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# Herbivore-induced changes in plant carbon allocation: assessment of below-ground C fluxes using carbon-14

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**Abstract** Effects of above-ground herbivory on short-term plant carbon allocation were studied using maize (*Zea mays*) and a generalist lubber grasshopper (*Romalea guttata*). We hypothesized that above-ground herbivory stimulates current net carbon assimilate allocation to below-ground components, such as roots, root exudation and root and soil respiration. Maize plants 24 days old were grazed (c. 25–50% leaf area removed) by caging grasshoppers around individual plants and 18 h later pulse-labelled with $^{14}CO_2$. During the next 8 h, $^{14}C$ assimilates were traced to shoots, roots, root plus soil respiration, root exudates, rhizosphere soil, and bulk soil using carbon-14 techniques. Significant positive relationships were observed between herbivory and carbon allocated to roots, root exudates, and root and soil respiration, and a significant negative relationship between herbivory and carbon allocated to shoots. No relationship was observed between herbivory and $^{14}C$ recovered from soil. While herbivory increased root and soil respiration, the peak time for $^{14}CO_2$ evolved as respiration was not altered, thereby suggesting that herbivory only increases the magnitude of respiration, not patterns of translocation through time. Although there was a trend for lower photosynthetic rates of grazed plants than photosynthetic rates of ungrazed plants, no significant differences were observed among grazed and ungrazed plants. We conclude that above-ground herbivory can increase plant carbon fluxes below ground (roots, root exudates, and rhizosphere respiration), thus increasing resources (e.g., root exudates) available to soil organisms, especially microbial populations.

**Key words** Herbivory · Carbon allocation · Photosynthetic rate · Root exudates · Rhizosphere respiration

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## Introduction

Greenfall, feces, urine, body parts, and nutrients leached from grazed leaves are traditionally considered the links between herbivores of grazing food webs and organisms of detrital food webs (Risley and Crossley 1988). Soil food webs are generally considered detrital systems because the resource base is non-living materials. However, it has become clear that non-detrital plant inputs to soil (e.g., roots and root exudates) are also important. If herbivory alters plant carbon allocation patterns and root exudation, then non-detrital plant inputs represent another link between herbivores of grazing food webs and the organisms of soil food webs.

Photosynthate allocated belowground can be stored in root carbohydrate pools, used for root growth and root respiration, or released into soil as root-derived exudates (soluble root exudates, mucilage, and dead root parts). The percentage of photosynthate released into the soil as root exudates is variable and depends in part on plant species, age, physiological status, and soil environmental factors (Hale and Moore 1979; Whipps 1984; Heal and Dighton 1985; Martin and Kemp 1986; van Veen et al. 1989). By using $^{14}C$-labelling techniques, the quantity of root exudates released into soil has been estimated for arable crops to be 10–40% of total net carbon assimilated (Barber and Martin 1976; Whipps and Lynch 1983; Whipps 1984; Helal and Sauerbbeck 1986; Keith et al. 1986; Liljeroth et al. 1990; Gregory and Atwell 1991; Martin and Merckx 1992). Once released into soil, root exudates are utilized by microbial populations as an energy source for growth and maintenance (van Veen et al.

1989; Helal and Sauerbeck 1986). Helal and Sauerbeck (1986) reported that 68% of soil microbial growth associated with maize plants was attributable to plant-C, while only 32% of growth was attributed to soil-C. Since soil microbial populations and, to a lesser extent, soil fauna are responsible for soil nutrient cycling, factors affecting root exudation are of importance to the functioning of soil ecosystems (van Veen et al. 1989, 1991).

If herbivory alters carbon allocated to roots and root exudates, then resources available to soil communities may change, since the primary carbon sources for soil microbial populations are root biomass (Fogel 1985; Milchunas et al. 1985) and root-derived exudates (Warembourg and Billes 1979; Helal and Sauerbeck 1986; Keith et al. 1986; Martin and Kemp 1986; van Veen et al. 1989). Even though above-ground herbivory may reduce root biomass and production (Chapin and Slack 1979; Richards 1984; Svejcar and Christiansen 1987; Ganskopp 1988), abundance of soil organisms may increase in response to foliage herbivory due to increased quality (e.g., increased nitrogen concentration of roots) of below-ground resources (Seastedt et al. 1988). Studies have shown indirectly that herbivory increases root respiration and root exudation (Bokhari and Singh 1974; Dyer and Bokhari 1976), and that herbivory can increase energy flow belowground (Dyer and Bokhari 1976; Doll 1991). However, other studies have reported translocation of root reserve carbon to shoots following defoliation (Ryle and Powell 1975), decreased root respiration of grazed plants (Detling et al. 1979), and decreased C allocation to roots following defoliation (Miller and Rose 1992). Defoliated plants are generally thought to mobilize and translocate below-ground nonstructural carbohydrate reserves to above-ground plant parts for regrowth, and reduce current carbon assimilate allocation to below-ground reserves following foliage removal (Donart and Cook 1970; Ryle and Powell 1975; Bokhari 1977; Chapin and Slack 1979; Chung and Trlica 1980; Miller and Rose 1992). However, other research has reported that root reserves do not significantly contribute to regrowth (Marshall and Sagar 1965; Hassan and Krueger 1980; Richards and Caldwell 1985; Oesterheld and McNaughton 1988), and that current photosynthate contributes the most to regrowth (Richards and Caldwell 1985).

The majority of changes in plant carbon allocation and translocation in response to herbivory have been assessed using response variables of plant biomass and total nonstructural carbohydrates (Bokhari and Singh 1974; Archer and Tieszen 1980; Caldwell et al. 1981; Richards and Caldwell 1985; Oesterheld and McNaughton 1988; Holland and Detling 1990). Only a few studies have used stable and radioactive isotopes ($^{13}C$, $^{11}C$, $^{14}C$) to construct carbon budgets (Bokhari 1977; Dyer et al. 1991; Miller and Rose 1992). In order to more precisely assess whole-plant carbon dynamics in response to herbivory, plant components such as shoot, root, below-ground respiration, and exudates need to be simultaneously incorporated into studies. The present study addresses short-term changes in whole-plant carbon allocation patterns on a time scale of hours and days. To our knowledge, this is the first study to report concurrent measurement of herbivore-induced changes in plant carbon allocated to shoot, root, root and soil respiration, root exudates, and soil using $^{14}C$-technology and real foliage herbivory with an emphasis on below-ground carbon fluxes *in situ* soil. Objectives of the research were to assess changes in plant carbon allocation patterns in response to above-ground herbivory using $^{14}C$-technology, and test the hypothesis that root-exudation and soil metabolism increase when plants are grazed, thereby linking above-ground herbivory with soil processes.

## Materials and methods

### Soil and growing plants

Maize (*Zea mays* L.; cultivar Pioneer 3320) plants were grown in conventionally tilled soil taken from the 0–15 cm layer of maize fields at the Horseshoe Bend Agroecosystem Research Site in Clarke County, Georgia, United States. The soil is characterized as a sandy clay loam, thermic Rhodic Kanhapludult, with a water holding capacity of 35% (w/w). The organic C, total Kjehldahl N, and available P (dilute $HCl$-$H_2SO_4$ extractable) of the soil are 1.13%, 0.11%, and 57.3 $\mu g\ g^{-1}$ respectively. Soil was sieved (2-mm mesh), homogenized, and air-dried before use in experiments. Further descriptions of the Horseshoe Bend Site are given by Beare et al. (1992), Blumberg and Crossley (1983), and Stinner et al. (1983).

Plants were grown in plastic (polyvinyl chloride, PVC) containers (5 cm internal diameter, 15 cm in height) with a capped bottom, air inlet tubing at the top, and air outlet tubing at the bottom of each container. Plastic containers were filled with 360 g of soil and two germinated seeds (incubated in petri dishes in the dark for 24 h) were planted approximately 2 cm deep in each container. After seedlings emerged from the soil, plants were thinned to one individual per container. Plants were grown for 24 days before experimentation. The first week of growth occurred outside in a mini-greenhouse. The mini-greenhouse did not allow control of temperature or photon flux, but did allow control of water and exclusion of herbivores. The remaining period of growth occurred in a growth chamber (photosynthetic photon flux density = 800 $\mu M\ s^{-1}\ m^{-2}$ at midcanopy) with a light-dark cycle of 15/9 h at 22°C. Soil moisture in each plant-soil-PVC container was maintained at approximately 20% (w/w) by weighing and adding water as needed. After 10 days of growth, each plant-soil column received 25 ml of double strength Hoagland's solution.

### Herbivory treatment

Herbivory treatments were applied to maize after 24 days of plant growth. Maize plants were in early stages of growth and leaves were juvenile. One day before applying herbivory treatments, each container was sealed at the soil surface of the plant with a mixture of petrolatum (petroleum jelly) and paraffin with a low melting point (53–55°C) in a proportion of 5:1 (w/w). To assure an air-tight seal, each plant container was submerged in water and air was pumped through the container. By sealing the containers prior to herbivory treatments, any interactions between grasshopper frass and soil were avoided. Grazing treatments were established by caging lubber grasshoppers, *Romalea guttata* (Houttuyn), around individual maize plants. A total of 12 plants were used in the experiment, 4 control and 8 grazed. Of the eight grazed plants, four received one grasshopper per plant and four received three grasshoppers per plant in order to create a gradient of leaf area removed. However, not all grasshoppers were actively feeding throughout the entire herbivory time period due to the low temper-

ature of the growth chamber. Nonetheless, shoot weights of the eight grazed plants were reduced by the removal of leaf area by the different numbers of grasshoppers (simple linear regression; ($F_{1,10}$ = 4.95, $P$ = 0.050). Just prior to the herbivory treatments, maize plants had four or five leaves branching from the stem. Grasshoppers fed on the plants for 8 h removing up to two leaves, corresponding to 25–50% leaf area removed. Following grazing, grasshoppers and cages were removed from plants, and 18 h later $^{14}CO_2$ labelling occurred (light-dark cycles were maintained as previously described).

### $^{14}CO_2$ labelling

The labelling apparatus consisted of (1) an air-tight Plexiglas chamber, (2) an air supply and dispensing system, (3) a $^{14}CO_2$-generating and infrared gas analyzer loop, and (4) two air mixing fans (see Cheng et al. 1993, 1994 for diagrammatic representation of equipment configuration). Sealed plant-soil containers were placed into a Plexiglas chamber (within growth chamber) after bringing soil water content to approximately 45% of field water holding capacity. Air flow through all soil containers was adjusted to 50 $cm^3$ $min^{-1}$. The Plexiglas chamber was closed, and the growth chamber lights were turned off prior to labelling and turned back on after injection of $^{14}CO_2$ and stabilization of the $CO_2$ concentration. Pulse labelling was begun by injecting $NaH^{14}CO_3$ (300 μCi $^{14}CO_2$) solution into the acid flask connected to the $^{14}CO_2$ injection loop. The lights were turned back on when $^{14}CO_2$ concentration in the chamber became constant (372 ppm). After the 20-min pulse-labelling period, the top of the Plexiglas chamber was removed. $^{14}C$ was traced in plant and soil components during the following 8 h. An overview of labelling methods of this type is given by Warembourg and Kummerow (1991).

### Sample analyses

Total root-soil respiration (root respiration and microbial respiration) was measured by trapping the $^{14}CO_2$ evolved from the plant-soil container. The $^{14}CO_2$ was trapped by continuously pumping room air at a rate of 50 $cm^3$ $min^{-1}$ through the container, and bubbling it through 4 ml of 4 M NaOH. The NaOH trap was changed every hour for 8 h following $^{14}CO_2$ pulse labelling of shoots. At the end of the $^{14}CO_2$ tracing period, root exudates or soluble $^{14}C$ were collected by vacuum pulling 40 ml water through the container and collecting the extract. The radioactivities in the $^{14}CO_2$ NaOH solution and the soluble $^{14}C$ water-extract solution were counted directly using Ecolite liquid scintillation counting (Beckman LS 3801).

After root exudates were collected, each plant shoot was cut at its base, root-soil columns were removed from PVC containers, and roots were hand-picked from soil. Rhizosphere soil was collected by gently shaking the roots, any soil adhering to the roots after shaking was treated as rhizosphere soil. Shoots, roots plus rhizosphere soils, and bulk soils were air-dried under a fume hood, then oven-dried at 60°C to a constant weight. Dry root, shoot, and soil samples were pulverized in a ball mill, and radioactivities were measured by liquid scintillation after combustion in an OX-300 Biological Oxidizer (R.J. Harvey Instrument Co., Hillsdale, N.J.). We used known $^{14}C$-glucose standards to correct for the loss of $^{14}C$ during combustion and trapping. The scintillation counting efficiencies of all samples were measured by internal standards.

### Statistical analyses

Data presented as kiloBecquerels were normalized for differences in total $^{14}CO_2$ assimilated by plants by using a correction factor. Correction factors were calculated for each plant and soil system by dividing the total $^{14}C$ recovered for each plant and soil system by the mean total $^{14}C$ recovered for the 12 plants. Each $^{14}C$ component (i.e., shoot, root, root exudates, respiration, bulk soil and rhizosphere soil) was then divided by its corresponding correction factor. These data in kiloBecquerels were analyzed using simple linear regression. Photosynthetic rates were analyzed using a pooled $t$-test [ungrazed ($n$ = 4) versus grazed ($n$ = 8)]. Regression analyses were performed using Statistical Analysis System for microcomputers (SAS Institute 1988).

## Results

Grasshoppers removed one to two leaves per plant, corresponding to 25–50% leaf area removed. Grasshopper grazing reduced shoot weights and increased plant root-to-shoot ratios (Table 1). Relative to the mean control shoot weight, herbivory reduced individual plant-shoot weights by 10–51%, which is in agreement with our estimates of leaf area removed. The reduction in shoot weights associated with herbivory did not significantly affect whole-plant photosynthetic rates (pooled $t$-test, $P$>0.05; $n$ = 4 for control ungrazed plants and $n$ = 8 for grazed plants).

Above-ground herbivory significantly altered plant carbon allocation patterns during the 8-h $^{14}C$ tracing period (Fig. 1). Herbivory significantly reduced carbon allocation to plant shoots ($F_{1,10}$ = 6.48, $P$ = 0.029); as shoot biomass decreased, or herbivory increased, $^{14}C$ recovered in shoots decreased (Fig. 1A). Herbivory significantly increased $^{14}C$ allocation to roots (Fig. 1B; $F_{1,10}$ = 5.38, $P$ = 0.043); as shoot-sink strength decreased with increasing herbivory, root-sink strength increased. In the ungrazed control plants, 73% of total $^{14}C$ was recovered in shoots and 17% in roots, while 66 and 23% of total $^{14}C$ was recovered in shoots and roots of high leaf area removed (LAR) plants, respectively (Fig. 2). This accounts for a 10% decrease in $^{14}C$ recovered in shoots, and a 35% increase in $^{14}C$ recovered in roots from control, ungrazed plants to high herbivory plants.

**Table 1** Dry weights of shoots and roots, root-to-shoot ratios (*R:S*), and photosynthetic rates of maize for control, and low and high leaf area removed (*LAR*) plants. Values are means (±1 SE) of four plants. Photosynthetic rates were enumerated by summing the total $^{14}C$ recovered for each plant and dividing by shoot mass. The high LAR plants were the four plants with the lowest plant weights, low LAR were the next four lowest plant weights, and control plants were ungrazed

| Treatment | Dry weight (g) | | R:S ratio | Photosynthetic rate |
|---|---|---|---|---|
| | Shoot | Root | | $^{14}C$ (kBq) · $g^{-1}$ · $min^{-1}$ |
| Control | 1.379±0.072 | 0.881±0.047 | 0.648±0.061 | 33.7±2.9 |
| Low herbivory | 1.167±0.075 | 1.036±0.089 | 0.909±0.120 | 26.6±2.5 |
| High herbivory | 0.816±0.067 | 0.753±0.095 | 0.917±0.056 | 28.3±1.8 |

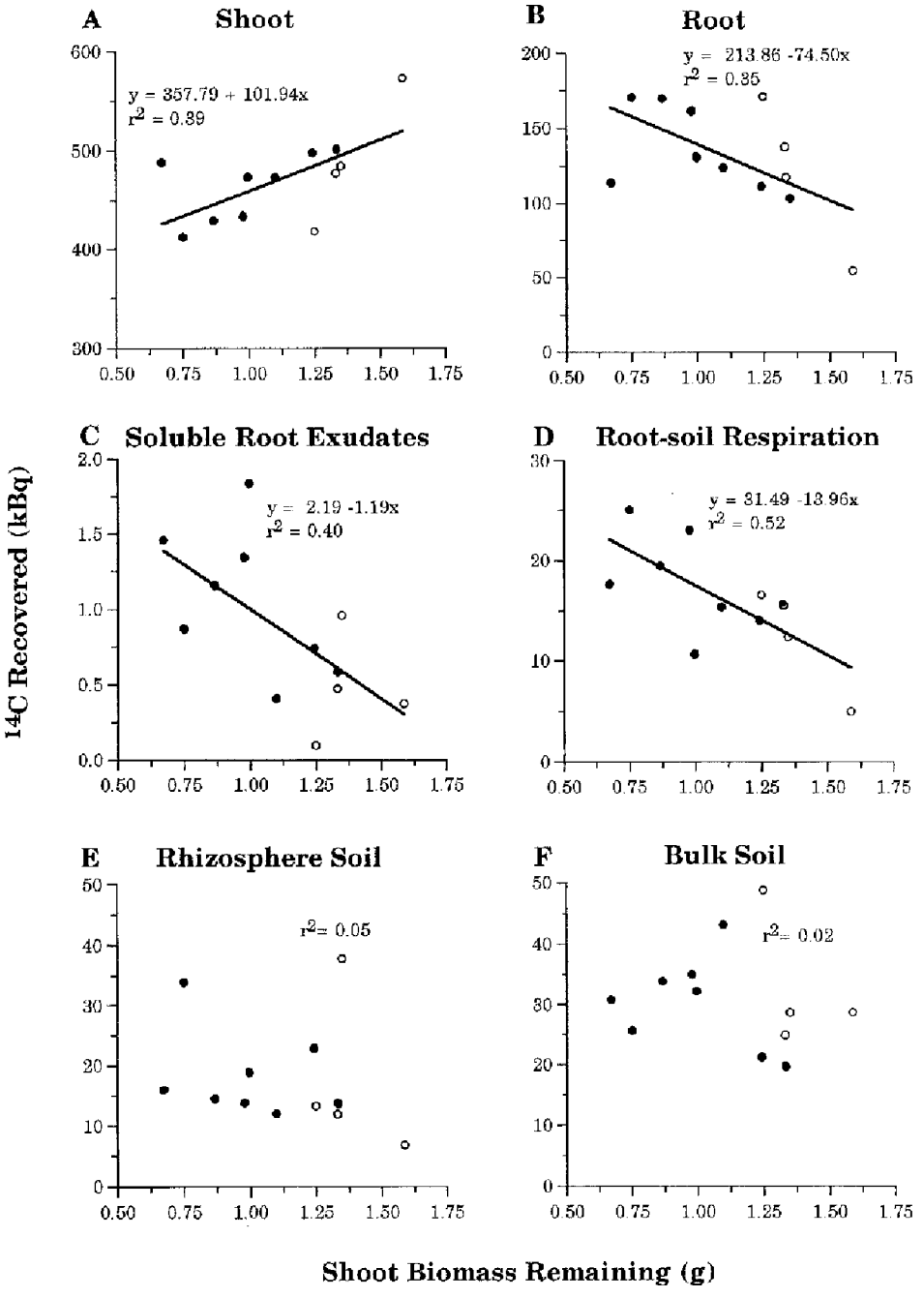


**Fig. 1A–F** $^{14}C$ recovered (kBq, kiloBequerel; normalized for differences in $^{14}CO_2$ uptake) as a function of shoot biomass in **A** shoots, **B** roots, **C** soluble root exudates, **D** root-soil respiration (root respiration plus microbial respiration), **E** rhizosphere soil, and **F** bulk soil. Shoot biomass is inversely related to leaf area removed by herbivore (i.e., as shoot biomass decreases, leaf area removed by herbivore increases). Graphs lacking simple linear regression equations and lines are not significant ($P>0.05$). 1 kB = 1000 disintegrations per second (*open circles* control, ungrazed plants, *solid circles* grazed plants)

Soluble root exudates significantly increased for grazed plants (Fig. 1C; $F_{1,10} = 6.69$, $P = 0.027$). For control and low and high LAR plants, soluble root exudates accounted for 0.07, 0.13, and 0.18% of total $^{14}C$ recovered, respectively (Fig. 2). This corresponded to an 86 and 157% increase in root exudation for low and high herbivory plants, respectively. Although soluble root exudates accounted for < 1% of total $^{14}C$ extracted from the soil at the end of the 8-h tracing period, up to 10% of total assimilated $^{14}C$ was released from roots and recovered in soil. These figures do not account for $^{14}C$ exudates that were released into the soil and subsequently metabolized and respired by soil microbes. Root-soil respiration (root respiration plus microbial respiration) also significantly increased as herbivory increased or shoot biomass decreased (Fig. 1D; Fig. 3; $F_{1,10} = 10.67$, $P = 0.009$). Rhizosphere respiration increased by 11% and 68% from control, ungrazed plants to low and high LAR plants, respectively (Fig. 2). Herbivory increased the total quantity of $^{14}CO_2$ released as rhizosphere respiration, but did not alter the pattern of translocation through time (Fig. 3). The $^{14}CO_2$ evolution rate of both ungrazed and grazed plants had similar time curves: $^{14}CO_2$ evolution rate increased rapidly following labelling; maximum $^{14}CO_2$ evolution for ungrazed and grazed plants peaked at similar times between 3 and 6 h after labelling; and $^{14}CO_2$ evolution began to decline before the end of the 8-h tracing period (Fig. 3).

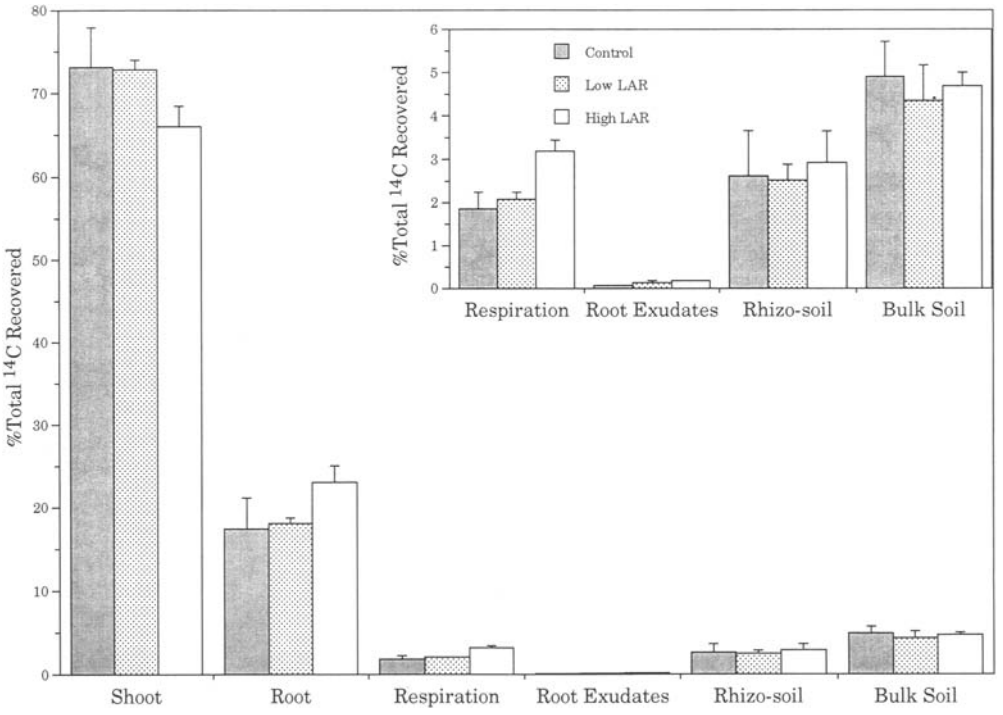


**Fig. 2** Distribution of $^{14}C$ in plant and soil components after a pulse labelling of maize and eight hours of subsequent measurement. The smaller graph within the larger graph is a magnification of the respiration, root exudates, and soil components of the larger graph. Values are means (±1 SE) of four replicates for ungrazed plants and low and high leaf area removed (*LAR*) plants. The high LAR plants were the four plants with the lowest plant weights, low herbivory were the next four lowest plant weights, and control plants were ungrazed with the greatest plant weights

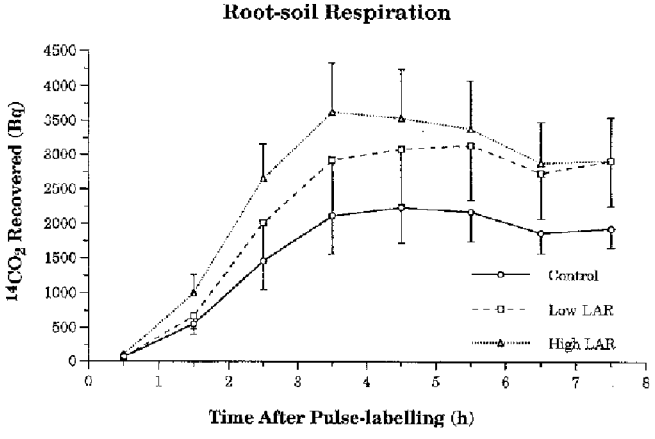


**Fig. 3** $^{14}CO_2$ (Bq; normalized for differences in $^{14}CO_2$ uptake) evolution from root-soil columns during 8 h of tracing following pulse-labelling. Values are means of four replicates for control, ungrazed plants (−1 SE) and low (−1 SE) and high (+1 SE) leaf area removed (*LAR*) plants. Control, low and high LAR plants are the same as in Fig. 2

Although herbivory increased $^{14}C$ allocated to roots, root exudates, and rhizosphere respiration, no relationship was observed between herbivory and $^{14}C$ recovered from soil (Fig. 1E,F). In addition, herbivory did not alter the proportion of $^{14}C$ recovered in below-ground components relative to total $^{14}C$ allocated belowground. The percentages of $^{14}C$ remaining in roots, respired, and total $^{14}C$ exuded from roots based on total $^{14}C$ allocated belowground for all plants were 66, 8, and 26%, respectively.

## Discussion

In this study, we assessed the effects of herbivory on short-term current assimilate partitioning in maize. While this study reports the concurrent changes in current carbon allocated to shoot, root, root-soil respiration, root exudates and soil two days after defoliation, it does not consider long-term plant responses to herbivory, nor does it assess changes in allocation of carbon fixed prior to herbivory (e.g., root reserves). Furthermore, changes in current assimilate allocation in maize, an annual crop plant, may not accurately reflect carbon dynamics in perenial plants or grazing-adapted plants. Future studies could improve our understanding of the effects of herbivory on carbon allocation by simultaneously assessing changes in current-assimilate partitioning and allocation of carbon fixed before defoliation.

Observed short-term changes in allocation of net carbon assimilation of grazed plants were not a function of photosynthetic rates, as there were no significant differences in whole-plant photosynthetic rates among grazed and ungrazed, control plants 18 h after defoliation. This is consistent with previous findings (Detling et al. 1979; Painter and Detling 1981; Meyer and Whitlow 1992), where immediately after defoliation photosynthetic rates remained unchanged or were slightly suppressed, while several days after defoliation photosynthetic rates of grazed plants increased. Direct comparisions of our measure of photosynthetic rates with other studies should be interpreted cautiously since most studies measure photosynthesis on a leaf area basis, while our study estimated photosynthesis on a whole plant basis. Nonetheless, the relative effects of herbivory on photosynthetic rates in our study are consistent with other findings.

In the system that we studied, herbivory increased current assimilate allocation to below-ground components and decreased allocation to shoots (Fig. 1). In a $^{14}C$ study of grazed and ungrazed grasslands, Doll (1991) concluded that more energy flows through belowground systems of grazed grasslands than of ungrazed grasslands. Using indirect evidence from a hydroponic medium study Dyer and Bokhari (1976) reported that foliage herbivory increased translocation of materials from above-ground components to crowns and roots. Additionally, Dyer et al. (1991) conducted a study on the short-term changes in plant carbon allocation using $^{11}C$-techniques and found that grazed plants translocated more labile carbon to roots. However, Miller and Rose (1992) found that autumn defoliation reduced $^{13}C$ allocation to roots in 1 of 2 years of the study, suggesting that time of defoliation during the growing season may affect carbon allocation patterns in response to grazing (Donart and Cook 1970; Hassan and Krueger 1980). Similarly, the changes in carbon allocation in this study were for maize in early stages of growth, which may differ for maize in later stages of growth. Nevertheless, the observed increase in carbon allocated to roots of grazed plants (Fig. 1) is consistent with prior studies (Marshall and Sagar 1965; Bokhari 1977; Dyer et al. 1991), and supports the idea that short-term storage of current carbon assimilates in roots following grazing, as opposed to shoots where the carbon reserves would be more accessible to grazers, may allow for rapid mobilization for regrowth (Dyer et al. 1991).

Over the 8 h tracing period, up to 10% of total $^{14}C$ was exuded from roots. This is consistent with the Helal and Sauerbeck (1986) study that reported maize releasing 11% of total photosynthate into soil. As with carbon allocated to roots, herbivory stimulated the quantity of exudates released from roots (Fig. 1C). We have not elucidated a direct mechanism to explain the observed increase in root exudation. Nonetheless, we speculate that increased carbon allocation to roots subsequently resulted in increased root exudation. To our knowledge, this is the first herbivory study conducted in a soil medium to simultaneously quantify carbon allocated to root exudates and shoots, roots, rhizosphere respiration, and soil. However, other studies have indirectly measured the effects of above-ground herbivory on root exudation. By measuring pH changes in a hydroponic medium containing grazed blue grama grass [*Bouteloua gracilis* (H.B.K.) Lag.], Dyer and Bokhari (1976) attributed the increased change in pH to increased release of organic acids from roots. Similarly, Bokhari and Singh (1974) reported greater quantities of reducing sugars in hydroponic solution of clipped western wheatgrass (*Agropyron smithii* Tydb.) plants, than for unclipped, control plants. In a defoliation experiment using sugar maple trees approximately 20 years of age, Smith (1972) reported that defoliation increased the quantity of root exudates without substantially altering the composition of the exudates. In a study of $^{14}C$ transfer from one plant to another via mycorrhizae, Waters and Borowicx (1994) found that when one plant was clipped, the quantity of $^{14}C$ recovered in the companion plant increased, suggesting greater carbon loss to mycorrhizal fungi for clipped plants.

Above-ground herbivory stimulated root-soil respiration (root respiration and microbial respiration) of maize plants (Fig. 1D). $^{14}CO_2$ recovered as respiration was a product of both root respiration and microbial uptake and subsequent metabolism of $^{14}C$ root exudates. Consequently, the observed increase in root-soil respiration in response to herbivory was likely a function of both root respiration (J.N. Holland, unpublished work; Fig. 1D) and microbial metabolism of $^{14}C$-root exudates (Fig. 1D). However, the magnitude of increased rhizosphere respiration may have been predominately a function of microbial respiration, since over 75% of rhizosphere respiration has been attributed to microbial metabolism (Helal and Sauerbeck 1989). Increased microbial respiration and metabolism are consistent with the observed increase in root exudates (Fig. 1C), which are a primary carbon resource for microbial populations (Warembourg and Billes 1979; Helal and Sauerbeck 1986; Keith et al. 1986; Martin and Kemp 1986; van Veen et al. 1989). Approximately one-third of all carbohydrates allocated to roots is used for root respiration to provide energy necessary for nutrient and ion uptake, growth, and translocation processes (Lambers et al. 1991). Stimulated root respiration following grazing would provide energy necessary for maintenance and additional uptake of ions and nutrients needed for regrowth following herbivory. Accordingly, Chapin and Slack (1979) reported that root respiration and phosphate absorption increased for tundra graminoids following defoliation. Other investigators have reported increased root respiration in response to herbivory (Dyer and Bokhari 1976; Chung and Trlica 1980), while still others have reported decreased or no change in root respiration (Bokhari 1977; Detling et al. 1979; Farrar and Jones 1986). Our conclusions about the effects of herbivory on root respiration are tentative, since $^{14}CO_2$ evolved from root respiration and microbial respiration were not separated. Nonetheless, herbivory did significantly increase rhizosphere respiration, indicating that above-ground herbivory stimulates soil metabolism and may increase below-ground energy flow (Doll 1991).

In conclusion, above-ground herbivory significantly decreased current carbon assimilates in shoots, and increased plant carbon allocation to roots, rhizosphere respiration, and root exudates. Results support our hypotheses that herbivory alters current plant carbon allocation patterns, and stimulates root exudation and soil metabolism (i.e., respiration). In addition, root exudates represent another link between herbivores of grazing food webs and organisms of soil communities. We further suggest that abundance of soil fauna may increase due to increased quality (greater nitrogen concentration) of roots of grazed plants (Seastedt et al. 1988) and due to increased microbial biomass produced by greater root exudation (Merckx et al. 1985, 1987; Helal and Sauerbeck 1986; Martens 1990). Investigators have reported greater soil microbial biomass associated with grazed

plants (Ruess and McNaughton 1987; Holland 1995), and greater abundance of soil fauna associated with grazed plants (Smolik and Dodd 1983; Ingham and Detling 1984; Leetham and Milchunas 1985). Furthermore, we hypothesize that previously observed increases in plant nitrogen in response to above-ground herbivory (e.g., Holland and Detling 1990) may be explained in part by the soil microbial loop described by Clarholm (1985a, b) where root exudates stimulate microbial growth (bacteria primarily), and protozoa graze the microbial biomass causing an increase in nitrogen mineralization and availability to plants.

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