SEASONAL TRANSFERS OF ASSIMILATED $^{14}$C IN GRASSLAND: PLANT PRODUCTION AND TURNOVER, SOIL AND PLANT RESPIRATION

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Summary—Six areas of native grassland were labelled with $^{14}$C during a growing season. Transfers from the foliage to the roots and root respiration were measured. Plant production and turnover rates were determined by sampling the labelled material at different periods following exposure to $^{14}$CO$_2$.

Above to beneath ground plant production ratios ranged between 1.1 and 1.9 with maximal translocation to the roots occurring during the drier summer months. The distribution of the photosynthates in the roots at different depths changed with time and soil moisture content. The upper part of the soil (0-10 cm) contained 49-77% of the labelled C found beneath the soil surface. Measurement of transfers with time of the above ground labelled C from living to dead plant and litter categories gave an insight into foliage dynamics and made it possible to estimate the seasonal shoot production at 130 g C m$^{-2}$ (1300 kg ha$^{-1}$). Root growth represented 100 g C m$^{-2}$ (1000 kg ha$^{-1}$).

Calculations of root and soil respiration were based on the CO$_2$ profiles in the soil. The fluxes of labelled and unlabelled CO$_2$ at the soil surface were estimated using the diffusion equation method. Respiration by roots and closely associated soil organisms accounted for 12 per cent of the net assimilation of CO$_2$ by the plants. This proportion was constant throughout the season and represented 19 per cent of the total CO$_2$ evolved at the soil surface.

INTRODUCTION

In agricultural systems, harvestable yield is a major criterion in assessing plant growth and soil management practices. In ecosystem studies, C and energy transfer, as measured by rates of photosynthesis, production of dry matter and respiration, are of special importance in interpreting the functioning of the system. In a grassland community, roots and soil organic matter account for a large part of the C storage. Harvest and CO$_2$ exchange methods of measuring primary production fail to give information concerning underground biomass changes if growth and decomposition occur simultaneously.

A detailed study of C transfers within the plant-soil system of grassland has been made possible by the application of radioisotopes (Dahlman, 1968; Warembourg and Paul, 1973). This involves labelling the plants in situ with $^{14}$CO$_2$ and following the labelled C through the different compartments of the system. This paper presents data for shoot production, C translocation to the roots, root and soil respiration and turnover rates of plant material after $^{14}$C labelling of plants during a season in the field.

MATERIALS AND METHODS

Studies were conducted on native grassland at the Matador site of the Canadian IBP in southwestern Saskatchewan. The vegetation is an Agropyron-Koeleria association and the soil a Sceptre heavy clay classified as Rego Brown Chernozem.

Prairie grass was labelled, in situ, with $^{14}$CO$_2$ under a hemispherical cellulose acetate-butyrate canopy (Warembourg and Paul, 1973). The temperature inside the canopy was adjusted to ambient by the use of sensors which controlled the circulation of refrigerant through cooling coils. $^{14}$CO$_2$ was maintained at a concentration of 0.03% (v/v) with a specific activity of 500 $\mu$Ci g$^{-1}$ by automatic addition of $^{14}$CO$_2$ as needed. Samples of soil atmosphere were taken from aluminium tubes (diffusion wells) installed at a 45° angle under the canopy at different depths in the soil.

Measurements of CO$_2$ concentration, using a gas chromatograph, permitted the calculation of the daily flux at the soil surface (de Jong and Schappert, 1972). $^{14}$CO$_2$ in the soil atmosphere samples were measured with a scintillation counter after NaOH absorption of the $^{14}$CO$_2$ in 10 ml of air. The moisture content of the soil was determined with neutron probes and from rainfall data.

Plant material was sampled by clipping the shoots. Visual observation was used to separate the shoots into three categories: green, yellow and gray or standing dead. Soil-root cores obtained with a hydraulic corer were washed with a reciprocating sieve washer. Plant C was measured by dry combustion and radioassays were done by scintillation counting of an aliquot of the NaOH solution used to trap the CO$_2$ from combustion (Warembourg and Paul, 1973).

Calendar of the labelling experiments

Six separate areas of the site were labelled during the growing season, 18 May and 31 May, 21 June, 5 July and 20 July, and 7 September. The period of exposure of the plants to $^{14}$CO$_2$ varied from 55 to 100 h. During each experiment, the soil atmosphere
was sampled once a day for CO₂ and ¹⁴CO₂. When no measurable radioactivity (less than 30 counts min⁻¹ per 10 ml of soil air) was detected, plant material was collected and measured for C and radioactivity. Root sampling consisted of three or four cores extracted from each labelled area per sampling date. In late September another set of plant samples was taken from each area.

Expression of the results

The quantities of biomass and specific activities (dpm g⁻¹ biomass C) were measured values. The activities g⁻¹ of ¹⁴C m⁻² were calculated by reference to the initial specific activity of the CO₂ used to label the plants.

RESULTS

Distribution of the labelled C between shoots and roots

The soil ¹⁴CO₂ was monitored during and after each period of exposure to radioactive CO₂. The production of ¹⁴CO₂ in the soil was attributed to roots and associated microbial respiration. When the soil atmosphere no longer contained measurable radioactivity, it was assumed that movement of ¹⁴C from the foliage to the roots had ceased and the root C had been deposited in growth or storage organs. At this state, the ¹⁴C content of above and beneath ground plant material was assumed to represent the net biomass increase attributable to ¹⁴C assimilation by the plants.

Because of differences between the duration of the labelling periods, season and weather during the different experiments, no comparisons between the absolute amount of ¹⁴C assimilated by the plants from one experiment to the next were made. But, for any one period, the proportion of ¹⁴C located above and beneath ground could be compared. The ratio between shoot and root growth, indicated that slightly more ¹⁴C was retained by the foliage than was stored in the roots (Table 1). The maximum occurred in the 18–20 May and 31 May to 4 June labellings when 65 per cent of the plant ¹⁴C was deposited above ground. This was the period of most active vegetative growth when the green biomass increased by 50 g m⁻². In the drier summer, 53 to 57 per cent of the label remained in the shoots.

Root respiration

The pattern of labelled C evolution after assimilation by the plants was related to the moisture conditions of the soil during the experiments (Figs. 1a and 1c). From May to early July when the soil was moist, utilization of ¹⁴C by the roots and consequently ¹⁴C evolution was extended over 3 to 4 weeks. Differences in diffusion rate caused by soil moisture changes affected the daily flux of CO₂. Wetting of the soil increased the resistance to CO₂ diffusion and diminished the CO₂ flux at the soil surface (Figs. 1a and 1b).

When the soil moisture content was below 27% (v/v) (15 atm tension, 1530 kPa) nearly all the evolution of labelled C occurred during the first week following assimilation. At higher soil moisture contents, ¹⁴CO₂ evolution occurred over a longer period. Measurements of specific activities of the soil CO₂ at different depths indicated a maximum near the soil surface (data not shown) where most roots were located. Specific activities of soil air sampled at depths >20 cm were higher under dry than wet conditions.

Total labelled C lost from the soil system was calculated from the daily fluxes at the soil surface (Table 2). Net assimilation of labelled C ranged from 932 to 6715 mg C m⁻² in 1971 and 8000 mg C in August 1970. Net assimilation was calculated as the ¹⁴C remaining in the plants at the conclusion of ¹⁴C root respiration plus ¹⁴C evolved by the roots during the period of measurement. ¹⁴CO₂ respiration by the aerial portion of the plants was not taken into account. Respiration by roots plus associated microorganisms accounted for 9.4 to 13% in 1971 and 14.8 per cent of the net assimilated ¹⁴C in August 1970. Root respired ¹⁴C represented 20 to 29% of the C translocated from the foliage to the roots. This relatively constant proportion throughout the year despite differences in the daily rate of evolution (Fig. 1c) indicated a higher rate of energy consumption over a short period of utilization under dry conditions.

Table 1. Biomass and labelled C in shoots and roots after labelling with ¹⁴CO₂ and completion of labelled root respiration

<table>
<thead>
<tr>
<th></th>
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</thead>
<tbody>
<tr>
<td>Sampling dates</td>
<td>31 May</td>
<td>28 June</td>
<td>20 July</td>
<td>1 August</td>
<td>12 August</td>
<td>21 Sept.</td>
</tr>
<tr>
<td><strong>ABOVE GROUND</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total standing Biomass C g m⁻²</td>
<td>130</td>
<td>237</td>
<td>150</td>
<td>182</td>
<td>182</td>
<td>160</td>
</tr>
<tr>
<td>Labelled C mg m⁻²</td>
<td>860 ± 30</td>
<td>3862 ± 150</td>
<td>2238 ± 100</td>
<td>5306 ± 200</td>
<td>2055 ± 100</td>
<td>485 ± 20</td>
</tr>
<tr>
<td>Percent of plant label</td>
<td>65</td>
<td>65.5</td>
<td>56</td>
<td>57</td>
<td>53</td>
<td>57</td>
</tr>
<tr>
<td><strong>BENEATH GROUND</strong></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass C g m⁻²</td>
<td>543 ± 150</td>
<td>705 ± 60</td>
<td>659 ± 70</td>
<td>658 ± 50</td>
<td>680 ± 75</td>
<td>718 ± 80</td>
</tr>
<tr>
<td>Percent of Biomass C</td>
<td>80</td>
<td>75</td>
<td>81</td>
<td>78</td>
<td>79</td>
<td>82</td>
</tr>
<tr>
<td>Beneath ground</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Labelled C mg m⁻²</td>
<td>463 ± 23</td>
<td>2031 ± 200</td>
<td>1772 ± 170</td>
<td>4044 ± 350</td>
<td>1803 ± 200</td>
<td>359 ± 40</td>
</tr>
<tr>
<td>Percent of plant label</td>
<td>35</td>
<td>34.5</td>
<td>44</td>
<td>43</td>
<td>47</td>
<td>43</td>
</tr>
</tbody>
</table>

* Long labelling period data only used for determining distribution of carbon.
Patterns of labelled-C distribution within the root system

The 33 measurements did not indicate a significant difference in the total root C and its distribution with depth during the 1971 growing season. Data are therefore presented as average total C (Table 3). The maximum quantity of underground material was concentrated in the 0 to 10 cm soil layer (50 per cent). There was a regular decrease of roots with depth but 4.5 per cent were still present below 100 cm.

A range of 73–77% of the root label was recovered in the 0–10 cm layer after the 18 May, 21 June, 5 and 20 July labelings; only 49 per cent was found in the 31 May and 55 per cent for 7 September labelings. A deeper penetration of the labelled C was recorded for these two experiments. Approximately 4.5 per cent of the root label was located below the 100 cm depth after the 31 May labelling. The small amount of 14C located below 40 cm (5 per cent) after the 18 May labelling was attributed to a soil temperature that was still <10°C at that depth.

Above ground labelled-C distribution

The amount of 14C utilized and the short term exposure should not have caused radiation damage

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Labelled C, net assimilation mg m⁻²</td>
<td>1467</td>
<td>6715</td>
<td>4562</td>
<td>4432</td>
<td>932</td>
<td>8016</td>
<td></td>
</tr>
<tr>
<td>Labelled C, root respiration mg m⁻²</td>
<td>144</td>
<td>833</td>
<td>552</td>
<td>574</td>
<td>88</td>
<td>1186</td>
<td></td>
</tr>
<tr>
<td>Labelled C translocated to the roots, mg m⁻²</td>
<td>607</td>
<td>2853</td>
<td>2324</td>
<td>2377</td>
<td>447</td>
<td>4886</td>
<td></td>
</tr>
<tr>
<td>Root respiration, percent of root translocation</td>
<td>23.7</td>
<td>28.8</td>
<td>23.8</td>
<td>24.2</td>
<td>19.7</td>
<td>24.3</td>
<td></td>
</tr>
<tr>
<td>Root respiration, percent of net assimilation</td>
<td>9.8</td>
<td>12.2</td>
<td>12.1</td>
<td>13.0</td>
<td>9.4</td>
<td>14.8</td>
<td></td>
</tr>
</tbody>
</table>
The measured transfer of labelled grass from the green to the standing dead categories between the times of the initial labelling and the sampling of the plant material was attributed to natural decay of the foliage.

The green plant material contained 100 per cent of the above ground label immediately after assimilation of $^{14}$C. The minimum transfer occurred in June and July with 8 per cent moving from green to yellow in 28 days (Table 4). It increased slightly near the end of July with 13 per cent in 23 days. The rate of transfer was maximum when the soil moisture was low as at the end of May, 13 per cent in 13 days, and during the late summer months when 31 per cent of the September grass was already yellow 14 days later. The second sampling of above ground material on 21 September indicated that none of the material synthesized in May was found in the green shoots. Only 8 per cent of the early June production was still in the green material by September.

The green material standing in June had been almost completely changed into yellow by the end of September. It can be assumed that the September green material was produced after June. On this basis, the foliage production was estimated as standing green in June plus May production already yellow in June plus green biomass standing in September corrected for the remainder from June. This accounted for a total of 107 g C m$^{-2}$.

A more general expression was used to ascertain foliage production. Growth between two sampling dates $t_1$ and $t_2$ is equal to the green biomass at time $t_1$ minus the proportion of green biomass measured at time $t_1$ that was still green at time $t_2$:

$$\text{foliage production} = V_{t_1} - (1 - n_1) V_{t_1-t_2}$$

where $V_{t_1}$ = green biomass at time $t_1$; $n_1$ = rate of transfer or rate of decay between $(t - 1)$ and $t$; $V_{t_1-t_2}$ = green biomass at time $(t - 1)$. The values for $V_t$ are given in Table 4 and those of $n_1$ were

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**Table 3. Distribution of labelled C in the roots**

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>0-10*</th>
<th>10-25</th>
<th>25-40</th>
<th>40-55</th>
<th>55-70</th>
<th>70-85</th>
<th>85-100</th>
<th>&gt;100</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total C g m$^{-2}$</td>
<td>336 ± 60</td>
<td>100 ± 28</td>
<td>64 ± 20</td>
<td>44 ± 15</td>
<td>42 ± 12</td>
<td>28 ± 11</td>
<td>12 ± 0</td>
<td>50 ± 10</td>
</tr>
<tr>
<td>Distribution per cent</td>
<td>50.4</td>
<td>15.0</td>
<td>9.6</td>
<td>6.6</td>
<td>6.3</td>
<td>4.2</td>
<td>3.3</td>
<td>7.0</td>
</tr>
</tbody>
</table>

* 0-10 cm includes roots plus rhizomes.

(Sauerbeck and Fuhr, 1963). The measured transfer of labelled grass from the green to the standing dead categories between the times of the initial labelling and the sampling of the plant material was attributed to natural decay of the foliage.

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**Table 4. Distribution of above ground labelled C after different periods following labelling with $^{14}$CO$_2$ (1971 grassland field experiments)**

<table>
<thead>
<tr>
<th>Sampling experiments</th>
<th>Dates</th>
<th>Time after labelling (days)</th>
<th>Green biomass g m$^{-2}$</th>
<th>Standing green</th>
<th>Standing yellow</th>
<th>Grey plus litter</th>
</tr>
</thead>
<tbody>
<tr>
<td>18 May</td>
<td>31 May</td>
<td>13</td>
<td>27</td>
<td>87</td>
<td>13</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>21 Sept.</td>
<td>126</td>
<td>33.5</td>
<td>1</td>
<td>68</td>
<td>31</td>
</tr>
<tr>
<td>31 May</td>
<td>28 June</td>
<td>28</td>
<td>9.3</td>
<td>92</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>21 Sept.</td>
<td>113</td>
<td>39.1</td>
<td>8</td>
<td>80</td>
<td>12</td>
</tr>
<tr>
<td>21 June</td>
<td>20 July</td>
<td>29</td>
<td>52.5</td>
<td>92</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>21 Sept.</td>
<td>92</td>
<td>30.2</td>
<td>28</td>
<td>63</td>
<td>12</td>
</tr>
<tr>
<td>20 July</td>
<td>12 Aug.</td>
<td>63</td>
<td>63</td>
<td>87</td>
<td>13</td>
<td>0</td>
</tr>
<tr>
<td>7 Sept.</td>
<td>21 Sept.</td>
<td>63</td>
<td>28.7</td>
<td>28</td>
<td>60</td>
<td>12</td>
</tr>
</tbody>
</table>

* 0-10 cm includes roots plus rhizomes.
Seasonal transfers of assimilated $^{14}$C in grassland

Table 5. Decrease of root $^{14}$C with time

<table>
<thead>
<tr>
<th>Sampling dates</th>
<th>12 Aug.</th>
<th>1 Aug.</th>
<th>20 July</th>
<th>28 June</th>
<th>31 May</th>
</tr>
</thead>
<tbody>
<tr>
<td>21 Sept.</td>
<td>40</td>
<td>51</td>
<td>63</td>
<td>86</td>
<td>113</td>
</tr>
<tr>
<td>21 Sept.</td>
<td>20</td>
<td>34</td>
<td>56</td>
<td>41</td>
<td>52</td>
</tr>
</tbody>
</table>

Period between sampling
$^{14}$C lost percentage

Calculated from the proportion of the label lost between the different sampling dates. For the period under study, a total of almost 100 g of C production per m$^2$ was calculated using this equation. This corroborates the above result and shows the application of $^{14}$CO$_2$ labelling experiments to productivity studies.

Transformation of yellow material into standing dead plus litter was indicated by the different proportions measured in September (Table 4). Thirty per cent of the May labelled production, 12 per cent of June’s and July’s and none of September’s were found in these categories at that date.

**Decrease of root labelled C as a function of time, root turnover**

As much as 50 per cent of the root label measured in May was not accounted for by September (Table 5). Less loss was recorded for the later experiments; 20 per cent of the 12 August label had disappeared by 21 September.

The rate of labelled C disappearance from the roots indicated an exponential relationship with time. The data, plotted on semi-logarithmic paper, are located along a straight line (Fig. 2) and the expression of root label variation with time is represented by the following regression equation:

$$V = V_0 e^{-6.45 \times 10^{-3} t}$$

in which $V$ is the root material remaining at time $t$, $V_0$ is the initial root biomass, $e$ is the base of the natural logarithm and $t$ the time (days). If $V$ is expressed in percent, $V_0$ the initial root production is equal to 100 per cent. The equation can be expressed as:

$$V = V_0 e^{-0.693 T / t},$$

with $T = \text{half life of roots}$

- 107 days.

Measurements of labelled C decrease in the roots at different depths indicate a slightly higher rate for the 0–10 cm, the lowest being below 40 cm depth.

**Transfer of labelled C from the roots to the shoots**

New shoots developing on the area previously clipped in May were sampled in September. Radioactivity measurements showed that 26.6 mg m$^{-2}$ of labelled C originated from the roots. This accounted for 6 per cent of the root label that was present at the end of May (data not shown). Even if transfer was accentuated by clipping the plants, these data indicate that root to shoot transfers were not negligible.

**Modelling the dynamics of C**

Relationships between the different compartments represented in Fig. 3 can be estimated on a time basis. After a certain period, the amount of C located in the various portions of the plants is dependent upon the balance between input and output. This can be expressed by:

$$\frac{\Delta V_i}{\Delta t} = k_i P_a - n V_i.$$  \hspace{1cm} (1)

The change of the green biomass is equal to the increase by growth $k_i P_a$ minus the decay or transfer into yellow material $n V_i$ that occurred during the same period. $P_a$ is the net photosynthesis or apparent assimilation per unit of time. The portion of apparent assimilation ($k_i$) that stayed above ground after completion of translocation to the roots was estimated from the above to beneath ground production ratio.

$$V = V_0 e^{-6.45 \times 10^{-3} t}$$

$$V = V_0 e^{-0.693 T / t},$$

$T = \text{half life of roots}$

- 107 days.

\hspace{1cm} Fig. 2. Decrease of root labelled C as function of time following completion of labelled root respiration (1971 grassland experiments).
(Table 1). After correction for root respiration, $k_1$ averaged 0.6 from May until the end of June and 0.5 from July to the end of September. The proportion of green biomass transferred into the yellow compartment ($n$) was calculated from Table 4 as $n = 0.01$ between 18 May and 31 May, 0.0027 between 1 June and 20 July, 0.0057 between 21 July and 12 August, 0.011 between 13 August and 7 September, and 0.022 after 8 September. These values were expressed per unit of time (in days).

The root biomass equation is:

$$\Delta V_2 = \frac{k'_1 P_n - n(t)V_1}{\Delta t}$$

This represents the variation of the root mass. It is equal to the increase by growth, $k'_1 P_n$ minus root decomposition, $(q_{(t-d_o)} V_2)$. $k_2$, the proportion of net assimilation that stayed in the roots was calculated from $k_1$ by the relation: $k_2 = [(1 - k_1) - r_2]$ with $r_2$ being the proportion of apparent net assimilation dissipated by root respiration per unit of time. According to the preceding data, root respiration averaged 12 per cent of net assimilation and lasted for 30 days for the period from May until 15 July and 15 days after that date. This gave $r_2$ a value of 0.004 day$^{-1}$ before 15 July, 0.008 after that date (for the purpose of modelling, it was assumed that a constant proportion of the 12 per cent root respiration was evolved each day). The expression $q_{(t-d_o)}$ represents the proportion of the root $^{14}$C lost by decomposition and was calculated from the equation $V = V_0 e^{-0.45 \times 10^{-5}}$ described earlier. $d_o$ represents the period of active root respiration. It was assumed that decomposition started after active root respiration ceased.

**Discussion**

Shoot production between 18 May and 21 September, was estimated at 103 g C m$^{-2}$ with a high rate
of transfer into yellow material between sampling dates. Despite this, no disappearance of the initial material from the total above ground vegetation occurred during the period of observation. The value of 103 g C m\(^{-2}\) can be corrected for the top growth that occurred after September. This accounted for 30 g C thus giving a value of 133 g C for the foliage in 1971.

Underground production, calculated from the \(^{14}C\) data, averaged 43 per cent of the net total production, or about 100 g C m\(^{-2}\). At Matador, total underground material averaged 660 g C m\(^{-2}\) (R.T. Coupland, personal communication). Fluctuations during 1971 were not statistically significant indicating that production was balanced by losses.

Root respiration was directly related to net assimilation and averaged 12 per cent of the net C assimilated by the plants. It amounted to 25 g m\(^{-2}\) during the period under study and was estimated to be 32 g m\(^{-2}\) for the growing season. A total of 132 g C m\(^{-2}\) were respired by the soil between May and September. The respiration by underground plant tissue and its associated microbial components represented 25/132 = 19 per cent of the total respiration during this period. The above calculation is based on the premise that all the \(^{14}CO_2\) evolved by the plant–root–soil system emanated from the plant roots and their closely associated organisms such as sap feeders and mycorrhiza. The \(^{14}CO_2\) was measured for a period of 10 to 30 days after labelling until \(^{14}CO_2\) in the soil dropped below measureable amounts. CO\(_2\) evolution by organisms other than plant roots no doubt occurred. This means that the 19 per cent figure is an overestimate. Recipping of sampled plots, however, showed translocation of root stored \(^{14}C\) to new shoots. A portion of this must have been respired and could have counter-balanced the \(^{14}CO_2\) not attributed to other organisms during the initial measurement period.

The estimates for root CO\(_2\) production are low when compared to literature values that range between 30 and 70 per cent of the total soil CO\(_2\) attributed to the plants (Brown et al., 1965; Lundegardh, 1927; Woldendorp, 1963). Generally, the latter information was obtained from differences between the respiration of bare and cropped soil or between sterile and non-sterile systems; therefore they are difficult to compare with \textit{in situ} values obtained in this study.

This tracer study shows the application of \(^{14}C\) techniques in studying C transfer through the soil–plant system. Other systems may not be as amenable to canopy techniques but the methods and principle used should with adaption be applicable to a number of other systems, especially cropland. Grasslands are subject to large variations in abiotic conditions and data from small plots obtained during one year must be interpreted with caution. The insights gained with \(^{14}C\) and the equations utilized should however be useful in further understanding C transfer processes in the soil–plant system.

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REFERENCES


