Carbon flow in an upland grassland: effect of liming on the flux of recently photosynthesized carbon to rhizosphere soil

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Abstract

The effect of liming on the flow of recently photosynthesized carbon to rhizosphere soil was studied using 13CO2 pulse labelling, in an upland grassland ecosystem in Scotland. The use of 13C enabled detection, in the field, of the effect of a 4-year liming period of selected soil plots on C allocation from plant biomass to soil, in comparison with unlimed plots. Photosynthetic rates and carbon turnover were higher in plants grown in limed soils than in those from unlimed plots. Higher δ13C% values were detected in shoots from limed plants than in those from unlimed plants in samples clipped within 15 days of the end of pulse labelling. Analysis of the aboveground plant production corresponding to the 4-year period of liming indicated that the standing biomass was higher in plots that received lime. Lower δ13C% values in limed roots compared with unlimed roots were found, whereas no significant difference was detected between soil samples. Extrapolation of our results indicated that more C has been lost through the soil than has been gained via photosynthetic assimilation because of pasture liming in Scotland during the period 1990–1998. However, the uncertainty associated with such extrapolation based on this single study is high and these estimates are provided only to set our findings in the broader context of national soil carbon emissions.

Keywords: 13C, carbon pools, carbon turnover, liming, rhizosphere soil, upland grassland

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Introduction

Soil is the major sink for carbon in terrestrial ecosystems (Saggar & Hedley, 2001). It is considered that the potential accumulation of C in soil could help mitigate the continuous increase of atmospheric CO2 because of its large capacity for C sequestration (Valentini et al., 2000; Oren et al., 2001; Schlesinger & Lichter, 2001). This is a central issue in international policy on C budgets and was widely discussed in the Kyoto Protocol to the United Nations Framework Convention on Climate Change, leading to commitment by the European Union to a reduction of 8% in CO2 emissions, based on a report on 1990 baseline emissions (Smith et al., 2000a). The UK is committed to a reduction of 12.5% of its 1990 greenhouse gas emissions by 2008–2012 (DETR, 1998; Smith et al., 2000b).

The mass of C in the terrestrial pool is more than twice that in the atmospheric pool (Schlesinger, 1997) and approximately three times greater than that in plant biomass (Mahieu et al., 1999). Consequently, any change in the soil C balance is expected to affect the global C balance. Most of the C in soil organic matter (SOM) is plant-derived through root exudates and decomposition of roots, shoots and litter (Johansson, 1991, 1992; Sindhoj et al., 2000; Kuzyakov & Domanski, 2002). The combination of these inputs and outputs (e.g. decomposition, erosion and leaching) determines the C balance in the SOM pool (Sindhoj et al., 2000) and, consequently, the productivity below- and above-ground, as well as impacting directly on the soil microbial
biodiversity. Environmental changes may directly affect allocation of C from plant to soil. For example, high atmospheric CO₂ concentrations could increase primary productivity and therefore C accumulation in soil, as long as the outputs are not counterbalanced by collateral effects (Niklaus et al., 2002). Management and change of land use can also influence the soil C cycle by increasing or decreasing the C stock (Webster et al., 2000; Guo & Gifford, 2002).

The flux of terrestrial C in managed ecosystems has been studied extensively, but few investigations have focussed on natural and seminatural environments, despite their importance in the global C cycle. For example, temperate grasslands, the subject of this study, account for 6% of the total land surface and approximately 8% of all terrestrial carbon is found in these soils (Schlesinger, 1997). In fact, soil C stocks in grasslands and agricultural land (ca. 10–15 kg C m⁻²) have been shown to be similar to those in forest areas (Korner, 2000), supporting their fundamental role in the global C budget (Goodale & Davidson, 2002; Jackson et al., 2002). Carbon flux studies in grassland ecosystems have provided information on quantification of C allocation from shoots to rhizosphere (Meharg & Killham, 1990, 1991; Meharg, 1994; Stewart & Metherell, 1999), changes in seasonal and annual C inputs (Saggar & Hedley, 2001), and the effects of elevated CO₂ upon C allocation from plants to the soil pool (Hungate et al., 1997; Kuzyakov et al., 1999, Domanski et al., 2001; Kuzyakov & Domanski, 2002). Field studies are less common, and the influence of land management strategies, such as liming, on C flow from plant to soil, has rarely been studied despite relevance to the UK and elsewhere (Chalmers, 2001). Between the mid-1980s and 1990s the average increase of lime use in tillage crops was 10–12% and in grasslands 4–7% in terms of total area limed (Chalmers, 2001). The potential loss of soil C associated with liming is so well accepted that it was a necessary category for inclusion under the land-use selection of national greenhouse gas inventories (IPCC, 1997). The use of lime affects nitrogen (N) mineralization, by increasing the microbial biomass and therefore N assimilation (Adams & Cornforth, 1973; Popovic et al., 1988; Chambers & Garwood, 1998). Lime application has been shown to increase plant production, microbial biomass and net N mineralization in areas with heathland herbs, grasses and Sitka-spruce plantations (Neale et al., 1997). Liming of upland pasture areas in northern Britain increased soil microbial activity and rates of microbial C and N transformations (Isabella & Hopkins, 1994; Hopkins, 1997). The effect of lime application on the increment of basal soil respiration and biomass C was detected in an upland soil pasture even 15 years after improvement (Webster et al., 2000). This study investigates whether the use of lime in seminatural temperate uplands modifies the C flow in such systems, thereby affecting the capacity of soils to retain high amounts of C. The specific objectives were to determine the effect of liming on C flow from plants to the rhizosphere soil in an upland grassland ecosystem, in particular to assess the fate of this C in terms of storage in soil and turnover, and to estimate soil C loss because of this form of land management. Rhizosphere soil is considered as the soil that is influenced by root presence and activity (Darrah, 1993). Assessment of C flow was achieved using the stable isotope ¹³C, pulsed as ¹³CO₂ for 1 or 3 days to limed and unlimed plots of a grassland soil, and subsequent tracking of the signal in shoots, roots, and rhizosphere soil for a period of 4 months.

Materials and methods

Study site

The study site (NT855196, 320 a.s.l.) is located at the Sourhope Research Station, to the South of Kelso in the Scottish Borders, UK. The vegetation of the site is typical for an acid upland grassland (with Agrostis capillaris as the dominant species) and brown forest soils (Davidson et al., 2002; more information of the site can be obtained from this reference and from the homepage of the NERC Soil Biodiversity Programme: http://www.nmw.ac.uk/soilbio/Sourhope.htm). The site is divided into five blocks, each subdivided into six plots equivalent to different treatments. Four blocks and two plots from each of them, corresponding to limed and unlimed treatments, were used in this investigation. Blocks were considered as replicates, providing a total of four replicates per treatment. Lime had been applied annually since 1999 at a rate of 600 g m⁻² per application as CaCO₃ each time (http://www.nmw.ac.uk/soilbio/Sourhope.htm). The dataset provided by the annual surveys made at the site (available at http://www.nmw.ac.uk/soilbio/Sourhope.htm), indicated that there were no major differences in plant composition between limed and unlimed plots. The pH values of unlimed and limed soils were 4.9 and 5.2, respectively. Aboveground plant production from limed and unlimed plots has been recorded during 1999–2002 (NERC Biodiversity Programme database; G. Burt-Smith, personal communication) and was used to calculate differences in plant production between plots.

Pulse labelling

A mobile Stable Isotope Delivery laboratory was used to pulse ¹³CO₂ into 400 mm diameter acrylic labelling
chambers in areas of vegetation in limed and unlimed plots (see Ostle et al., 2000 for details of pulse-labelling laboratory). Two $^{13}$CO$_2$ pulse-labelling experiments were conducted during the growing season in July 2002. A $^{13}$CO$_2$ tracer (up to 99 at% $^{13}$C) was pulsed at a CO$_2$ concentration between 300 and 400 mL/L for periods of approximately 5 h on July 10, 2002 (short pulse labelling experiment) and over 3 consecutive days between July 10 and 12 (long pulse labelling experiment). Plots were not mown during the experiment.

**Sampling**

Samples were taken 1, 7, 15, 29, 57 and 113 days after completion of pulse labelling to encompass both the time when the first $^{13}$C signals were expected in soil and its turnover in the whole plant-soil system. At each sampling, aboveground plant biomass was clipped in each plot from areas corresponding to two soil cores; plant biomass samples were pooled and stored at $-20^\circ$C until further analyses. Two soil cores (2.5 cm diameter, 15 cm depth) per plot were taken at each sampling time, pooled and homogenized. Roots and soil were separated by hand, washed to remove all debris and remaining soil particles and stored frozen. Soil samples (5 g) were oven-dried at 80 $^\circ$C for 12 h to determine water content and the remaining soil was frozen for further analyses. At the end of the sampling period, nonlabelled plant material and soil samples were taken from limed and unlimed plots for estimation of $^{13}$C natural abundance and to determine bulk density.

**Sample processing and analyses of C, N and $^{13}$C**

Plant and soil samples were dried overnight at 80 $^\circ$C and ground in a mill for preparation for C, N, and $^{13}$C determinations. Shoot and root samples were weighed in 1–5 ng amounts and soils in 5–10 ng amounts in tin cups (8 mm x 5 mm). Analyses were carried out by isotope ratio mass spectrometry at the Scottish Crop Research Institute, Invergowrie, Scotland. $^{13}$C enrichments were expressed as $\delta^{13}$C in parts per thousand (%), referring to the difference in ratios between $^{12}$C and $^{13}$C and calculated as described by Biggs et al. (2002):

$$\delta^{13}$C(in%) = [(R$_{\text{sample}}$/R$_{\text{standard}}$) - 1] x 1000,$

where $R = ^{13}$C/$^{12}$C, and the reference standard material is Pee Dee Belemnite (Wang & Hsieh, 2002).

**Statistical analyses**

Data were analysed by ANOVA using the Statistical Package MINITAB. When required, results were transformed by ranking to fulfil the assumption of homogeneity of the variance.

**Results**

Similar trends between the short- and long-pulse-labelling experiments were observed, but as $^{13}$C enrichment levels in samples from the long-pulse experiment were higher, only the results from this experiment are included and discussed in the paper.

**Aboveground plant production and C pools during 4 years of liming**

Lime application to Sourhope soil plots during the period 1999–2002 resulted in higher aboveground plant production than in unlimed plots (Table 1; $P<0.001$ for all years); the difference in productivity between limed and unlimed plots increased approximately fourfold from 0.77 t ha$^{-1}$ yr$^{-1}$ in 1999 to 3.01 t ha$^{-1}$ yr$^{-1}$ in 2002. This resulted in an indirect effect on shoot C (t C ha$^{-1}$), which was also higher in limed plots. With the exception of year 1999, C contents were statistically higher: $P = 0.002$; $P<0.001$; $P<0.001$ for 2000–2002, respectively. The difference in C contents increased substantially during the 4-year period, from 0.16 t C ha$^{-1}$ yr$^{-1}$ in 1999 to 1.00 t C ha$^{-1}$ yr$^{-1}$ in 2002.

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**Table 1 Aboveground plant production and C pool values**

<table>
<thead>
<tr>
<th>Treatment</th>
<th>1999</th>
<th>2000</th>
<th>2001</th>
<th>2002</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant production (t ha$^{-1}$ yr$^{-1}$)</td>
<td>3.27/4.04 ± 0.31</td>
<td>3.7/4.93 ± 0.24</td>
<td>6.43/9.49 ± 0.35</td>
<td>4.29/7.30 ± 0.42</td>
</tr>
<tr>
<td>Difference in production*</td>
<td>0.77</td>
<td>1.18</td>
<td>3.05</td>
<td>3.01</td>
</tr>
<tr>
<td>Shoot C (t C ha$^{-1}$ yr$^{-1}$)</td>
<td>1.32/1.48 ± 0.12</td>
<td>1.52/1.86 ± 0.10</td>
<td>2.60/3.58 ± 0.15</td>
<td>1.73/2.74 ± 0.16</td>
</tr>
<tr>
<td>C (t C ha$^{-1}$)*</td>
<td>0.16</td>
<td>0.34</td>
<td>0.98</td>
<td>1.00</td>
</tr>
</tbody>
</table>

* Differences in biomass and C contents represent the difference between values from limed and unlimed plots. Values indicate mean and standard error of the difference.
At the time of the $^{13}$CO$_2$ pulse labelling and during the sampling period, aboveground plant biomass was greater in limed than in unlimed plots (Fig. 1a), although no statistical difference was found. No difference in root biomass between treatments was found (Fig. 1b). Nevertheless, significant variations ($P < 0.001$) in root biomass with sampling time were detected, most likely as a result of a peak in the biomass in both treatment plots, observed in the samples collected on day 57 after completion of the pulse labelling. Shoots ($P < 0.001$), roots ($P < 0.001$) and soil ($P = 0.04$) samples from unlimed plots contained higher levels of C than their counterparts sampled from limed plots (Fig. 2). Root C content was significantly greater in limed plots throughout the sampling period ($P = 0.042$).

$\delta^{13}$C$\%$ values in the shoots of plants from both treatments was detected by the first sampling compared with natural abundance values (Fig. 3, Table 2). No statistical differences were found between $\delta^{13}$C$\%$ values of shoots from limed plants and those from greater in limed than in unlimed plots (Fig. 1a), although no statistical difference was found. No difference in root biomass between treatments was found (Fig. 1b). Nevertheless, significant variations ($P = 0.001$) in root biomass with sampling time were detected, most likely as a result of a peak in the biomass in both treatment plots, observed in the samples collected on day 57 after completion of the pulse labelling. Shoots ($P < 0.001$), roots ($P < 0.001$) and soil ($P = 0.04$) samples from unlimed plots contained higher levels of C than their counterparts sampled from limed plots (Fig. 2). Root C content was significantly greater in limed plots throughout the sampling period ($P = 0.042$). C concentrations in the other fractions were similar throughout the experiment.

$\delta^{13}$C$\%$ distribution

A rapid increase in $\delta^{13}$C$\%$ in the shoots of plants from both treatments was detected by the first sampling compared with natural abundance values (Fig. 3, Table 2). No statistical differences were found between $\delta^{13}$C$\%$ values of shoots from limed plants and those from...
Nevertheless, analysis of the $^{13}$C% values detected in shoots from plants collected in the first three samplings, corresponding to 15 days after the end of pulse labelling, indicated that shoots from limed plots had statistically higher $^{13}$C values than shoots from unlimed plots ($P = 0.042$). The initial enrichment of $^{13}$C detected in these first three samplings was followed by a significant decrease ($P = 0.021$) that reached the lowest values at the last two sampling times. The amounts of $^{13}$C were always higher than natural abundance levels. In roots, $^{13}$C% increased significantly ($P = 0.043$) with time. There was a significant effect of liming ($P = 0.033$) on enrichment of $^{12}$C, with lower $^{13}$C% in roots of limed plants. $^{13}$C% values in roots of both treatments were higher than natural abundance values throughout the experiment. Analysis of soil samples demonstrated a small enrichment of $^{13}$C after completion of pulse labelling in both limed and unlimed plots compared with unlabelled soils. There were no significant differences in the $^{13}$C% values between limed and unlimed soils, with only small increases in $^{13}$C% values detected in limed plots, with a peak of $^{13}$C enrichment at 57 days.

%N and C/N ratios

Lime had no effect on N concentrations in shoots, but N concentration was lower in plant roots ($P = 0.002$) and in soil ($P = 0.008$) from limed plots (Fig. 4). No significant difference in the N pools was detected with time in any of the fractions. Shoots from unlimed plots presented higher C/N ratios ($P = 0.090$) than those from limed plots, while the ratios determined in roots and soil varied with time ($P < 0.001$ and $P = 0.026$ for roots and soil, respectively) but not between treatments (Fig. 5).

Discussion

Application of lime to acidic soil plots of upland grassland during the period 1999–2002 substantially increased aboveground biomass production and C pools, except for year 1999 where no statistical difference between shoot C pools was found. Compared with this 4-year period of liming, when aboveground biomass collection was intense, no difference was observed in vegetation biomass from limed and unlimed plots in this study, probably because of the short period of sampling (4 months). The well-known Park Grass liming experiment at Rothamsted in the UK, which began in 1856 by fertilizing a pasture area, followed in 1903 by regular liming to most plots, aimed to counteract increasing acidity observed on fertilized plots. Although a very different soil type to that used in

### Table 2 $^{13}$C% natural abundance values and total C, N and C/N ratios from nonlabelled samples

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Fraction</th>
<th>$^{13}$C%</th>
<th>%C</th>
<th>%N</th>
<th>C/N</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>natural</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>abundance</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Limed</td>
<td>Shoots</td>
<td>−28.56 ± 0.44</td>
<td>36.12 ± 1.48</td>
<td>1.51 ± 0.23</td>
<td>24.23 ± 5.46</td>
</tr>
<tr>
<td></td>
<td>Roots</td>
<td>−28.37 ± 0.27</td>
<td>30.68 ± 0.14</td>
<td>1.04 ± 0.25</td>
<td>30.30 ± 6.48</td>
</tr>
<tr>
<td></td>
<td>Soil</td>
<td>−29.13 ± 0.34</td>
<td>11.73 ± 3.18</td>
<td>0.92 ± 0.17</td>
<td>12.86 ± 0.95</td>
</tr>
<tr>
<td>Unlimed</td>
<td>Shoots</td>
<td>−29.12 ± 0.44</td>
<td>38.51 ± 1.48</td>
<td>1.28 ± 0.23</td>
<td>30.75 ± 5.46</td>
</tr>
<tr>
<td></td>
<td>Roots</td>
<td>−28.70 ± 0.27</td>
<td>42.05 ± 0.14</td>
<td>1.40 ± 0.25</td>
<td>30.61 ± 6.48</td>
</tr>
<tr>
<td></td>
<td>Soil</td>
<td>−29.41 ± 0.34</td>
<td>18.21 ± 3.18</td>
<td>1.29 ± 0.17</td>
<td>13.89 ± 0.95</td>
</tr>
</tbody>
</table>

Values represent mean and standard error of the difference.

Fig. 4 Nitrogen content in shoots (a), roots (b) and rhizosphere soil (c) from limed (solid circles) and unlimed (open circles) plots. Bars represent standard errors of the difference.
this study, Park Grass provides many useful insights into plant–soil response to liming. In unlimed Park Grass plots, pH values ranged from 3.5 to 5.7 and the rate of organic matter decomposition was lower than in limed plots, with accumulation of 'peaty', partly decomposed material visible on the surface. These acidic plots also contained no earthworms and demonstrated the lowest vegetation diversity. Liming of these plots, to maintain soil pH at 5, 6 and 7 (as happened in 1965–1968 on previously unlimed plots) led to disappearance of the 'peaty' layer, indicating increased decomposition of organic matter and of C loss (Warren & Johnston, 1964; Thurston et al., 1976; Poulton, 1996). Other investigations where lime has been applied to seminatural ecosystems have demonstrated significant modifications of SOM compared with corresponding, nonimproved areas. For instance, greater rates of mineralization of organic matter were observed in an experiment where lime was added to a Molinia grassland in comparison with a nonimproved area (Cuttle & James, 1995). A survey in a seminatural valley grassland, dominated by Nardus, Agrostis and Festuca, where soils were improved by supply of lime, also indicated that soil solutions from these pastures contained higher contents of organic carbon than those from unimproved sites (Hornung et al., 1986). Liming of forest ecosystems has become a common practice in Nordic countries and Germany to counteract soil acidification. A recent study indicated that lime caused a decrease in the C/N and C/S ratios in the organic horizon (Oe + Oa), and higher heterotrophic CO2 respiration, indicating a strong decline in soil C storage (Nilsson et al., 2001). Our study indicated that soil from limed plots had lower C and N concentrations than unlimed plots, although the C/N ratio did not differ between them. This suggests that organic matter decomposition has been higher in limed than in unlimed soil.

To estimate the potential impact of liming of organic soils in Scotland on the national soil carbon emissions, a simple extrapolation was performed using the measured soil C pool, bulk density and plant biomass production (calculated from reported vegetation productivity obtained during the years 1999–2002; NERC Soil Biodiversity Programme; G. Burt-Smith, personal communication). Over 4 years, liming led to a mean yearly C loss from Sourhope soil at depths of 10 and 20 cm of 1.27 and 2.55 t C ha⁻¹, respectively. If these results are assumed to be representative, and considering a yearly increase of 1100 ha yr⁻¹ of improved pasture on organic soils in Scotland during 1990–1998 based on a Countryside Survey data (R. Milne, Personal Communication), our results suggest that up to 2800 t C yr⁻¹ has been lost as a result of liming in Scotland, while only 960 t C yr⁻¹ has been assimilated via photosynthesis. However, because of the small areas involved, this accounts for less than 0.1% of Scotland’s total soil C emissions (3.04 Mt C; Milne et al., 2002). If all natural ecosystems on organic soils (a total of 1738 k ha) in Scotland were converted to improved grasslands by liming, soil C emissions could increase by between 73% and 146%, but such a dramatic conversion is unlikely, particularly as some of these systems have high conservation value. These calculations suggest that soil C emissions will increase in proportion to the extent of liming, with considerable impacts on the already high soil C emissions reported. The uncertainty associated with such extrapolation based on a single study is, however, high and these estimates are provided only to set our findings in the broader context of national soil carbon emissions.

The use of 13C pulsed as 13CO₂ to plants grown in limed and unlimed plots enabled detection of the effect of lime on recently photosynthesized C and its turnover and transfer between the different pools (i.e. shoots, roots and soil) compared with unlimed samples. Furthermore, the strategy used in this study enabled experimentation in the field, with only minor disturbance to the site during pulse labelling and sampling.

Fig. 5 C/N ratios of shoots (a), roots (b) and rhizosphere soil (c) from limed (solid circles) and unlimed (open circles) plots. Bars represent standard errors of the difference.
found in all aboveground biomass samples after \(^{13}\)CO\(_2\) pulse labelling for 3 days, compared with the natural abundance levels from nonlabelled samples. Shoots from limed plots, clipped during the first three samplings, presented a higher \(\delta^{13}\)C\(_{\text{soil}}\) mean value than shoots from unlimed soils. This suggests that photosynthetic rates of plants exposed to liming were greater than in unlimed plots. The rapid decline in \(^{13}\)C levels observed after 7 days of pulse labelling in plants from limed plots suggests that either shoot respiration or \(^{13}\)C turnover was higher in these plants. If \(^{13}\)C allocation from shoots to roots in plants from limed soils was higher than in unlimed ones, root \(^{13}\)C levels would be expected to be greater. Nevertheless, allocation of \(^{13}\)C from shoots to roots had a clear tendency to increase during the experiment in both limed and unlimed samples, but roots from plants growing in unlimed soils had higher \(\delta^{13}\)C\(_{\text{soil}}\) values than those from limed plants. A possible explanation of these results is that plants grown in limed plots lost C at a greater rate. This is in accordance with expected higher rates of respiration and exudation as soil pH increases, as found in previous studies using \textit{Lolium perenne} and \(^{13}\)C pulse labelling in plots (Meharg & Killham, 1990). The \(^{13}\)C data from shoots and roots confirmed that liming had a strong effect on the physiology of the plant, in accordance with previous investigations demonstrating effects on plant chemical composition and uptake and tissue concentration of mineral elements (Edmeades et al., 1983; Mandal et al., 1998; Tyler & Olsson, 2001). It was not possible to measure plant and soil \(^{13}\)CO\(_2\) respiration during and after completion of pulse labelling, although it is recognized that this would have greatly assisted in evaluating the dynamics of C flow from plants to soils.

Although no clear difference in \(^{13}\)C levels was detected between limed and unlimed soils at any sampling time point, the \(\delta^{13}\)C\(_{\text{soil}}\) values were always higher than natural abundance levels. This indicates that exudation of recently photosynthesized \(^{13}\)C compounds started even before completion of pulse labelling. C root exudates are difficult to measure in the field because of their low concentrations in comparison with the SOM, but also because of their fast decomposition by soil micro-organisms, and their appearance only in the rhizosphere soil (Kuzyakov & Domanski, 2000). Furthermore, Meharg & Killham (1990) found that rhizodeposition could vary from 8% to 67% of the assimilated \(^{13}\)C\(_2\) in \textit{L. perenne}, depending on the stage of development of the plant. The steady but slight increase in \(\delta^{13}\)C\(_{\text{soil}}\)% in limed soils, observed until 57 days after pulse labelling in this study, which was not observed in unlimed soils, was not statistically significant. Nevertheless, that slight trend in \(^{13}\)C enrichment observed particularly in limed soil throughout the experiment indicated a continuous flow of root-derived C, which was then potentially used by the micro-organisms present in the rhizosphere soil. The main factor driving biological interactions belowground is C flow through the rhizosphere (Killham & Yeomans, 2001); however, in spite of its pivotal importance in soil microbial cycling processes, the linkage between C flow and soil microbial biodiversity remains unclear. Johnson et al. (2002) studied C fluxes from plant to arbuscular-mycorrhizal (AM) fungi in a limed upland grassland and found that liming increased fixation of C by the plant and allocation to roots and AM fungi. A more detailed study, however, is needed to determine the extent to which liming affects the whole microbial community in the rhizosphere soil (i.e. bacteria and saprotrophic fungi). In conclusion, these results indicate that liming increases plant biomass production, and consequently the pool and the turnover of C in the plant. The rapid turnover of C, observed particularly in shoots from limed plants and detected by the fast decrease in \(^{13}\)C levels during the first samplings, indicates a greater photosynthetic rate and transfer of C through the plant, in comparison with unlimed plants. Interestingly, the \(^{13}\)C levels in limed roots were lower than in unlimed roots while the levels in soil were similar. Therefore, assuming that the root systems from both treatments had similar respiration rates, the results suggest that the use of \(^{13}\)C exudates by rhizosphere micro-organisms from the managed soils was faster. However, this assumption needs to be tested with respiration measurements of root and soil samples. At the large scale, a potential increase in the use of lime to improve plant productivity of the natural areas in Scotland would cause a substantial increase in soil C emissions by 70–140% compared with the already high emissions reported for the country, although such a major effect has not been observed during the 1990s and more thorough studies are required to confirm this assumption. At the soil microbial level, we hypothesize that the flow of C from limed plots drives changes in soil biodiversity. Recent techniques, such as \(^{13}\)C-enriched polar-lipid-derived fatty acids (Boschker et al., 1998; Boschker & Middelburg, 2002) and stable isotope probing (Radajewski et al., 2000; Manefield et al., 2002a, b) that relate bacterial profiles to their ecological function, are currently being used to test this hypothesis.

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