



## Defoliation affects rhizosphere respiration and rhizosphere priming effect on decomposition of soil organic matter under a sunflower species: *Helianthus annuus*

Shenglei Fu<sup>1,2,3</sup> & Weixin Cheng<sup>1</sup>

<sup>1</sup>Department of Environmental Studies, University of California, Santa Cruz, CA 95064, USA. <sup>2</sup>Department of Nematology, University of California, Davis, CA 95616, USA. <sup>3</sup>Corresponding author\*

Received 15 September 2003. Accepted in revised form 16 December 2003

**Key words:** C-cycle, clipping, decomposition, herbivory, soil biota

### Abstract

In the present study, 'natural <sup>13</sup>C tracer method' was used to partition the belowground respiration into rhizosphere respiration and soil microbial respiration to test the hypothesis that defoliation affects rhizosphere respiration and rhizosphere priming effect on decomposition of soil organic matter (SOM). A C<sub>3</sub> plant species, *Helianthus annuus* (sunflower), was grown in 'C<sub>4</sub>' soil in microcosms so that the CO<sub>2</sub> evolved from plant-soil system can be partitioned. Four levels of defoliation intensities were established by manual clipping. CO<sub>2</sub> evolved from plant-soil system was trapped during 0–4 h after defoliation (HAD), 5–22 HAD and 23–46 HAD using a closed circulating system, respectively. We found that both rhizosphere respiration and soil microbial respiration of the clipped plants were either unchanged or significantly enhanced compared to unclipped plants at 45% defoliation level during all sampling intervals. Soil microbial respiration increased significantly at all defoliation levels during 0–4 HAD, however, both rhizosphere respiration and soil microbial respiration decreased significantly during 5–22 HAD or 23–46 HAD when 20% or 74% clearly demonstrated that the defoliation treatments modified the rhizosphere priming effect on SOM decomposition. The total cumulative rhizosphere priming effects on SOM decomposition during 0–46 HAD were 146%, 241%, 204% and 205% when 0%, 20%, 45% and <74%.

### Introduction

Most plants lose part of their tissues (e.g., leaves, stems, roots, flowers, or seeds) because of herbivory during their life cycles (Crawley, 1983; Reichman and Smith, 1991). In general, about 10% of terrestrial plant production is consumed by herbivores (Moore, 1995). Plant-herbivory interactions have been studied using two common approaches: animal grazing (e.g., insect or mammal) and manual clipping. Most studies have indicated that both animal grazing and manual clipping produce the same effects on plant responses (Johansson, 1993; Donaghy and Fulkerson, 1998; Lawson et al., 2000; Paterson and Sim, 2000; Slack et al., 2000), except that a few have considered

the impacts of animal grazing on plants to be different from manual clipping (Dyer, 1982, 1991).

A variety of plant growth responses to herbivory have been reported, ranging from a high degree of damage to growth overcompensation (Quinn and Hall, 1992; Belsky, 1986). The direct impacts of herbivory on plants may include changes in growth rate, biomass production, and plant height (Louda et al., 1990). Indirect impacts may include changes in root:shoot ratios (Vranjic and Gullan, 1990; Guitian and Bardgett, 2000), altered photosynthetic activity (Harrison and Maron, 1995) and levels of chemical defense (Karban and Niiho, 1995). Plant-herbivory interactions are heavily dependent on the degree (frequency and intensity) of herbivory, plant phenology or pattern of tissue loss, presence of competitors, history of herbivory, and the environmental conditions (nu-

\*FAX No: (530) 752-5809.

E-mail: fushenglei@hotmail.com or sfu@ucdavis.edu

trient level and water stress) that affect plant growth and the ability of plants to compensate or tolerate herbivorous attack (Bryant et al., 1983; Belsky, 1986, 1987; McNaughton, 1986; Anderson, 1987; Maschinski and Whitham, 1989; Doak, 1992; Marquis, 1992; Mauricio et al., 1993; Guitian and Bardgett, 2000; Fu et al., 2001). Most studies have focused on the aboveground responses of the plants to herbivory. Belowground responses to aboveground herbivory have received limited attention (Holland, 1995; Donaghy and Fulkerson, 1998; Paterson and Sim, 2000; Bardgett et al., 2001; Hamilton and Frank, 2001). Root exudation, soil microbial biomass and soil respiration were increased under defoliation of the plants in a few cases (Holland, 1995; Paterson and Sim, 2000; Hamilton and Frank, 2001). Timing and frequency of defoliation are found very important for maintaining a more active root system (Donaghy and Fulkerson, 1998). However, little information is available on the responses of rhizosphere respiration and SOM decomposition to defoliation (Robinson and Scrimgeour, 1995).

The rhizosphere is one of the 'hot spots' where soil biota aggregate and resources are more abundant with a faster mass and energy transformation (Beare et al., 1995; Coleman and Crossley, 1996). Through rhizosphere processes, many important aspects of plant-soil interactions are mediated (Uren and Reisenauer, 1988; Sallih and Bottner, 1988; Cheng and Coleman, 1990; Baker, 1991; Yeates et al., 1998; Fu and Cheng, 2002). The objective of this study was to test the hypothesis that defoliation affects rhizosphere respiration and rhizosphere priming effects on SOM decomposition.

## Materials and methods

### Soil

The soil was obtained from Konza Prairie, Kansa, USA, where  $C_4$  grasses dominated, and it was then defined as 'C<sub>4</sub> soil' in the present study. 'C<sub>4</sub> soil' had a  $\delta^{13}C$  of  $-14.6\%$ , C and N contents of  $20 \text{ g kg}^{-1}$  and  $1.9 \text{ g kg}^{-1}$ , and a pH of 7.1. The soil was homogenized through a 4-mm mesh sieve before use.

### Plant-soil system

A  $C_3$  plant, sunflower (*Helianthus annuus*), was grown in each PVC (polyvinyl chloride) pot (10 cm in diameter, 20 cm in height, capped bottom, with air

outlet tubing at the bottom) filled with one kg of Kansas 'C<sub>4</sub> soil'. Soil moisture was adjusted to  $250 \text{ g kg}^{-1}$  (ca. 90% of WHC) prior to planting. Planting was conducted on June 15, 2001 with multiple seeds but only one plant in each pot was kept for later measurements. The 'no-plant' controls for 'C<sub>4</sub> soil' were set in the same way without plants.

Soil moisture in each pot was maintained at  $250 \text{ g kg}^{-1}$  by weighing the pots frequently. Daily water loss and need were calculated and water was added to each pot to maintain the moisture. This experiment was conducted in a greenhouse where photoperiod was set as 14 h with supplement lighting as needed during the period of plant growth. Temperature was maintained at  $22 \text{ }^\circ\text{C}$  to  $25 \text{ }^\circ\text{C}$ , relative humidity was maintained at 45% during the day and 75% during the night.

### Sampling and measurements

Sampling was conducted from September 20 to 22, 2001 when plants were healthy and were in flowering stage. There were four replicated pots for each treatment. Sampling included CO<sub>2</sub> trapping, clipping treatment, plant biomass harvesting and soil collection.

For CO<sub>2</sub> trapping, two pieces of half-circle Plexiglas sheets connected with Tygon tubing (3.2 mm I.D.) were placed and fitted around the plant base and taped together. Low melting point paraffin wax was melted and poured on the top of the Plexiglas sheets to seal the top of the PVC pot. The Tygon tubing connected to the plexiglas sheet served as the air inlet during CO<sub>2</sub> trapping. Each pot was tested for possible air leaks by pumping air into the pot through the air inlet and submerging the air outlet tubing into water. The CO<sub>2</sub> accumulated in the PVC pot was completely flushed out by pumping before the start of the CO<sub>2</sub> trapping. Then, all CO<sub>2</sub> evolved from the plant-soil system were trapped for 20 min at a 4-h interval with a closed circulating system (Cheng, 1996; Fu and Cheng, 2002). The closed circulating system consisted of three major components: plant-soil system, CO<sub>2</sub> absorber, and an airflow controlling and pressure relief set. All gases (including CO<sub>2</sub>) evolved from the plant-soil system were pumped through a CO<sub>2</sub> trap (50 mL of 0.5 N NaOH solution in a plastic bottle). No CO<sub>2</sub> was detected with an infrared gas analyzer (commonly called IRGA) after all gases traveled through the CO<sub>2</sub> trap. The rest of the gases passed through a needle valve, a flow meter and a Mylar balloon (filled with

Table 1. Defoliation intensity based on leaf mass loss (%)

Intensity	Leaf mass loss of the replicates (%)				Mean $\pm$ S.E (%)
Low	20	17	21	22	20 $\pm$ 1
Medium	43	44	43	48	45 $\pm$ 1
High	72	70	75	78	74 $\pm$ 2

CO<sub>2</sub>-free air, served as a pressure relief and oxygen source), and was brought back to the plant-soil system. Possible air contamination during the trapping process was corrected by using some blank CO<sub>2</sub> traps with the same set-ups but bypassing the plant-soil system. The CO<sub>2</sub> traps were brought back to laboratory and the inorganic C content of a sub-sample of the solution was measured with a TOC analyzer (Shimadzu TOC-5050A). Another sub-sample was used to form the SrCO<sub>3</sub> precipitate with SrCl<sub>2</sub>, excess SrCl<sub>2</sub> was added to insure a complete precipitation of the carbonate. The SrCO<sub>3</sub> precipitate was washed with de-ionized water until its pH was 7 to minimize the air contamination to the sample (preventing further absorption of air CO<sub>2</sub>) and then dried in an oven (Harris, 1997). CO<sub>2</sub> trapping was conducted during three periods after defoliation: 0–4 (11 a.m. to 3 p.m. on 09/20), 5–22 (3 p.m. 09/20 to 9 a.m. 09/21), and 23–46 (9 a.m. 09/21 to 8 a.m. 09/22) hours after defoliation (HAD).

Clipping treatment was done immediately after the plant-soil systems were sealed with paraffin but right before CO<sub>2</sub> trapping. Since timing and intensity of defoliation had been found to be critical for the responses of root system, root exudation and soil microbial biomass to defoliation (Holland, 1995; Donaghy and Fulkerson, 1998; Paterson and Sim, 2000; Hamilton and Frank, 2001), the responses of rhizosphere respiration and decomposition of SOM to defoliation were then investigated during different intervals after defoliation and under various intensities of the defoliation.

To establish a gradient of defoliation intensity, the tips of all leaves of each sunflower plant were clipped with scissors. The area of the leaf tip to be clipped was estimated according to specific intensities. A hypothetical gradient of 0%, 20%, 50%, 80% of leaf mass loss was attempted but the real gradient 0%, 20  $\pm$  1%, 45  $\pm$  1% and 74  $\pm$  2% of leaf mass loss was established based on the weights of the oven-dry leaves harvested (Table 1). The whole clipping procedure was completed in less than 15 min.

Immediately after the third trapping, plant materials were harvested and categorized into shoots and root. Plant roots were washed with de-ionized water and collected in brown paper bags, and dried in an oven at 70 °C. One composite soil sample was taken from each PVC pot and a sub-sample was dried in an oven at 105 °C. All oven-dried materials (SrCO<sub>3</sub> precipitate, plant roots and soils) were ground with a SPEX mill (Certiprep 8000), and their  $\delta^{13}\text{C}$  values were measured with a PDZ Europa (Cheshire, UK) 'Hydra 20–20' continuous flow isotope ratio mass spectrometer. The samples were combusted at 1000 °C and the combustion products (N<sub>2</sub> and CO<sub>2</sub>) fed into the IRMS via a chromatography column which separated N<sub>2</sub> and CO<sub>2</sub>. The isotope ratios were compared to those of reference gas injections.

#### Calculation and statistics analysis

In our study, the 'natural <sup>13</sup>C tracer method' was used to partition the belowground respiration into rhizosphere respiration and soil microbial respiration (Fu and Cheng, 2002). When growing a C<sub>3</sub> plant in a 'C<sub>4</sub> soil', the carbon derived from C<sub>3</sub> plant and from 'C<sub>4</sub> soil' will have a different  $\delta^{13}\text{C}$  value and plant derived CO<sub>2</sub>-C can be partitioned using a two end-member mixing model:  $C_3 = C_t (\delta_t - \delta_4) / (\delta_3 - \delta_4)$  (Cerri et al., 1985; Cheng, 1996). In the equation, C<sub>3</sub> is the amount of 'root-derived CO<sub>2</sub>-C' (derived from both C<sub>3</sub> plant roots and rhizosphere microbes who decompose root-associated materials), C<sub>4</sub> is the amount of 'soil-derived CO<sub>2</sub>-C' (derived from microbial decomposition of SOM in 'C<sub>4</sub> soil'), C<sub>t</sub> is the total CO<sub>2</sub>-C from soil respiration which is the sum of 'root-derived CO<sub>2</sub>-C' and 'soil-derived CO<sub>2</sub>-C' (or  $C_t = C_3 + C_4$ ),  $\delta_t$  is the  $\delta^{13}\text{C}$  value of C<sub>t</sub>,  $\delta_3$  is the  $\delta^{13}\text{C}$  value of the 'root-derived CO<sub>2</sub>-C' and  $\delta_4$  is the  $\delta^{13}\text{C}$  value of the 'soil-derived CO<sub>2</sub>-C'.  $\delta^{13}\text{C}$  value of plant roots was used for  $\delta_3$  here since Cheng (1996) found that total rhizosphere CO<sub>2</sub> has the same  $\delta^{13}\text{C}$  value as that of plant roots, i.e. isotope fractionation does not occur during rhizosphere respiration.  $\delta_4$  referred to  $\delta^{13}\text{C}$  value of CO<sub>2</sub> evolved from control soil without plant. Although CO<sub>2</sub> evolved from each plant-soil system was partitioned using  $\delta^{13}\text{C}$  values from individual plant-soil system, only the mean  $\delta^{13}\text{C}$  values of the plant-soil systems, of plant roots and of SOM were summarized (Table 2). For a specific defoliation intensity, the same  $\delta^{13}\text{C}$  values of plant roots were used for all three trapping intervals because the same plant-soil systems were used to trap CO<sub>2</sub> during different

Table 2.  $\delta^{13}\text{C}$  value (‰) of  $\text{CO}_2$  evolved from soil, plant roots and plant-soil systems after defoliation

Defoliation intensity (%)	$\text{CO}_2$ origin	0–4 HAD <sup>a</sup>	5–23 HAD	24–46 HAD
0	System <sup>b</sup>	$-22.92 \pm 0.853$	$-23.31 \pm 0.31$	$-23.89 \pm 0.15$
	Root <sup>d</sup>	$-28.82 \pm 0.19$	$-28.82 \pm 0.19$	$-28.82 \pm 0.19$
	Soil <sup>e</sup>	$-15.00 \pm 0.40$	$-15.53 \pm 0.16$	$-15.24 \pm 0.32$
20	System	$-19.60 \pm 0.28$	$-23.15 \pm 0.64$	$-24.24 \pm 0.42$
	Root	$-28.84 \pm 0.22$	$-28.84 \pm 0.22$	$-28.84 \pm 0.22$
	Soil	$-15.00 \pm 0.40$	$-15.53 \pm 0.16$	$-15.24 \pm 0.32$
50	System	$-20.36 \pm 0.45$	$-23.22 \pm 0.43$	$-23.86 \pm 0.31$
	Root	$-28.39 \pm 0.45$	$-28.39 \pm 0.45$	$-28.39 \pm 0.45$
	Soil	$-15.00 \pm 0.40$	$-15.53 \pm 0.16$	$-15.24 \pm 0.32$
80	System	$-20.40 \pm 0.21$	$-23.30 \pm 0.40$	$-24.73 \pm 0.41$
	Root	$-28.43 \pm 0.17$	$-28.43 \pm 0.17$	$-28.43 \pm 0.17$
	Soil	$-15.00 \pm 0.40$	$-15.53 \pm 0.16$	$-15.24 \pm 0.32$

<sup>a</sup>HAD refers to hours after defoliation.

<sup>b</sup>System refers to plant-soil system.

<sup>c</sup>Mean values and standard error ( $n = 4$ ).

<sup>d</sup>Delta values of plant roots are used as delta value of  $\text{CO}_2$  evolved from plant roots (Cheng, 1996).

<sup>e</sup>Delta value of  $\text{CO}_2$  evolved from no-plant control soil.

intervals (Table 2). Standard errors of  $\delta^{13}\text{C}$  values of  $\text{CO}_2\text{-C}$  from the plant-soil systems ranged from 0.15 to 0.85 (per mil) with a mean of 0.40 (per mil). The difference in  $\delta^{13}\text{C}$  values between the two end members (Root-derived  $\text{CO}_2\text{-C}$  and SOM-derived  $\text{CO}_2\text{-C}$ ) was 13.35‰. The accuracy of the ‘natural  $^{13}\text{C}$  tracer method’ used in this study ranged from 80% to 96% with a mean of 90%, using a 95% confidence interval analysis ( $t_{0.025} = 3.182, n = 4-1$ ).

‘Root-derived  $\text{CO}_2\text{-C}$ ’ and ‘soil-derived  $\text{CO}_2\text{-C}$ ’ were defined as rhizosphere respiration and soil microbial respiration, respectively. Rhizosphere priming effect was expressed by the following equation:

$$\text{RPE} (\%) = (C_1 - C_2) * 100 / C_2,$$

where, RPE refers to rhizosphere priming effect on SOM decomposition,  $C_1$  is the ‘soil-derived  $\text{CO}_2\text{-C}$ ’ from soil with a plant, and  $C_2$  is the ‘soil-derived  $\text{CO}_2\text{-C}$ ’ from soil without any plant.

Statistical analyses for all data were performed using SAS software (SAS Institute, 1985) GLM procedure. Defoliation intensity and timing of  $\text{CO}_2$  trapping were set as main effects. The Fisher’s least significant difference (LSD) procedure was used to separate the means and significance levels were set at  $P < 0.05$  and  $P < 0.01$ .

## Results

### Rhizosphere respiration

During 0–4 h after defoliation (HAD), rhizosphere respiration increased significantly only when 74% of the leaves were removed from the plants; it did not change when 20% or 45% leaves were removed.

During 5–22 and 23–46 HAD, rhizosphere respiration decreased significantly when 20% or 74% of leaves were removed. Rhizosphere respiration was at the same level as that of unclipped plants during 5–22 HAD but increased significantly during 23–46 HAD when 45% leaves were removed (Figure 1).

### Rhizosphere priming effect

In consistency with the previous study (Fu and Cheng, 2002), sunflower plants induced a significant positive rhizosphere priming effect on SOM decomposition compared to no-plant control. The total cumulative rhizosphere priming effects during 0–46 HAD were 146%, 241%, 204% and 205% when 0%, 20%, 45% and 74% of the leaves were removed (Figure 2). This also clearly demonstrated that the defoliation treatments modified the rhizosphere priming effect. However, the modification of defoliation on rhizosphere priming effect varied with the timing and the intensity of defoliation. During 0–4 HAD, the rhizosphere priming effects were 127%, 530%, 307% and

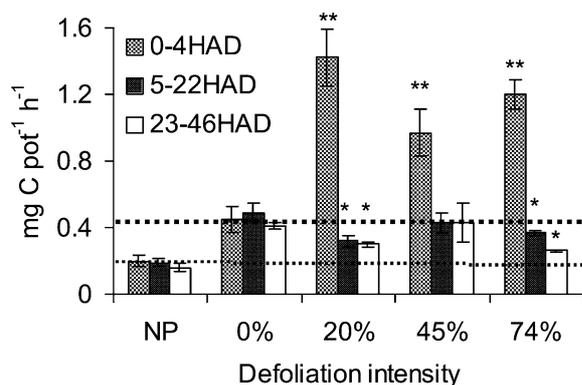


Figure 1. Rhizosphere respiration (root-derived CO<sub>2</sub>-C) in response to defoliation. Defoliation intensity refers to the percentages of the leaf mass removed. Bars and error bars are means and standard errors ( $n = 4$ ). \* or \*\* indicate significance level of  $P < 0.05$  or  $P < 0.01$ , respectively.

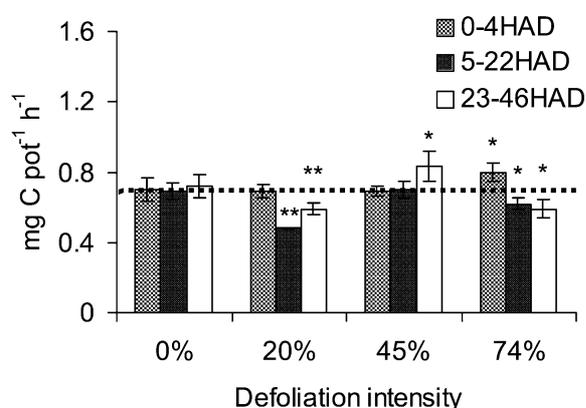


Figure 2. Soil microbial respiration (soil-derived-CO<sub>2</sub>-C) in response to defoliation. Defoliation intensity refers to the percentages of the leaf mass removed. NP refers to no-plant control. Values of the bars above the fine dotted line indicate rhizosphere priming effects. The modification of the rhizosphere priming effect due to defoliation can be visualized by comparing with that of 0% defoliation control indicated by the coarse dashed line. Bars and error bars are means and standard errors ( $n = 4$ ). \* or \*\* indicate significance level of  $P < 0.05$  or  $P < 0.01$ , respectively.

421% when 0%, 20%, 45% and 74% plant leaves were removed, respectively. In other words, the rhizosphere priming effect on SOM decomposition was enhanced by defoliation during 0–4 HAD. However, the rhizosphere priming effects were 158%, 68%, 126% and 95% during 5–22 HAD and 156%, 88%, 169% and 63% during 23–46 HAD when 0%, 20%, 45% and 74% plant leaves were removed, respectively. This illustrated that the rhizosphere priming effect was suppressed during these two periods when 20% and 74% of plant leaves were clipped but it did not change when 45% of plant leaves were removed (Figure 2).

## Discussion

Several studies showed a consistent pattern that soil microbial biomass and root exudation increased in the rhizosphere soils where plants were defoliated (Holland, 1995; Holland et al., 1996; Guitian and Bardgett, 2000; Paterson and Sim, 2000; Hamilton and Frank, 2001). Hamilton and Frank (2001) performed a <sup>13</sup>C pulse-chase experiment on a grazing tolerant grass to follow carbon flow into the rhizosphere and microbial biomass. They observed that the belowground respiration rate (microbes + roots) and rhizosphere microbial C were significantly higher in clipped pots 24 h after clipping compared to unclipped pots although this was not observed 7 d after clipping treatment. Paterson and Sim (2000) found that defoliation transiently (3–5 d) increased the exudation of soluble organic compounds from roots, and increased significantly cumulative rhizodeposition over the experimental period by growing plants in an axenic microcosm and clipping the plants repeatedly to an even height of 4 cm. Guitian and Bardgett (2000) found that defoliation of all tested plant species led to an increase in soil microbial biomass and C use efficiency in the rhizosphere. However, none of these studies attempted to partition soil respiration into rhizosphere respiration and soil microbial respiration, therefore, the respective response of rhizosphere respiration and soil microbial respiration to defoliation was not known. In the present study, we were able to monitor the separate response of rhizosphere respiration and soil microbial respiration to defoliation by using natural <sup>13</sup>C tracer method. We found that both rhizosphere respiration and soil microbial respiration of the clipped plants were either unchanged or significantly enhanced compared to unclipped plants at 45% defoliation level during all sampling intervals, and soil microbial respiration increased significantly at all defoliation levels during 0–4 HAD. It seemed logical to infer that defoliation stimulated the root exudation and caused a flush of soil microbial growth during 0–4 HAD, consequently resulted in a significant increase in rhizosphere respiration and soil microbial respiration. However, it was very difficult to use this logic to explain why both rhizosphere respiration and soil microbial respiration decreased significantly during 5–22 or 23–46 HAD when 20% or 74% of leaves were removed.

Kuzyakov and Cheng (2001) found that both rhizosphere respiration and rhizosphere priming effects increased tremendously with lighting and decreased

Table 3. The change and coupling of rhizosphere respiration and rhizosphere priming effect in response of defoliation

Defoliation (%)	Hours after defoliation (HAD)					
	0–4		5–22		23–46	
	RR <sup>a</sup>	RPE	RR	RPE	RR	RPE
0	0 <sup>b</sup>	0	0	0	0	0
20	0	+	–	–	–	–
45	0	+	0	0	+	0
74	+	+	–	–	–	–

<sup>a</sup>RR: rhizosphere respiration; RPE: rhizosphere priming effect.

<sup>b</sup>0, + and – indicate ‘no change, increase and decrease’ at a significant level ( $P < 0.05$ ) compared to the results from 0% defoliation, respectively.

significantly with prolonged shading. They concluded that plant photosynthesis is an important controlling factor for soil CO<sub>2</sub> efflux and rhizosphere processes and hypothesized that any factors that affect photosynthesis such as water stress and herbivory activity are important determinants of soil CO<sub>2</sub> efflux and rhizosphere processes. In the present study, the changes of rhizosphere respiration and rhizosphere priming effect on SOM decomposition to defoliation occurred in the same direction (Table 3). These responses reflected different mechanisms or physiological strategies of plants to maintain their activity and vitality in response to defoliation. Based on the findings and hypotheses of Kuzyakov and Cheng (2001), we proposed two possible mechanisms for what we found in the present study: 1) At low level of defoliation (i.e., 20%), the primary strategy for plant roots to maintain their normal activity was to conserve its energy by respiring less C when less photosynthates were available for roots due to defoliation. When defoliation reached to a certain level (i.e., 45%), the compensation mechanism was triggered. The compensation mechanism might be a high-cost process of energy use. Plants (including roots) had to maintain their vigor by using a lot of energy in storage for respiration. C source might be reallocated to roots disproportionately; 3) When defoliation reached to a severe level (i.e., 74%), an ‘injury repair’ might occur immediately after defoliation but the photosynthetic capability of the plant decreased rapidly and significantly later and was beyond the compensation threshold. Therefore, an enhanced rhizosphere respiration was observed during 0–4 HAD but a significantly reduced rhizosphere respiration was found during 4–22 HAD and 23–46 HAD.

Guitian and Bardgett (2000) established three levels of defoliation by cutting plants weekly (high), biweekly (low) or uncut (control). They found that soil microbial biomass increased only at high level of defoliation and did not change at low level of defoliation. Bardgett et al. (2001) measured a range of soil microbial properties across successional transitions derived from sheep grazing in three biogeographic regions and showed that soil microbial biomass was maximal at low-to-intermediate levels of grazing and that the phenotypic evenness of the microbial community declined as the intensity of grazing increased. Donaghy and Fulkerson (1998) found that the persistence and productivity of perennial ryegrass (*Lolium perenne* L.) were optimized when defoliation occurred at the 3-leaf stage of regrowth and around a stubble height of 50 mm. This optimal defoliation strategy enabled a greater proportion of water-soluble carbohydrate (WSC) to be allocated to maintain a more active root system. Since the criteria of defoliation gradient varied with studies, it was very difficult to directly interpret and compare the findings between different studies. For instance, leaf area loss was used as criteria to establish defoliation gradient in some studies (Holland, 1995; Fu et al., 2001), leaf mass loss was used in the present study, but grass height remaining was used in some other studies (Donaghy and Fulkerson, 1998). Nevertheless, all studies suggested that soil or rhizosphere processes were optimized at a certain level of defoliation.

In conclusion, our findings clearly demonstrated that defoliation affected rhizosphere respiration and rhizosphere priming effect on SOM decomposition. The magnitude and directions of these effects depended upon the intensity of defoliation and the time after defoliation.

### Acknowledgements

We thank Nicol Alcain, Nicol Krause and Jacqueline Bishop for their greenhouse and laboratory assistance. This research was supported by a CSREES/NRI grant from the United States Department of Agriculture (Award # 98-35107-7013).

### References

- Anderson D 1987 Below-ground herbivory in natural communities: A review emphasizing fossorial animals. *Quart. Rev. Biol.* 62, 261–286.

- Baker R 1991 Induction of rhizosphere competence in the biocontrol fungus *Trichoderma*. In *The Rhizosphere and Plant Growth*. Eds. D L Keister and P B Cregan. pp. 221–228. Kluwer Academic, Dordrecht, The Netherlands.
- Bardgett R D, Jones A C, Jones D L, Kemmitt S J, Cook R and Hobbs P J 2001 Soil microbial community patterns related to the history and intensity of grazing in sub-montane ecosystems. *Soil Biol. Biochem.* 33, 1653–1664.
- Beare M H, Coleman D C, Crossley Jr. D A, Hendrix P F and Odum E P 1995 A hierarchical approach to evaluating the significance of soil biodiversity to biogeochemical cycling. *Plant Soil* 170, 5–22.
- Belsky A J 1986 Does herbivory benefit plants? A review of evidence. *Am. Nat.* 127, 870–892.
- Belsky A J 1987 The effects of grazing: Confounding of ecosystem, community and organism scales. *Am. Nat.* 129, 777–783.
- Bryant J P, Chapin III F S and Klein D R 1983 Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40, 357–368.
- Cerri C C, Feller C, Balesdent J, Victoria R L and Plenecassagne A 1985 Application du tracage isotopique naturel en  $^{13}\text{C}$  à l'étude de la dynamique de la matière organique dans les sols. *C.R. Acad. Sci. Paris* 300, 423–428.
- Cheng W 1996 Measurement of rhizosphere respiration and organic matter decomposition using natural  $^{13}\text{C}$ . *Plant Soil* 183, 163–168.
- Cheng W and Coleman D C 1990 Effect of living roots on soil organic matter decomposition. *Soil Biol. Biochem.* 22, 781–787.
- Coleman D C and Crossley Jr. D A 1996 *Fundamentals of soil ecology*. Academic Press. 148 pp.
- Crawley M J 1983 *Herbivory: the dynamics of animal-plant interactions*. Blackwell Scientific, Oxford, England.
- Doak D F 1992 Lifetime impacts of herbivory for a perennial plant. *Ecology* 73, 2086–2099.
- Donaghy D J and Fulkerson W J 1998 Priority for defoliation of water-soluble carbohydrate reserves during regrowth of *Lolium perenne*. *Grass Forage Sci.* 53, 211–218.
- Dyer M I, Detling J K, Coleman D C, Hilbert D W 1982 The role of herbivores in grasslands. In *Grasses and Grasslands*. Eds J R Estes, R J Tyrl and J N Brunken. pp. 255–296. University of Oklahoma Press, Norman, Oklahoma.
- Dyer M I, Acra M A, Wang G M, Coleman D C, Freckman D W, McNaughton S J, Strain B R 1991 Source-sink carbon relations in two *Panicum coloratum* ecotypes in response to herbivory. *Ecology* 72, 1472–1483.
- Fu S and Cheng W 2002 Rhizosphere priming effects on the decomposition of soil organic matter in  $\text{C}_4$  and  $\text{C}_3$  grassland soils. *Plant Soil* 238, 289–294.
- Fu S, Kisselle K W, Coleman D C, Hendrix P F, Crossley Jr. D A 2001 The short-term impacts of aboveground herbivory (grasshopper) on the abundance and  $^{14}\text{C}$  activity of soil nematodes in conventional tillage and no-till agroecosystems. *Soil Biol. Biochem.* 33, 1253–1258.
- Guitian R and Bardgett R D 2000 Plant and soil microbial responses to defoliation in temperate semi-natural grassland. *Plant Soil* 220, 271–277.
- Hamilton III E W and Frank A D A 2001 Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. *Ecology* 82, 2397–2402.
- Harrison S and Maron J L 1995 Impacts of defoliation by tussock moths (*Orgyia vetusta*) on the growth and reproduction of bush lupine (*Lupinus arboreus*). *Ecol. Entomol.* 20, 223–229.
- Harris D, Porter L K and Paul E A 1997 Continuous flow isotope ratio mass spectrometry of carbon dioxide trapped as strontium carbonate. *Commun. Soil Sci. Plant Anal.* 28, 747–757.
- Holland J N 1995 Effects of aboveground herbivory on soil microbial biomass in conventional and no-till agroecosystems. *Appl. Soil Ecol.* 2, 275–279.
- Holland J N, Cheng W and Crossley Jr. D A 1996 Herbivory induced changes in plant carbon allocation: assessment of below-ground C fluxes using carbon-14. *Oecologia* 107, 87–94.
- Johnsson G 1993 Carbon distribution in grass (*Festuca pratensis* L.) during regrowth after cutting-utilization of stored and newly assimilated carbon. *Plant Soil* 151, 11–20.
- Karban R and Niiho C 1995 Induced resistance and susceptibility to herbivory: Plant memory and altered plant development. *Ecology* 76, 1220–1225.
- Kuzyakov Y and Cheng W 2001 Photosynthesis controls of rhizosphere respiration and organic matter decomposition. *Soil Biol. Biochem.* 33, 1915–1925.
- Lawson A R, Kelly K B and Sale P W G 2000 Defoliation frequency and cultivar effects on the storage and utilisation of stolon and root reserves in white clover. *Aust. J. Agri. Res.* 51, 1039–1046.
- Louda S M, Keeler K H and Holt R D 1990 Herbivore influences on plant performance and competitive interactions. In *Perspectives on Plant Competition*. Eds. J B Grace and D Tilman. pp. 413–444. Academic Press, New York.
- Marquis R J 1992 The selective impact of herbivores. In *Plant resistance to herbivores and pathogens*. Eds. R S Fritz and E L Simms. pp. 301–325. University of Chicago Press, Chicago, Illinois, USA.
- Maschinski J and Whitham T G 1989 The continuum of plant responses to herbivory: The influence of plant association, nutrient availability, and timing. *Am. Nat.* 134, 1–19.
- Mauricio R, Bowers M D and Bazzaz F A 1993 Pattern of leaf damage affects fitness of the annual *Raphanus sativus* (Brassicaceae). *Ecology* 74, 2066–2071.
- McNaughton S J 1986 On plant and herbivores. *Am. Nat.* 128, 765–770.
- Moore P 1995 Citation records show plant herbivory taking root as hot research topic. *The Scientist* 9, 12.
- Paterson E and Sim A 2000 Effect of nitrogen supply and defoliation on loss of organic compounds from roots of *Festuca rubra*. *J. Exp. Bot.* 51, 1449–1457.
- Quinn M A and Hall M H 1992 Compensatory response of a legume root-nodule system to nodule herbivory by *Sitona hispidulus*. *Entomol. Exp. Appl.* 64, 167–176.
- Reichman O J and Smith S C 1991 Responses to simulated leaf and root herbivory by a biennial, *Tragopogon dubius*. *Ecology* 72, 116–124.
- Robinson D and Scrimgeour L B 1995 The contribution of plant C to soil  $\text{CO}_2$  measured using  $\delta^{13}\text{C}$ . *Soil Biol. Biochem.* 27, 1653–1656.
- SAS Institute Inc. 1985 *SAS Procedure guide for personal computers*, version 6. Cary, North Carolina.
- Sallih Z and Bottner P 1988 Effects of wheat (*Triticum aestivum*) roots on mineralization rates of soil organic matter. *Biol. Fert. Soil.* 7, 67–70.
- Slack K, Fulkerson W J and Scott J M 2000 Re-growth of Prairie grass (*Bromus willdenowii* Kunth) and perennial ryegrass (*Lolium perenne* L.) in response to temperature and defoliation. *Aust. J. Agri. Res.* 51, 555–561.
- Uren N C and Reissenauer H M 1988 The role of root exudates in nutrient acquisition. *Adv. Plant Nutr.* 3, 79–114.

Vranjic J A. and Gullan P J 1990 The effect of a sap-sucking herbivore, *Ericoccus coriaseus* (Homoptera: Ericoccidae), on seedling growth and architecture in *Eucalyptus blakelyi*. *Oikos* 59, 159–162.

Yeates G W, Saggar S, Denton C S and Mercer C F 1998 Impact

of clover cyst nematodes (*Heterodera trifolii*) infection on soil microbial activity in the rhizosphere of white clover (*Tifolium repens*) – a pulse labeling. *Nematologica* 44, 81–90.

*Section editor: Y.-G. Zhu*