Experimental warming and clipping altered litter carbon and nitrogen dynamics in a tallgrass prairie

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ABSTRACT

Litter carbon (C) and nitrogen (N) dynamics are important processes in regulating C and N cycling in ecosystems. However, it is not well understood how global climate change and land use practice interactively affect litter C and N dynamics in ecosystems. We conducted a field experiment in a tallgrass prairie in Oklahoma, USA, to study effects of climate warming and clipping (as mimic of agricultural hay harvest) on litter C and N dynamics in association with litter production and decomposition of dominant species C_4 grass and C_3 forb. Warming did not significantly affect specific decomposition and N immobilization/mineralization rates of either species but increased C_4 and decreased C_3 litter production. Increased C_4 litter production, together with its intrinsic low decomposition, resulted in 16–47% increase in litter mass. Warming decreased N concentrations, litter N production, litter N pool and litter N output (i.e., litter N loss). Clipping significantly increased specific decomposition rates of C_4 litter but decreased litter production, litter mass and litter N contents. Our results suggest that indirect effects of climate change via shifts in plant species composition and decreases in litter quality are much more important than its direct effects on litter decomposition and subsequent C and N turnovers.

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1. Introduction

Global warming due to anthropogenic buildup of atmospheric CO_2 and other greenhouse gases has increased the earth's surface temperature by more than 0.74 °C over the past century and is predicted to increase by 1.1–6.4 °C over the period from 1990 to 2100 (IPCC, 2007). Meanwhile, land use practice results in net release of about 1.6 Pg of C to the atmosphere (Hougthton, 2007), enhancing climate warming. Global warming and associated land use practice are expected to significantly influence carbon (C) and nitrogen (N) cycling in terrestrial ecosystems (Luo, 2007; Parton et al., 2007; Chapin et al., 2008). As a key process of the ecosystem C and N cycles, litter decomposition can be considerably altered under global warming and land use practice (e.g., Quested et al., 2007; Chapin et al., 2008; Day et al., 2008). Decomposition of dead organic matter controls the release of nutrients (particularly, N) for plant growth as well as the C release to the atmosphere. Thus, potential changes in decomposition rates and associated C loss and N release and/or immobilization from litter under global change may have significant consequences for plant productivity and global C cycling (e.g., Aerts and De Caluwe, 1997; Cornelissen et al., 2007). Although impacts of climate warming and other environmental changes on litter production, decomposition, and quality have been examined (e.g., Hobbie, 1996; White et al., 2004; Quested et al., 2007; Day et al., 2008; Pleguezuelo et al., 2009), little effort has been made to quantitatively relate litter decomposition to C and N dynamics in litter pools at an ecosystem scale under warming and land use practice.

Here we focus on the consequences of warming and land use practice (clipping, as mimic of agricultural hay harvest) for litter decomposition processes related to litter C and N dynamics. Litter decomposition is strongly related to environmental parameters such as soil temperature and moisture as well as litter quality (e.g., litter N, C:N ratios) (e.g., Meentemeyer, 1978; Aerts, 2006). Climate warming can directly alter the soil environment, particularly soil temperature and moisture (Hobbie, 1996; Aerts, 2006). Alterations in soil temperature and moisture can affect litter decomposition rates at very short time-scales due to the high sensitivity of biological processes to temperature and water availability (Nadelhoffer et al., 1992; Aerts, 2006). Nadelhoffer et al. (1992), for example, have reported that increasing temperature can enhance litter decomposition rates directly by stimulating microbial activity. But

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decomposition rates could be hindered if litter moisture substantially declines with increased temperature (e.g., Shaw and Harte, 2001). At the same time, warming has been reported to decrease plant litter quality (Bontti et al., 2009) and alter plant species composition that has inherently different litter quality (Chapin et al., 1995; Shaw and Harte, 2001). Litter quality, in particular its initial litter N concentrations and C:N ratios or lignin:N ratios, often determines the litter decomposition rates and the N immobilization or N release from plant litter (Guo and Sims, 1999; Billings et al., 2003; Seneviratne, 2000; Tagliavini et al., 2007). The alterations in litter quality and species composition under warming thus will have indirect impacts on litter decomposition (Hobbie, 1996; Cornelissen et al., 2007). Changes in litter decomposition rates will probably affect litter C and N cycling rates, which may lead to appreciable changes in C and N pool at an ecosystem scale (Frederiksen et al., 2001; Aerts, 2006; Cornelissen et al., 2007; Pleguezuelo et al., 2009). Therefore, understanding the response of litter decomposition to climatic warming is critical for accurate prediction of long-term ecosystem C and N cycling in future climatic scenarios.

Land use practice also has great impact on terrestrial ecosystems, profoundly altering C and N cycles (e.g., Quested et al., 2007). Land practices that include biomass removal can significantly reduce aboveground net primary productivity (ANPP) (Luo et al., 2009) and plant C substrate input to soil (Wan and Luo, 2003), and also affect soil temperature and soil moisture (Wan et al., 2002; Klein et al., 2005). Thus, harvesting for hay, a major agricultural land management practice in the Southern Great Plains of the USA, may considerably affect the direct impacts of warming on litter decomposition, primarily through altering soil microclimate and community composition and structure. Although a few studies have reported effects of land use change on litter decomposition (e.g., Quested et al., 2007), little experimental evidence exists on how warming and land use practice interactively affect litter decomposition in association with litter C and N dynamics under future climatic conditions.

This study was designed to examine effects of climate warming and land use practice (clipping as mimic of agricultural hay harvest) on litter C and N dynamics in a tallgrass prairie. We took an advantage of a long term, ongoing experimental warming and clipping experiment in a tallgrass prairie, which was initiated on 21 November 1999 in Central Oklahoma, USA (Luo et al., 2001). Our previous studies in this field experiment have shown that warming caused (1) shifts towards more C_4-grass dominated plant community structure (Luo et al., 2009), (2) increase in aboveground biomass (Wan et al., 2005), and (3) increased the C/N ratios of litter (An et al., 2005). In this study, we build on our previous findings and assess whether decomposition rates of functional groups (C_3 an C_4) are useful for understanding changes in *in situ* ecosystem litter C and N dynamics under warming and clipping with a mix of new data and synthesis of published results. The specific objective of this work was to test the following hypotheses: (i) warming and clipping would increase/decrease litter decomposition not only directly via changes in soil microclimate, but also indirectly via changing litter quality and species composition, and (ii) warming and clipping would influence litter C and N dynamics by altering the balance between litter production and litter decomposition. We conducted a 2-year experiment to determine litter decomposition rates of two representative dominant species from the C_3 and C_4 functional groups (*Schizachyrium scoparium*, C_4 grass and *Ambrosia psilostachya*, C_3 forb) under warming and clipping from 2001 to 2003. Litter mass at the soil surface was measured in May 2003 and October 2006, respectively. Using published results (An et al., 2005; Luo et al., 2009) and unpublished data (Niu, unpublished data), we estimated effects of warming and clipping on litter N concentration, litter production and litter N production over a 6-year period

from 2001 to 2006. We also used the litter decomposition rates and litter input to estimate litter C and N pool and output (loss) at the ecosystem scale.

2. Materials and methods

2.1. Site description

The experiment was located at the Great Plain Apiaries (34°58′54″N, 97°31′14″W), 40 km from the Norman campus of the University of Oklahoma, USA. Detailed description of the site characteristics and design of the experiment have been reported elsewhere (see Luo et al., 2001; Wan et al., 2002). Briefly, the site is a tallgrass prairie primarily dominated by C_4 grasses including *S. scoparium* (Michx.) Nash-Gould, and *Sorghastrum nutans* (L.) Nash., and a few C_3 forbs, including *A. psilostachya* DC., *Hemiachyris dracunuloides*, *Solidago rigida*, *Solidago nemoralis*, and *Aster ontarionis* Wieg. *S. scoparium* comprise over 80% of the cover and *A. psilostachya* was the most dominant C_3 forb in this community. Mean annual temperature is 16.0 °C with monthly mean temperature of 3.1 °C in January and 28.0 °C in July. Mean annual precipitation is 911.4 mm (Oklahoma Meteorological Survey). The soil is part of the Nash–Lucien complex, which is characterized by a low permeability, high available water capacity, and deep, moderately penetrable root zone (USDA Soil Conservation Service and Oklahoma Agricultural Experiment Station, 1963).

2.2. Experimental design

This experiment used a paired factorial design with warming as the main factor nested by clipping factor. Each treatment had five replicates (i.e., five pairs). Each pair had two plots of 2 m × 2 m. One plot had been subjected to continuous warming since 12 November 1999 to present while the other was the control with ambient temperature. One 165 cm × 15 cm radiant infrared heater (Kalglo Electronics Inc., Bethlehem, PA, USA) with an output of 100 W m^{-2} was suspended at 1.5 m above the ground in each warmed plot as the heating device. Reflector surface of the heaters were adjusted so as to generate evenly distributed radiant input to soil surface (Kimball, 2005). As a result, temperature increments generated by the infrared heaters were relatively even over the entire areas of plots and similar at different soil depths (Wan et al., 2002). A "dummy heater" with the same shape and size as the infrared heater was suspended at the same height in the control plots to simulate the shading effect of the heater on the plant canopy. For each paired plot, the distance between warmed and control plots was approximately 5 m to avoid heating of the control plots. The distance between the paired plots varied from 20 to 60 m.

Each 2 m × 2 m plot was divided into four 1 m × 1 m subplots. Plants in the two diagonal subplots were clipped at the height of 10 cm above the ground yearly to remove biomass, usually in August. Clipping in manner effectively mimics agricultural hay mowing, a widely practiced land use in the southern Great Plains. Usually farmers and ranchers in the southern Great Plains mow pasture once or twice per year, depending on rainfall. Clipping also simulates biomass harvest for biofuel feedstock production although the study was not originally designed to study bioenergy production. The other two diagonal subplots were unclipped. The four treatments in the experiment were unclipped control (UC), clipped control (CC), unclipped warming (UW), and clipped warming (CW).

2.3. Soil temperature and moisture

Soil temperature was measured using thermocouples installed at the depth of 2.5 cm at the centers of one clipped and one

unclipped subplot in each plot. All the thermocouples were connected to a CR10 datalogger (Campbell Scientific Inc., Utah, US). Soil temperature was measured every ten minutes, and then averages within one hour were stored in an SM196 Storage Module (Campbell Scientific Inc., Utah, US). In addition, soil temperature at the depth of 5 cm was measured twice a month using a thermocouple connected to Li-Cor 6400 (Luo et al., 2001) at the same time as soil moisture (% volumetric) at 0–15 cm was measured using Time Domain Reflectometry (Soilmoisture Equipment Corp., Santa Barbara, CA).

2.4. Litter decomposition

Litter decomposition was measured using the litter-bag method. The most dominant C_4 grass, *S. scoparium*, and the most dominant C_3 forb, *A. psilostachya*, were chosen to represent two types of litter materials in the ecosystem. Because the major input of aboveground litter on annual basis is leaf litter, we only collected the dead standing leaf samples of *S. scoparium* and *A. psilostachya* grown under ambient temperature conditions out of but very close to the plots in February 2001. Before filling the bags with litter, all the litter material was air-dried at room temperature to constant weight. The moisture content of the litter was measured to calibrate the dry weight of the litter material from air-dried to oven-dried weight before filling the bags.

The litter bags were made of fiberglass mesh (1.5 mm × 1.0 mm). This mesh size could allow most fungi, bacteria, and soil organisms to colonize the detritus but exclude larger organisms such as isopods and earthworms (Swift et al., 1979). One 15 cm × 20 cm bag was sewed into two halves, one half for *S. scoparium* sample (5 g), another half for *A. psilostachya* sample (4 g). The initial weights of litter-bag contents were recorded for future use. On 1 June 2001, the litter bags for *S. scoparium* and *A. psilostachya* were anchored on the soil surface with iron wire to make sure of complete contact between the litter bags and the surface soil. In each of the four subplots within one plot, we placed 3 bags of *S. scoparium* and *A. psilostachya* litter on the soil surface. We had a total of 120 bags (10 plots × 4 subplots × 3 bags) of *S. scoparium* and *A. psilostachya* litter in these plots, i.e., 30 litter bags of each species for each treatment. We measured 6 times after 2, 4, 8, 12, 17 and 24 months of decomposition on 1 August 2001, 3 October 2001, 3 February 2002, 3 June 2002, 6 November 2002, and 2 June 2003, respectively. We retrieved five litter bags from each treatment each time.

After the litter bags were collected, they were gently scraped to remove surface debris, dried at 65 °C for 48 h, and then brushed lightly to remove remaining debris. Mass of each litter-bag content was measured. After weighing, subsamples of the initial litter material for each litter type were milled, and sent to the Water and Forage Analytical Laboratory of the Oklahoma State University (WFAL-OSU) for analysis of C and N concentration. Litter C concentration was determined using a dry combustion carbon analyzer (Nelson and Sommers, 1996), and N concentration using a dry combustion Nitrogen Analyzer (LECO 428, National Forage Testing Association, 1993). In addition, the lignin content of the initial litter materials was analyzed for the acid-insoluble C fraction using the methods formulated by the Association of Official Analytical Chemists (Association of Official Analytical Chemists, 1990) in A&L laboratories, Inc. (Memphis, TN).

Specific decomposition rates (k) were determined by fitting an exponential function to data of mass remaining at different times of decomposition measurements (Weider and Lang, 1982) as:

$$\ln\left(\frac{M_t}{M_0}\right) = -kt + c \tag{1}$$

where M_t is the mass remaining at time t, M_0 is the initial mass, t is the time in years, k is the decay constant, c is the intercept of the

regression and is constrained between 95% and 105% (Harmon et al., 2009). This model was used to calculate one specific decomposition rate, k, for each species under each treatment. The residence time (RT) of litter remaining in the litter pool is $1/k$.

2.5. Litter mass, estimated carbon and nitrogen input and loss from litter pool

Litter mass on the soil surface of the same experimental plots was collected on 2 June 2003 and 4 April 2006. Collected litter was separated into C_3 and C_4 species according to morphological traits. The separated C_3 and C_4 litter materials were cleaned with a soft brush in the laboratory before oven-dried at 65 °C to constant weight and then weighed. After a small fraction of litter materials were used for chemical analysis, the majority of litter was returned to plots to minimize disturbance on the biogeochemical cycles.

To estimate annual litter C and N dynamics in association with litter production and litter decomposition rates, we estimated carbon input into the litter pool from both C_3 and C_4 plant debris (i.e., C_3 and C_4 litter production). The annual litter production in the unclipped (UC and UW) plots was estimated from peak aboveground biomass (AGB) in summer (July or August), which represent the annual aboveground net primary production according to primary criteria of virtually no carryover of living biomass from previous year due to a distinct dormant season and negligible decomposition of biomass produced during the growing season (Knapp et al., 2007). Peak biomass in the clipped (CC and CW) plots was removed from the ecosystem and could not be considered as litter input to the soil surface. Instead, the annual litter production was estimated from AGB in autumn since the virtually annual litter input in clipped plots was the plant re-growth following the clipping at peak biomass. AGB of C_3 and C_4 plants in both the unclipped and the clipped plots was estimated by a pin-frame method (Frank and McNaughton, 1990; McNaughton et al., 1996) and described in detail by Luo et al. (2009). In this study, we used an average of AGB of C_3 and C_4 plants from 2001 to 2006 times their respective carbon concentrations as estimated carbon input of C_3 and C_4 litter to the ecosystem. The estimated annual litter C pool size was the sum of C_3 and C_4 litters, which were products of their respective annual litter inputs and their residence times ($1/k$), assuming that all other of C_3 forbs and C_4 grasses have the same decay rates as our study C_3 forb and C_4 grass. The estimated annual litter losses of C_3 and C_4 litter were calculated by the amounts of C_3 and C_4 litters in the litter input pool times their respective annual rates of decomposition (k).

The estimated annual litter N input into the ecosystem was estimated by annual litter C input divided by C:N ratio of senescent plant materials. The estimated annual litter N pool was estimated by annual litter C pool divided by litter C:N ratio. The estimated annual litter N output (i.e., annual litter loss) was calculated as: estimated annual litter C loss/litter C:N ratio. C and N concentrations of senescent leaf of C_3 and C_4 plants in clipped plots were analyzed at WFAL-OSU with a LECO CXS-200 Elemental Analyzer (LECO Corp., St Joseph, MI, USA) after they were oven-dried at 65 °C for 48 h. As the unclipped subplots were designed to have minimal disturbances over the long term, no plant materials were taken from the unclipped plots.

2.6. Statistical analyses

Analysis of variance (ANOVA) of paired plot design (one pair of plots being considered a block) was used to examine the statistical significance of warming, clipping, time, and their interactive effects on the overall mass remaining percentages, decomposition rates (k), N remaining percentages, average soil temperature and soil moisture, litter C concentrations and C:N ratios, litter C input, litter
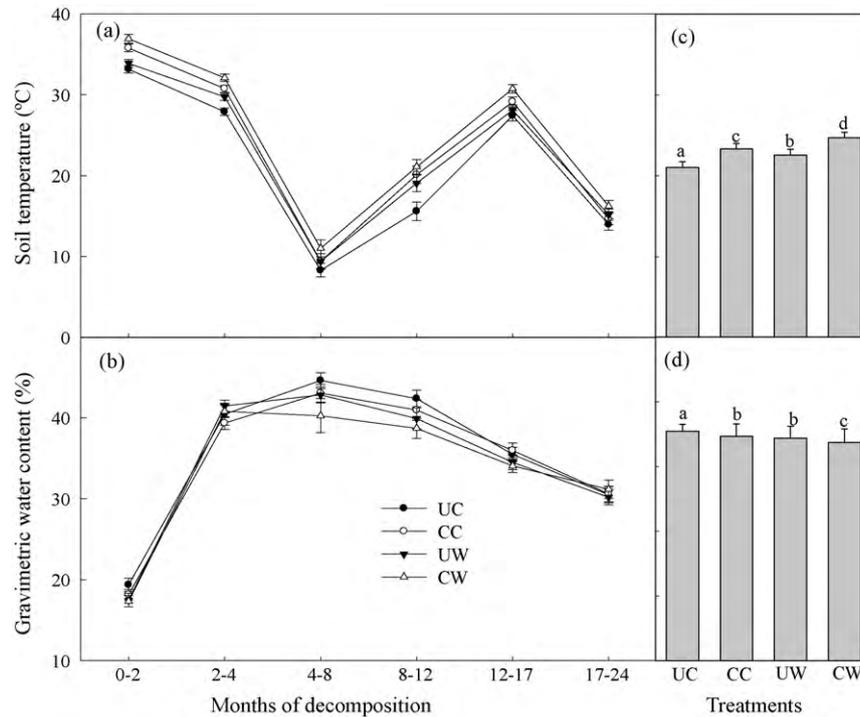
Fig. 1. The temporal variations of soil temperature (a) and soil moisture (b), and average soil temperature (c) and soil moisture (d) (mean ± SE) under four treatments. Letters a–d indicate statistical significance at P < 0.05 among the four treatments. *Abbreviations*: UC, unclipped control; CC, clipped control; UW, unclipped warming; CW, clipped warming.

Table 1
The initial litter chemical properties of the two representative dominant C₄ species (*S. scoparium*) and C₃ species (*A. psilostachya*).

Litter type	Total C (%)	Total N (%)	C:N ratio	Lignin (%)	Lignin:N ratio
C$_4$ (*S. scoparium*)	48.10 ± 0.38ᵃ	0.35 ± 0.01ᵇ	139.6 ± 4.3ᵃ	13.4 ± 1.0ᵃ	38.5 ± 2.1ᵃ
C$_3$ (*A. psilostachya*)	47.77 ± 0.40ᵃ	0.77 ± 0.02ᵃ	62.3 ± 1.2ᵇ	15.6 ± 0.7ᵃ	20.4 ± 1.1ᵇ

Values are mean (n = 5) with standard error. Different suffixes indicate significant differences among treatments (one-way ANOVA, P < 0.05).

C pool, litter C output, litter N input, litter N pool, litter N output, and litter mass. The differences in senescent leaf N concentrations and C:N ratios between warmed and control plots of each species, and the differences in initial litter C and N concentrations between the two litter types were analyzed using one-way ANOVA. All the statistical analyses were carried out with SAS software package (SAS Institute, Cary, NC).

3. Results

3.1. Soil microclimate

Warming and clipping altered soil temperature and moisture during the 2 years decomposition. On average, clipping, warming and clipping plus warming increased soil temperature by average 2.25, 1.52, and 3.62 °C, respectively, in comparison with the control (Fig. 1a and c). Clipping, warming and clipping plus warming

decreased soil moistures by average 2.2, 3.1, and 5.1% compared with the control, respectively (Fig. 1b and d).

3.2. Initial litter quality and changes in senescent leaf N and litter N concentrations

The initial litter quality of the 2 standard litter types differed significantly (P < 0.05) (Table 1). The carbon concentrations were not significantly different between the two litter types whereas the N concentration of *S. scoparium* (0.35%) was significantly lower than that of *A. psilostachya* (0.77%). Accordingly, C:N ratio of *S. scoparium* was significantly higher than that of *A. psilostachya*. There were no significant differences in lignin concentration between *S. scoparium* and *A. psilostachya*. However, lignin:N ratio of *S. scoparium* was significantly higher than *A. psilostachya*. Overall, warming significantly decreased N concentration in senescent leaf of C₃ and C₄ species on average data over 6 years from 2001 to 2006, whereas warming sig-

Table 2
The N concentrations in senescent leaf and litter of C₃ and C₄ species under four treatments.

Variable	Species	UC	UW	CC	CW
Senescent leaf N (%)	C$_4$	–	–	0.45 ± 0.04ᵃ	0.41 ± 0.05ᵇ
	C$_3$	–	–	1.15 ± 0.15ᵃ	1.04 ± 0.13ᵇ
Litter N (%)	C$_4$	0.62 ± 0.1ᵃ	0.53 ± 0.08ᵇ	0.70 ± 0.12ᵃ	0.57 + 0.09ᵃ
	C$_3$	0.65 ± 0.12ᵃ	0.54 ± 0.2ᵃ	0.71 ± 0.15ᵃ	0.63 ± 0.07ᵃ

UC, unclipped control; CC, clipped control; UW, unclipped warming; CW, clipped warming. Data are expressed as mean ± SE. Suffixes a, b and c indicate statistical significance at P < 0.05 among the treatments.
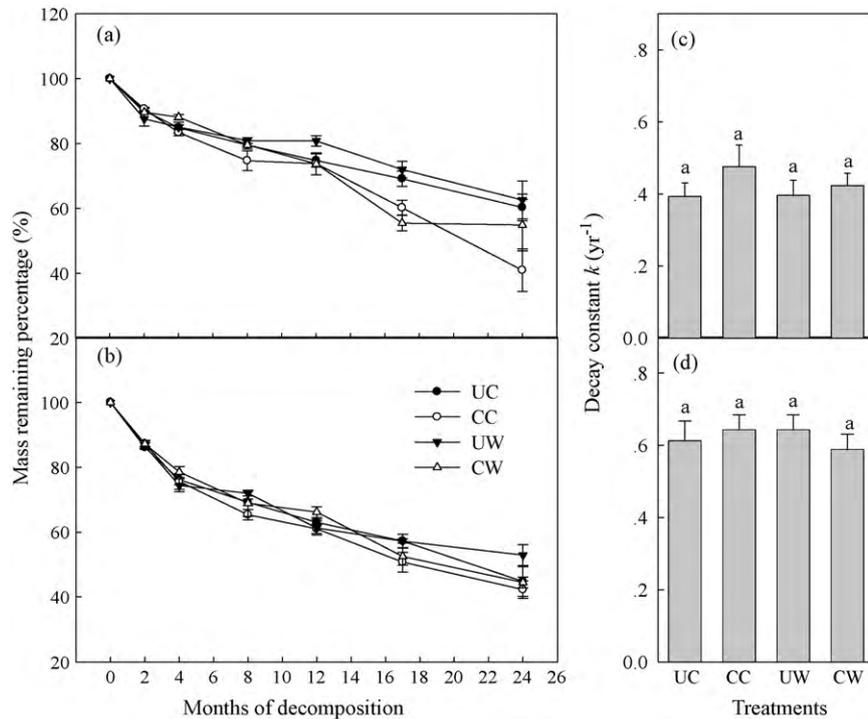
Fig. 2. The mass remaining percentages of C_4 (*S. scoparium*, a) and C_3 (*A. psilostachya*, b), and average decay constant (k) values of C_4 (*S. scoparium*, c) and C_3 (*A. psilostachya*, d) (mean ± SE) under four treatments during 2-year decomposition. Letters a–d indicate statistical significance at $P < 0.05$ among the four treatments. See Fig. 1 for abbreviations.

nificantly decreased litter N concentration of C_4 species ($P < 0.05$; Table 2).

3.3. Litter decomposition rates

The interactive effects of warming and clipping on litter decomposition were significant for *S. scoparium* during the 2 years of study ($P = 0.007$; $F_{3,6} = 26.8$; Fig. 2a and c), but not for *A. psilostachya* ($P = 0.056$; $F_{9,34} = 2.1$; Fig. 2b and d). Warming did not significantly affect litter decomposition of either species ($P > 0.05$) during 2 years of decomposition (Fig. 2). Clipping significantly increased decomposition of C_4 (*S. scoparium*) litter ($P < 0.01$; Fig. 2a and c), but not for C_3 (*A. psilostachya*) litter ($P > 0.05$; Fig. 2b and d).

Litter decomposition rates differed significantly between C_3 and C_4 litter types ($P = 0.00001$; $F_{6,27} = 14.8$; Fig. 2). The decomposition rate of *S. scoparium* litter was significantly lower than that of *A. psilostachya* ($P < 0.0001$; Fig. 2a vs. b). Accordingly, the decay constant k of *A. psilostachya* (0.59–0.64 year^{-1}) was generally higher than that of *S. scoparium* (0.39–0.48 year^{-1}) ($P < 0.0001$; Fig. 2c vs. d).

3.4. Nitrogen immobilization and mineralization during decomposition

Neither warming nor clipping significantly affected net N immobilization or mineralization as indicated by the N remaining percentages for either species during 2 years of decomposition ($P = 0.24$; $F_{36,121} = 1.19$; Fig. 3). However, two litter types differed significantly in their timing and patterns of net N immobilization and mineralization during the 2 years of decomposition study ($P = 0.003$; $F_{6,27} = 14.4$). C_4 (*S. scoparium*) leaf litter did not release any N during the 2 years of decomposition whereas C_3 (*A. psilostachya*) released about 30% of their original N concentrations in the 4th month of decomposition (Fig. 3). The final N remaining percentage of *S. scoparium* (170–250%) was much higher than those of *A. psilostachya* (120–160%).
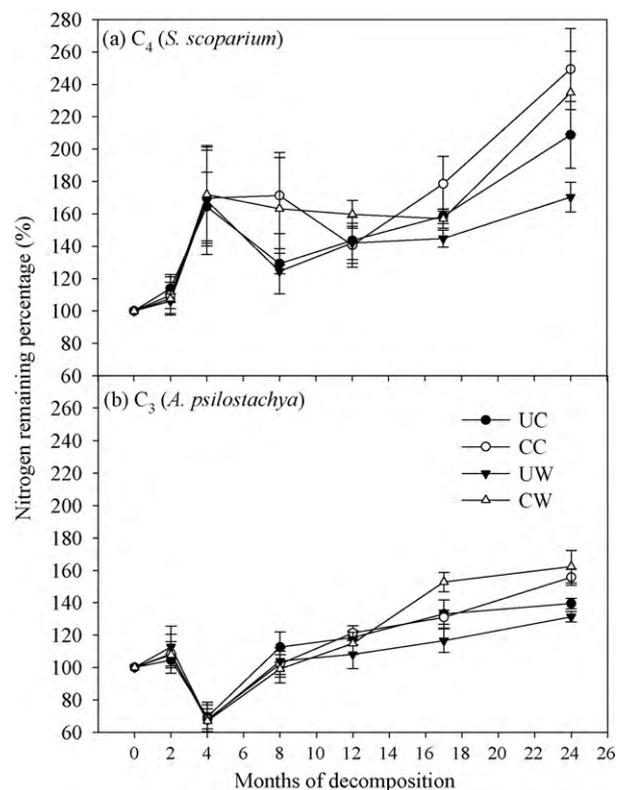
Fig. 3. The N remaining percentages (mean ± SE) of *S. scoparium* (a) and *A. psilostachya* (b) under four treatments during 2-year decomposition. See Fig. 1 for notes and abbreviations.

3.5. Litter mass, estimated carbon and nitrogen cycling in litter pool

Warming increased total litter mass by 22% without clipping and 69% with clipping, whereas clipping decreased total litter mass by 81% without warming and 74% with warming based on average on data over 2003 and 2006 (Fig. 4).

Estimated C input into the litter pool was $53 \pm 5\,\mathrm{g\,C\,m^{-2}\,year^{-1}}$ from C_3 plants and $192 \pm 16\,\mathrm{g\,C\,m^{-2}\,year^{-1}}$ from C_4 plants in the control plots. Warming increased the estimated total annual litter C pool by 12% without clipping ($P < 0.05$) and 28.2% with clipping ($P < 0.05$) on average of data over 6 years (Fig. 5). The increases in litter C pool under warming resulted from larger warming-induced increment by 22% in C_4 litter input than C_4 litter output (15%), although warming decreased C_3 litter input and output on average of data over 6 years (Fig. 5). Clipping significantly decreased estimated annual litter C input, litter C pool and annual litter C output by average 68% ($P < 0.05$; Fig. 5).

Warming resulted in no significant increases in the estimated C_4 litter N input and output, whereas warming significantly decreased C_3 litter N input and output (Fig. 6). As a consequence, warming significantly decreased estimated litter N pool in the unclipped plots (Fig. 6). Clipping significantly decreased estimated annual litter N input, litter N pool and litter N output by average 34–67% (Fig. 6).

4. Discussion

4.1. Effects of climate warming and clipping on litter decomposition rates

Experimental warming in our study did not significantly affect specific decomposition rates of either C_3 or C_4 litters (Fig. 2), probably due to counteracting effects of temperature and moisture (Fig. 1). Although increased temperature under climate warming may accelerate litter decomposition at a given soil moisture (e.g., Hobbie, 1996; Shaw and Harte, 2001), warming also decreased soil moisture, which strongly depress soil microbial activity (Griffin,
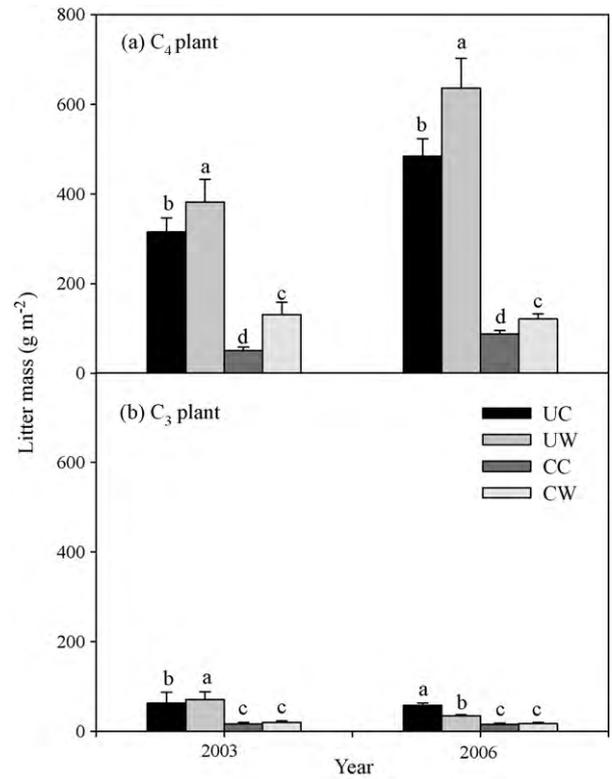
Fig. 4. C_4 and C_3 plant litter mass (mean ± SE) under four treatments in 2003 and 2006. See Fig. 1 for notes and abbreviations. Letters a–d indicate statistical significance at $P < 0.05$ of each species among the four treatments.

1981; Shaw and Harte, 2001). In the present study, the decreases in soil moisture by 2–5% volumetrically under warming may depress litter decomposition and thus offset the potential stimulating litter decomposition by warming (Figs. 1 and 2), leading to little changes in decomposition rates. Similar to our study, other studies
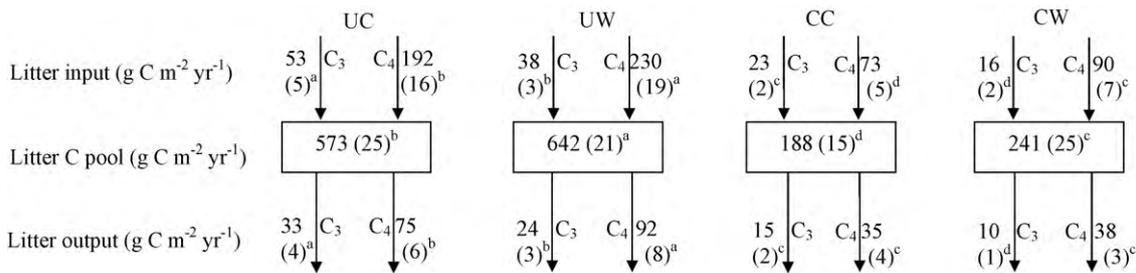
Fig. 5. Effects of warming and clipping on litter input, litter pool and litter loss on average over 6 years from 2001 to 2006. *Notes*: Values are mean ($n = 6$) with standard error (in parentheses). Letters a–d indicate statistical significance at $P < 0.05$ of each species among the four treatments. See Fig. 1 for abbreviations.
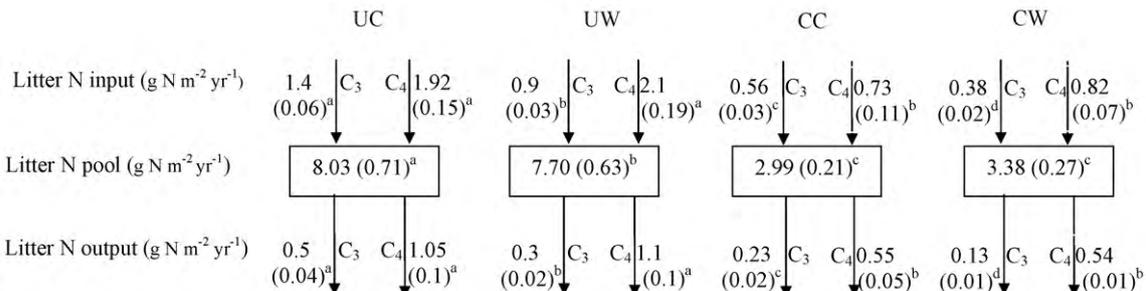
Fig. 6. Effects of warming and clipping on litter N input, litter N pool and litter N loss on average over 6 years from 2001 to 2006. *Notes*: Values are mean ($n = 6$) with standard error (in parentheses). Letters a–d indicate statistical significance at $P < 0.05$ of each species among the four treatments. See Fig. 1 for abbreviations.

have reported that the litter decomposition rates were lower under soil warming than under control in dry habitats and dry seasons, because the decreased soil moisture offset the effect of increased temperature on decomposition (e.g., Shaw and Harte, 2001; O'Neill et al., 2003).

Despite no warming effects, clipping significantly increased decomposition rates of C_4 (*S. scoparium*) litter (Fig. 2a). Previous studies found that the degree to which soil microclimate controls litter decomposition rates depends on litter quality and the degree of climatic variability and severity (e.g., Fierer et al., 2005). The clipping caused higher soil temperature compared to warming, and reduced substrate input to soil microbes (Wan and Luo, 2003) which may have caused soil microbes to be more active in exploring new substrates (litter) on the soil surface. Thus, our results suggested that climate warming by about 1 °C might not be warm enough to cause dramatic difference in litter decomposition due to the moisture offset effects during dry seasons, whereas reduction in plant C substrate input to soil and higher temperature (about 2–3 °C) caused by clipping may substantially increase C_4 litter decomposition.

Climatic warming can also indirectly affect litter decomposition by altering litter quality and species composition (e.g., Aerts, 2006). The litter quality and in particular initial litter N concentrations appear to control the decomposition rates (Aerts, 1997; Parton et al., 2007). Litter with higher N concentrations and lower C:N ratios or lignin:N ratios usually decompose faster (Köchy and Wilson, 1997; Aerts et al., 2006; Vargas et al., 2006). Thus, the decomposition rate of a C_4 litter species ($k = 0.39–0.48\,year^{-1}$) was lower than that of a C_3 species ($k = 0.59–0.64\,year^{-1}$) (Table 1; Fig. 2). The shifts of species from C_3 to C_4 species (Fig. 4; Wan et al., 2005; Luo et al., 2009), together with the decreased N concentrations of plant senescent leaf and litter (Table 2; An et al., 2005) will probably result in overall low litter quality and decomposability under climate warming at ecosystem scale in long term.

4.2. Ecosystem carbon and nitrogen dynamics in litter pool

Warming-induced changes in community composition and structure can strongly alter the ratio of litter accumulation vs. decomposition, and hence influence C and N dynamics at the ecosystem level (Figs. 5 and 6; Dorrepaal et al., 2005; Aerts et al., 2006; Cornelissen et al., 2007). Studies conducted in the same experiment have found that warming has induced strong shifts in plant functional types with increased C_4 grasses and decreased C_3 forbs (Wan et al., 2005; Luo et al., 2009). These shifts in plant growth under warming resulted in increased production of C_4 litter with low quality and decreased production of C_3 litter with high quality (An et al., 2005; Table 1), leading to reduced decomposition of bulk litter at the ecosystem scale (Fig. 4). Indeed, warming increased litter mass of C_4 plants at the soil surface by average 47.2% (Fig. 4a) and decreased litter mass of C_3 plants by average 19.1% (Fig. 4b). This result might reflect differences in the litter decomposition rates of two functional groups (Fig. 2). The C_4 species with lower N concentrations were more recalcitrant to decomposition, leading to a buildup of litter, whereas the C_3 species decomposed more quickly, resulting in less litter accumulation. Because C_4 species is a major component of aboveground litter in the tallgrass prairie (Wan et al., 2005; Luo et al., 2009), warming increased C_4 litter input (22%) more than C_4 litter output (15%) (Fig. 5), leading to average 47% increase in bulk litter mass at the soil surface in comparison with that in the control plots (Fig. 4).

Although litter N immobilization rates of the two litter types during the 2 years of decomposition study were not affected by warming and clipping, C_4 litter, which had initial lower N concentration (Table 1), immobilized much more N than C_3 litter (Fig. 3). This finding was consistent with general findings among studies

that litter of low initial litter N concentration usually immobilized more N from soil into litter (Aerts and De Caluwe, 1997; Curtis et al., 2005; Aerts et al., 2006; Zhang et al., 2008). Warming-induced increases in C_4 litter production together with high N immobilization of C_4 litter during decomposition (Figs. 3 and 4) presumably resulted in N accumulation and/or immobilization in litter pool under warming (An et al., 2005).

However, the litter N pool is regulated not only by litter decomposition rates but also by changes in the litter N concentrations (e.g., Billings et al., 2003; An et al., 2005). We found warming significantly decreased the whole litter N pool in the unclipped plots (Fig. 6), probably because warming-induced decreases in litter N concentrations overshadowed any enhancement in litter mass (Table 2; Fig. 5). Similarly, warming significantly decreased the whole ecosystem litter N input and output (i.e., loss) (Fig. 6). Being consistent with previous studies (Rustad et al., 2001; An et al., 2005), our results indicated that warming-induced decreases in litter N pool and flux rates could slow N releases from litter pool to soil available N pool. Indeed, warming decreased the total soil N content by 14% compared with the control plots without clipping (Niu, unpublished data). The decrease in soil N content may result partly from the redistribution of N between plant and soil pools and partly from increased plant N use efficiencies in C_4 species (An et al., 2005) resulting in soil N losses under warming. Thus, we suggested that soil N availability from litter in a tallgrass prairie could be a limiting factor for plant growth and hence could potentially affect ecosystem production in the further greenhouse warming.

Land use practice (clipping) was proposed to affect terrestrial ecosystems and profoundly alters C and N cycles and feedback to climatic change (Luo et al., 2009). The increased litter N concentrations of both species under clipping (Table 2) indicated that clipping might lead to higher litter quality and accelerate litter decomposition. Reduced litter production (Fig. 5) combined with increased C_4 litter decomposition rates (Fig. 2) significantly decreased litter C and N pool by an average of 77.9%, and 75.5% in warmed and unwarmed plots, respectively, over the 6 years (Figs. 5 and 6). Decreases in litter C and N contents under clipping for hay harvest in the Southern Great Plains of the USA would decrease C and N input into soil (Luo et al., 2009) and hence potentially affects terrestrial production and C cycling.

5. Conclusion

To our knowledge, this is the first study to relate the effects of warming and land use practice (clipping, as mimic of agricultural hay harvest) on litter decomposition to litter C and N dynamics in a tallgrass prairie. Although warming did not directly affect litter decomposition of either species, warming significantly enhanced total litter mass by increasing annual C_4 (*S. scoparium*) litter (low decomposition rate) input and decreasing annual C_3 (*A. psilostachya*) litter (high decomposition rate) input. Warming decreased litter N input and litter N pool, possibly because warming-induced decreases in N concentrations in senescent leaf and litter likely overshadowed any enhancements in litter production and litter mass. Warming also significantly decreased the whole ecosystem litter N release, due to largely decreased C_3 litter N loss. Clipping-induced decreases in litter input plus increases in C_4 litter decomposition rate significantly decreased litter C and N pool in warmed and unwarmed plots. Thus, our results highlighted the fact that changes in species composition driven by global change may strongly control litter decomposition and production and its subsequent C and N cycling in terrestrial ecosystems (e.g., Hobbie, 1996; Shaw and Harte, 2001; Vivanco and Austin, 2006). Finally, we acknowledged that the plant–air water vapor pressure gradients (VPGs) problem identified for infrared heating

of experimental plots might not sufficiently address the possible global warming effects on terrestrial ecosystems (Kimball, 2005). To predict the effects of global warming on ecosystem processes, we need use models to correct VPGs problem to project future changes in ecosystem C and N cycles in response to multifactor global change.

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References

Aerts, R., De Caluwe, H., 1997. Nutritional and plant-mediated controls on leaf decomposition of *Carex* species. Ecology 78, 244–260.

Aerts, R., 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79, 439–449.

Aerts, R., 2006. The freezer defrosting: global warming and litter decomposition rates in cold biomes. J. Ecol. 94, 713–724.

Aerts, R., van Logtestijn, R.S.P., Karlsson, P.S., 2006. Nitrogen supply differentially affects litter decomposition rates and nitrogen dynamics of sub-arctic bog species. Oecologia 146, 652–658.

An, Y., Wan, S., Zhou, X., Subedar, A., Wallace, L.L., Luo, Y., 2005. Plant nitrogen concentration, use efficiency, and contents in a tallgrass prairie ecosystem under experimental warming. Global Change Biol. 11, 1733–1744.

Billings, S.A., Zitzer, S.F., Weatherly, H., Schatter, S.M., Charlet, T., Arnone III, J.A., Evans, R.D., 2003. Effects of elevated carbon dioxide on green leaf tissue and leaf litter quality in an intact Mojave Desert ecosystem. Global Change Biol. 9, 729–735.

Bontti, E.E., Decant, J.P., Munson, S., Gathany, M.A., Przeszlowska, A., Haddix, M.L., Owens, S., Burke, I.C., Parton, W.J., Harmon, A.E., 2009. Litter decomposition in grasslands of Central North America (US Plains). Global Change Biol. 15, 1356–1363.

Chapin, F.S., Shaver, G.R., Giblin, A.E., Nadelhoffer, K.G., Laundre, J.A., 1995. Response of arctic tundra to experimental and observed changes in climate. Ecology 76, 694–711.

Chapin, F.S., Randerson, J.T., McGuire, A.D., Foley, J.A., Field, C.B., 2008. Changing feedbacks in the climate–biosphere system. Front. Ecol. Environ. 6, 313–320.

Cornelissen, J.H.C., van Callaghan, P.M., Aerts, R., Callaghan, T.V., van Logtestijn, R.S.P., Alatalo, J., Chapin, F.S., Gerdol, R., Gudmundsson, J., Gwynn-Jones, D., Hartley, A.E., Hik, D.S., Hofgaard, A., Jónsdóttir, I.S., Karlsson, S., Klein, J.A., Laundre, J., Magnusson, B., Michelsen, A., Molau, U., Onipchenko, V.G., Quested, H.M., Sandvik, S.M., Schmidt, I.K., Shaver, G.R., Solheim, B., Soudzilovskaia, N.A., Stenström, A., Tolvanen, A., Totland, Ø., Wada, N., Welker, J.M., Zhao, X., Team, M.O.L., 2007. Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. Ecol. Lett. 10, 619–627.

Curtis, C.J., Emmett, B.A., Grant, H., Kernan, M., Reynolds, B., Shilland, E., 2005. Nitrogen saturation in UK moorlands: the critical role of bryophytes and lichens in determining retention of atmospheric N deposition. J. Appl. Ecol. 42, 507–517.

Day, T.A., Ruhland, C.T., Xiong, F.S., 2008. Warming increases aboveground plant biomass and C stocks in vascular-plant-dominated Antarctic Tundra. Global Change Biol. 14, 1827–1843.

Dorrepaal, E., Cornelissen, J.H.C., Aerts, R., Wallén, B., van Logtesijn, R.S.P., 2005. Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient? J. Ecol. 93, 817–828.

Fierer, N., Craine, J.M., Mclauchlan, K., Schimel, J.P., 2005. Litter quality and the temperature sensitivity of decomposition. Ecology 86, 320–326.

Frank, D.A., McNaughton, S.J., 1990. Above-ground biomass estimation with the canopy intercept method—a plant-growth form caveat. Oikos 57, 57–60.

Frederiksen, H., Rønn, R., Chriatensen, S., 2001. Effect of elevated atmospheric CO_2 and vegetation type on microbiota associated with decomposition straw. Global Change Biol. 7, 313–321.

Griffin, D.M., 1981. Water and microbial stress. In: Alexander, M. (Ed.), Advances in Microbial Ecology. Plenum, New York, USA, pp. 91–136.

Guo, L.B., Sims, R.E.H., 1999. Litter decomposition and nutrient release via litter decomposition in New Zealand eucalypt short rotation forests. Agric. Ecosyst. Environ. 75, 133–140.

Harmon, M.E., Silver, W.L., Fasth, B., Chen, H., Burke, I.C., Parton, W.J., Hart, S.C., Currie, W.S., LIDET, 2009. Long-term patterns of mass loss during the decomposition of leaf and fine root litter: an intersite comparison. Global Change Biol. 15, 1320–1338.

Hobbie, S.E., 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. Ecol. Monogr. 66, 503–522.

Houghthon, R.A., 2007. Balancing the global carbon budget. Annu. Rev. Earth Planet. Sci. 35, 313–347.

Klein, J.A., Harte, J., Zhao, X.Q., 2005. Dynamic and complex microclimate responses to warming and grazing manipulations. Global Change Biol. 11, 1440–1451.

Kimball, B.A., 2005. Theory and performance of an infrared heater for ecosystem warming. Global Change Biol. 11, 2041–2056.

Knapp, A.K., Briggs, J.M., Childers, D.L., Sala, O.E., 2007. Estimating aboveground net primary production in grass-and herbaceous-dominated ecosystems. In: Fahry, T.J., Knaoo, A.K. (Eds.), Principles and Standards for Measuring Primary Production. Oxford University Press, Oxford, pp. 27–48.

Köchy, M., Wilson, S.D., 1997. Litter decomposition and nitrogen dynamics in aspen forest and mixed-grass prairie. Ecology 78, 732–739.

IPCC, 2007. Climate Change 2007: The Scientific Basis. Cambridge University Press, New York, USA.

Luo, Y., Wan, S., Hui, D., Wallace, L.L., 2001. Acclimatization of soil respiration to warming in tallgrass prairie. Nature 413, 622–625.

Luo, Y., 2007. Terrestrial carbon—cycle feedback to climate warming. Annu. Rev. Ecol. Evol. Syst. 38, 683–712.

Luo, Y., Sherry, B., Zhou, X., Wan, S., 2009. Terrestrial carbon-cycle feedback to climate warming: experimental evidence on plant regulation and impacts of biofuel feedstock harvest. Global Change Biol. Bioener. 1, 62–74.

McNaughton, S.J., Milchunas, D.G., Frank, D.A., 1996. How can net primary productivity be measured in grazing ecosystems? Ecology 77, 974–977.

Meentemeyer, V., 1978. Microclimate and lignin control of litter decomposition rates. Ecology 59, 465–472.

Nadelhoffer, K.J., Giblin, A.E., Shaver, G.R., Linkins, A.E., 1992. Microbial processes and plant nutrient availability in arctic soils. In: Chapin, F.S., Jeffries III, R.L., Reynolds, J.F., Shaver, G.R., Svoboda, J. (Eds.), Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective. Academic Press, San Diego, California, USA, pp. 281–300.

Nelson, D.W., Sommers, L.E., 1996. Total carbon, organic carbon, and organic matter. In: Spark, D.L. (Ed.), Methods of Soil Analysis. Part 3. Chemical Methods SSSA Book Ser. 5. SSSA and ASA, Madison, WI, pp. 961–1010.

O'Neill, E.G., Johnson, D.W., Ledford, J., Todd, D.E., 2003. Acute seasonal drought does not permanently alter mass loss and nitrogen dynamics during decomposition of red maple (*Acer rubrum* L.) litter. Global Change Biol. 9, 117–123.

Parton, W., Silver, W.L., Burke, I.C., Grassens, L., Harmon, M.E., Currie, W.S., King, J.Y., Adair, E.C., Brandt, L.A., Hart, S.C., Fasth, B., 2007. Global-scale similarities in nitrogen release patterns during long-term decomposition. Science 315, 261–264.

Pleguezuelo, C.R.R., Zuazo, V.H.D., FernÁndez, J.L.M., Peinado, F.J.M., Tarifa, D.F., 2009. Litter decomposition and nitrogen release in a sloping Mediterranean subtropical agroecosystem on the coast of Granada (SE, Spain): effects of floristic and topographic alteration on the slope. Agric. Ecosyst. Environ. 134, 79–88.

Quested, H., Eriksson, O., Fortunel, C., Garnier, E., 2007. Plant traits relate to whole-community litter quality and decomposition following land use change. Funct. Ecol. 21, 1016–1026.

Rustad, L.E., Cambell, J.L., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartly, A.E., Cornelissen, J.H.C., Gurevitch, J., 2001. A meta-analysis of the response of soil respiration, net mineralization, and aboveground plant growth to experimental warming. Oecologia 126, 543–562.

Seneviratne, G., 2000. Litter quality and nitrogen release in tropical agriculture: a synthesis. Biol. Fertil. Soils 31, 60–64.

Shaw, M.R., Harte, J., 2001. Control of litter decomposition in a subalpine meadow sagebrush species ecotone under climate change. Ecol. Appl. 11, 1206–1223.

Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in Terrestrial Ecosystems. University of California Press, Berkeley.

Tagliavini, M., Tonon, G., Scandellari, F., Quiones, A., Palmieri, S., Menarbin, G., Paola, G., Masia, A., 2007. Nutrient recycling during the decomposition of apple leaves (*Malus domestica*) and mowed grasses in an orchard. Agric. Ecosyst. Environ. 118, 191–200.

Vargas, D.N., Bertiller, M.B., Ares, J.O., Carrera, A.L., Sain, C.L., 2006. Soil C and N dynamics induced by leaf-litter decomposition of shrubs and perennial grasses of the Patagonian Monte. Soil Biol. Biochem. 38, 2401–2410.

Vivanco, L., Austin, A.T., 2006. Intrinsic effects of species on leaf litter and root decomposition: a comparison of temperate grasses from North and South America. Oecologia 150, 97–107.

Wan, S., Luo, Y., Wallace, L.L., 2002. Changes in microclimate induced by experimental warming and clipping in a tallgrass prairie. Global Change Biol. 8, 754–768.

Wan, S., Luo, Y., 2003. Substrate regulation of soil respiration in a tallgrass prairie: results of a clipping and shading experiment. Global Biogeochem. Cycles 17, 1–12.

Wan, S., Hui, D., Wallace, L., Luo, Y., 2005. Direct and indirect effects of experimental warming on ecosystem carbon processes in a tallgrass prairie. Global Biogeochem. Cycles 19, GB2014.

Weider, R.K., Lang, G.E., 1982. A critique of the analytical methods used in examining decomposition data obtained from litter bags. Ecology 63, 1636–1642.

White, T.A., Barker, D.J., Moore, K.J., 2004. Vegetation diversity, growth, quality and decomposition in managed grasslands. Agric. Ecosyst. Environ. 101, 73–84.

Zhang, D., Hui, D., Luo, Y., Zhou, G., 2008. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. J. Plant Ecol. 1, 85–93.