0001
L : N	$\ln k=-1.287-0.012(\mathrm{L:N})$	0.13	0.03
Root			
%L	$k=0.304-0.006(\%\mathrm{L})$	0.63	<0.0001
L : N	$k=0.327-0.006(\mathrm{L:N})$	0.60	<0.001

Analyses include all sites together (three mesic and three xeric sites). Leaf *k* was transformed because it did not meet the assumptions for regression analysis.

%L in the root material increased across both xeric and mesic sites ($P<0.0001$ and $P<0.001$, respectively).

Climate vs. litter quality variables

Climate variables showed a relation with root litter decomposition but not with leaf litter decomposition. Accordingly, climate and litter quality variables were tested to predict root decomposition with a best mixed model regression where site and species were random variables, and MAP and %L were a combination of explanatory variables based on the lowest $\mathrm{AIC_c}$. Analyses showed that %L was the best predictor of root decomposition ($F=76$, $P<0.03$), followed by MAP ($F=29$, $P<0.01$). Rates of root litter decomposition increased with corresponding increases in litter quality and with greater precipitation levels.

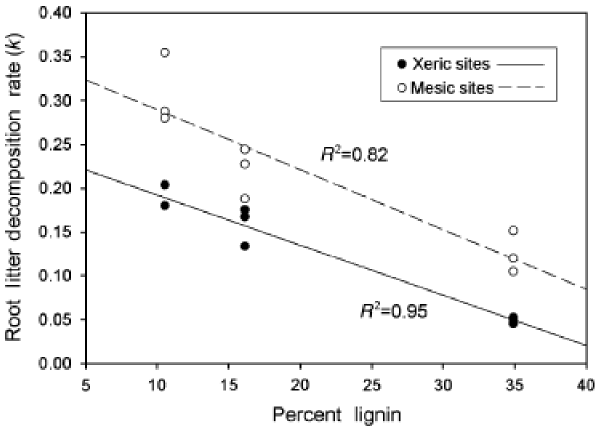

Fig. 2 Relationship between percent lignin and root decomposition rate (*k*) by species in six grasslands included in the Long-Term Intersite Decomposition Experiment Team (LIDET) experiment. Analyses were performed for xeric sites and mesic sites separately ($P<0.001$ in xeric as well as in mesic sites).

Table 4 Mixed model regression of leaf vs. root decomposition parameters by species in six grasslands included in the Long-Term Intersite Decomposition Experiment Team (LIDET) experiment

Parameter	*P*
Drypetes glauca	
MAP	0.13
Place	0.03
MAP × Place	0.62
Pinus spp.	
MAP	0.98
Place	0.01
MAP × Place	0.05
Dowels	
MAP	0.02
Place	<0.001
MAP × Place	0.22

Place refers to the position: above- or belowground.

Leaf vs. root decomposition

Root litter decomposed more slowly than leaves of the same species (*DRGL*) or genus (*Pinus* spp.) (Table 4). Leaf decomposition rates were not related to MAP, but increased root decomposition rates were related to increased MAP. *Pinus* spp. litter decomposition showed a significant interaction between MAP and place of decomposition (above- or belowground, Table 4).

Above- vs. belowground decomposition

Climatic variables significantly influenced belowground but not aboveground decomposition rates of

Table 5 Regressions of climatic variables with decomposition rates (k) of dowels ($n = 6$) in six grasslands included in the Long-Term Intersite Decomposition Experiment Team (LIDET) experiment

Parameter	Linear regression	R^2	P
Aboveground dowels			
Climatic variables			
MAP	$k = 0.00769 + 0.000547(\mathrm{MAP})$	0.60	0.07
MAT	$k = 0.0545 - 0.00139(\mathrm{MAT})$	0.08	0.60
AET	$k = 0.00548 + 0.000633(\mathrm{AET})$	0.59	0.07
CDI*	$k = 0.00845 + 0.150(\mathrm{CDI})$	0.62	0.06
Belowground dowels			
Climatic variables			
MAP	$k = 0.0382 + 0.000839(\mathrm{MAP})$	0.81	0.01
MAT	$k = 0.133 - 0.00421(\mathrm{MAT})$	0.40	0.18
AET	$k = 0.0357 + 0.000953(\mathrm{AET})$	0.76	0.02
CDI	$k = 0.0419 + 0.218(\mathrm{CDI})$	0.74	0.03

*CDI decomposition factor explained in 'Materials and Methods'.

homogeneous substrate (dowels) (Table 5). MAP best explained belowground decomposition rates, followed by AET and CDI (Table 5).

Discussion

The results of this study suggest that key controls of grassland decomposition differ from global scale controls and do not support the hypothesis of increased decomposition as a result of increased global temperature (Kirschbaum, 1995). Even though there is strong evidence of global influence of climate and litter quality on litter decomposition (Meentemeyer, 1978; Melillo *et al.*, 1982), decomposition patterns in grasslands has proven to be more complex, with studies showing contrasting results (Berg *et al.*, 2000; Hamadi *et al.*, 2000; Epstein *et al.*, 2002; Yahdjian *et al.*, 2006). Some of these discrepancies might relate to the lack of separation between direct and indirect effects of precipitation on decomposition (Yahdjian *et al.*, 2006).

Previous analyses in the US Great Plains, which assumed that abiotic factors affected leaf and root decomposition equally, showed that MAP explained a higher proportion of decomposition variability compared with MAT or soil texture (Epstein *et al.*, 2002). This study through a different experimental approach helped detecting different responses of leaf and root litter decomposition to climatic factors, which would allow more accurate predictions of litter decomposition in grasslands under global climatic change.

The effect of climate on litter decomposition observed in this study highlighted the difficulty of applying global predictors to a regional scale. A comparison with previous LIDET analyses on pine and hardwood litter at a global scale (Gholz *et al.*, 2000), revealed that different controls on root decomposition rates emerged at a regional level. In grasslands, which are comparatively more water limited than many other ecosystems, simple (MAP) and complex climatic variables that include moisture or precipitation (CDI and AET) best explained root decomposition rates.

These results also suggest that the negative relationship between MAT and soil organic carbon reported in the US Great Plains (Burke *et al.*, 1989) might be an effect of lower litter quality observed under higher MAT and MAP, which was attributed to higher nutrient use efficiency under these climatic conditions (Murphy *et al.*, 2002).

The importance of precipitation influence on root decomposition found in this study supports increasing evidence that higher rates of decomposition may occur under increased global temperature only when and where soils are not water limited (Giardina & Ryan, 2000; Epstein *et al.*, 2002; Aerts, 2006).

The general global circulation models predict increases in temperature under double CO_2 (Hansen *et al.*, 1983; Manabe & Wetherald, 1987; Wilson & Mitchell, 1987). Increased temperatures might also intensify water deficits in some areas (Lauenroth *et al.*, 2004), which would decrease root decomposition rates and increase carbon storage in moisture-limited grasslands.

Even though this study integrated a range of annual precipitation in a system that is well-recognized for its water limitation (Sala *et al.*, 1988; Lauenroth & Sala, 1992), leaf decomposition rates exhibited no response to MAP. However, Moore *et al.* (1999) showed a strong relationship between leaf litter decomposition and MAT and MAP in a global experiment in upland forests spanning from the arctic to the prairie border in Canada. These contrasting results may stem from differences in higher latitude biomes in terms of the litter decomposition response to temperature.

Factors other than moisture and temperature appeared to drive leaf decomposition. Leaf decomposition proceeded at a faster rate than root decomposition in comparisons between leaf and root litter of the same species (DRGL and *Pinus* spp.). This might be a consequence of lower %L in leaves compared with roots. Ultraviolet radiation or macroarthropods are other factors that might explain these differences in decomposition rates as well as the lack of relationship between leaf decomposition and MAT. UV radiation was found to accelerate litter decomposition in semiarid ecosystems (Austin & Vivanco, 2006; Parton, 2007). In this study, sites with low MAP may had received high UV radiation loads and thus had high decomposition rates. This study did not directly investigate any of these factors, and the effect of UV radiation could vary depending on the ecosystem, the plant species, and the soil microbial community composition, in particular of fungi (Gehrke *et al.*, 1995). Nevertheless, UV radiation might account for the higher than expected decomposition in Jornada ($\mathrm{MAP} = 298.1\,\mathrm{mm\,yr^{-1}}$ and $k = 0.276$), a site where direct radiation was high because of low vegetation cover. Here, macroarthropods (termites) might also have given rise to higher than expected leaf decomposition rates because they play an important role in leaf fragmentation that was shown to favor decomposition in deserts (Whitford *et al.*, 1981).

Initial litter quality emerged as the primary control on both leaf and root decomposition rates. Other studies have also shown the importance of litter quality on both leaf (Melillo *et al.*, 1982) and root decomposition (Silver & Miya, 2001). This stresses the importance of plant species traits that ultimately determine litter quality and drives litter decomposition (Cornwell *et al.*, 2008). Litter that is high in %L contains a large amount of decay-resistant carbon material and a relatively small proportion of easily decomposable compounds (Murphy *et al.*, 1998). Litter with greater amounts of %L will therefore decompose at relatively slower rates. Vinton & Burke (1997) suggested that litter quality was only important for biogeochemical cycling in wet grasslands. However, in this study litter quality was also important in dry grasslands that exhibited slower decomposition rates in litters with low (high %L) compared with high (low %L) quality. The predominant control of %L on decomposition suggests that increased temperatures in these grasslands might decrease decomposition indirectly through decreased litter quality, which was attributed to higher nutrient use efficiency under higher temperatures (Murphy *et al.*, 2002). This trend would likely enhance carbon storage under increased CO_2 scenarios.

Before concluding, it is important to point out that, despite other studies reporting home field advantage on litter decomposition (Gholz *et al.*, 2000; Wardle, 2006; Vivanco & Austin, 2008), the original experimental design of this study did not allow to test that hypothesis. Plant species might promote certain microbial communities and conditions that favor decomposition of their litter, and future studies should address the question by using native species' litter in order to predict litter decomposition more accurately in grasslands.

Conclusions

This study indicate that complex climate variables which combine moisture and temperature (i.e. CDI) to explain global scale root decomposition are not the main predictors of belowground decomposition of roots at the regional scale of central North American grasslands. Furthermore, this study showed the importance of differential impact of litter quality and precipitation on leaf and root decomposition. The influence of litter quality and precipitation on leaf and root decomposition, and the differences in controls between above- and belowground decomposition rates are particularly important because most of the current literature has focused on aboveground decomposition but grasslands have large belowground carbon inputs.

Models that predict litter decomposition in grasslands under global warming must account for %L as the main control on leaf and root decomposition and precipitation as the secondary control on root decomposition. The unexplained variation in aboveground decomposition suggests that other biotic and abiotic factors (i.e. macroarthropods, ultraviolet radiation) should be evaluated in future long-term studies and included in models to predict aboveground decomposition in grasslands.

Acknowledgements

This study was supported by grants from the NSF (DEB-0217631 SGS LTER, DEB-9108329, and DEB-9806493). These synthesis efforts were supported by the LTER Network Office, the Kaye and Ward Richardson Endowment, and the Bullard Fellowship of Harvard University. This work was conducted as part of the Decomposition working Group supported by NCEAS funded by the NSF (DEB-0072909), the UC at Santa Barbara, and the State of California. The authors received funding from the department of FRWS at CSU, from SGS LTER project (NSF Grant No. 0217631), from the CAE Station, Project #COL00650, and from NSF (DEB-0444880).

References

Aber JD, Melillo JM (1982) Nitrogen immobilization in decaying hardwood leaf litter as a function of initial nitrogen and lignin content. *Canadian Journal of Botany – Revue Canadienne De Botanique*, **60**, 2263–2269.

Aerts R (2006) The freezer defrosting: global warming and litter decomposition rates in cold biomes. *Journal of Ecology*, **94**, 713–724.

Allen RG, Pereira LS, Raes D, Smith M (1998) *Crop evapotranspiration: guidelines for computing crop requirements*.Irrigation Paper. FAO, Rome, Italy.

Austin A, Vivanco L (2006) Plant litter decomposition in a semiarid ecosystem controlled by photodegradation. *Nature*, **442**, 555–558.

Berg B, Johansson M, Meentemeyer V (2000) Litter decomposition in a transect of Norway spruce forests: substrate quality and climate control. *Canadian Journal of Botany – Revue Canadienne De Botanique*, **30**, 1136–1147.

Burke IC, Yonker CM, Parton WJ, Cole CV, Flach K, Schimel DS (1989) Texture, climate, and cultivation effects on soil organic-matter content in US grassland soils. *Soil Science Society of America Journal*, **53**, 800–805.

Cornwell WK, Cornelissen JHC, Amatangelo K *et al.* (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology letters*, **11**, 1065–1071.

Del Grosso SJ, Parton WJ, Mosier AR, Holland EA, Pendall E, Schimel DS, Ojima DS (2005) Modeling soil CO_2 emissions from ecosystems. *Biogeochemistry*, **73**, 71–91.

Epstein H, Burke I, Lauenroth W (2002) Regional patterns of decomposition and primary production rates in the US Great Plains. *Ecology*, **83**, 320–327.

Gehrke C, Johanson U, Callaghan TV, Chadwick D, Robinson CH (1995) The impact of enhanced ultraviolet-B radiation on litter quality and decomposition processes in Vaccinium leaves from the Subarctic. *Oikos*, **72**, 213–222.

Gholz H, Wedin D, Smitherman S, Harmon M, Parton W (2000) Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. *Global Change Biology*, **6**, 751–765.

Giardina CP, Ryan MG (2000) Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature*, **404**, 858–861.

Gill RA, Burke IC (2002) Influence of soil depth on the decomposition of *Bouteloua gracilis* roots in the shortgrass steppe. *Plant and Soil*, **241**, 233–242.

Hamadi Z, Steinberger Y, Kutiel P, Lavee H, Barness G (2000) Decomposition of *Avena sterilis* litter under arid conditions. *Journal of Arid Environments*, **46**, 281–293.

Hansen J, Russell G, Rind D *et al.* (1983) Efficient three-dimensional global models for climate studies: models I and II. *Monthly Weather Review*, **111**, 609–662.

Kirschbaum M (1995) The temperature-dependence of soil organic-matter decomposition, and the effect of global warming on soil organic-C storage. *Soil Biology and Biochemistry*, **27**, 753–760.

Lang GE, Forman RT (1978) Detrital dynamics in a mature oak forest – Hutcheson Memorial Forest, New Jersey. *Ecology*, **59**, 580–595.

Lauenroth WK, Epstein HE, Paruelo JM, Burke IC, Aguiar MR, Sala OE (2004) Potential effects of climate change on the temperate zones of North and South America. *Revista Chilena De Historia Natural*, **77**, 439–453.

Lauenroth WK, Sala OE (1992) Long-term forage production of North American shortgrass steppe. *Ecological Applications*, **2**, 397–403.

LIDET (Long-Term Intersite Decomposition Experiment Team) (1995) *Meeting the challenges of long-term, broad-scale ecological experiments*.Publication No. 19. U.S. LTER Network Office, Seattle, WA.

Liski J, Nissinen A, Erhard M, Taskinen O (2003) Climatic effects on litter decomposition from arctic tundra to tropical rainforest. *Global Change Biology*, **9**, 575–584.

Manabe S, Wetherald R (1987) Large-scale changes of soil wetness induced by an increase in atmospheric carbon dioxide. *Journal of the Atmospheric Sciences*, **44**, 1211–1235.

Meentemeyer V (1978) Macroclimate and lignin control of litter decomposition rates. *Ecology*, **59**, 465–472.

Melillo J, Aber J, Muratore J (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology*, **63**, 621–626.

Milchunas DG, Lauenroth WK (2001) Belowground primary production by carbon isotope decay and longterm root biomass dynamics. *Ecosystems*, **4**, 139–150.

Mokany K, Raison RJ, Prokushkin AS (2006) Critical analysis of root: shoot ratios in terrestrial biomes. *Global Change Biology*, **12**, 84–96.

Moore TR, Trofymow JA, Taylor B *et al.* (1999) Litter decomposition rates in Canadian forests. *Global Change Biology*, **5**, 75–82.

Murphy K, Burke I, Vinton M *et al.* (2002) Regional analysis of litter quality in the central grassland region of North America. *Journal of Vegetation Science*, **13**, 395–402.

Murphy KL, Klopatek JM, Klopatek CC (1998) The effects of litter quality and climate on decomposition along an elevational gradient. *Ecological Applications*, **8**, 1061–1071.

Olson JS (1963) Energy-storage and balance of producers and decomposers in ecological-systems. *Ecology*, **44**, 322–331.

Parton B (2007) *Effects of ultraviolet radiation on the early stages of litter decomposition in three contrasting grassland ecosystems*. ESA/SER Joint Meeting.

Parton WJ, Schimel DS, Ojima DS, Cole CV (1994) A general model for soil organic matter dynamics: sensitivity to litter chemistry, texture and management. In: *Quantitative Modeling of Soil Forming Processes* (eds Bryant RB, Arnold RW), pp. 147–167. SSSA Special Publication No. 39. Soil Science Society of America, Madison, WI.

Sala OE, Parton WJ, Joyce LA, Lauenroth WK (1988) Primary production of the central grassland region of the United States. *Ecology*, **69**, 40–45.

SAS Institute Inc. (1989) *SAS/STAT Guide for Personal Computers: Version 6 Edition*. SAS Institute, Inc., Cary, NC.

Silver W, Miya R (2001) Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia*, **129**, 407–419.

Vandermaarel E, Titlyanova A (1989) Above-ground and belowground biomass relations in steppes under different grazing conditions. *Oikos*, **56**, 364–370.

Vinton MA, Burke IC (1997) Contingent effects of plant species on soils along a regional moisture gradient in the Great Plains. *Oecologia*, **110**, 393–402.

Vivanco L, Austin AT (2008) Tree species identity alters forest litter decomposition through long-term plant and soil interactions in Patagonia, Argentina. *Journal of Ecology*, **96**, 727–736.

Wardle DA (2006) The influence of biotic interactions on soil biodiversity. *Ecology Letters*, **9**, 870–886.

White RP, Murray S, Rohweder M, Prince SD, Thompson KMJ (2000) *Grassland Ecosystems*. World Resources Institute, Washington, DC.

Whitford W, Meentemeyer V, Seastedt T *et al.* (1981) Exceptions to the AET model – deserts and clear-cut forest. *Ecology*, **62**, 275–277.

Wilson C, Mitchell J (1987) A doubled CO_2 climate sensitivity experiment with a global climate model including a simple ocean. *Journal of Geophysical Research – Atmospheres*, **92**, 13315–13343.

Yahdjian L, Sala O, Austin A (2006) Differential controls of water input on litter decomposition and nitrogen dynamics in the Patagonian steppe. *Ecosystems*, **9**, 128–141.