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Estimating seasonal and annual carbon inputs, and root decomposition rates in a temperate pasture following field ^{14}C pulse-labelling

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Abstract

Using a ^{14}C pulse-labelling technique, we studied the seasonal changes in assimilation and partitioning of photoassimilated C in the plant–root–soil components of a temperate pasture. Pasture and soil samples were taken after 4-h, and 35-day chase periods, to examine these seasonal ^{14}C fluxes. Total C and ^{14}C were determined in the shoot, root and soil system. The amounts of C translocated annually to roots and soil were also estimated from the seasonal ^{14}C distribution and pasture growth. The *in situ* field decomposition of newly formed roots during different seasons, also using ^{14}C-labelling, was studied for one year in undisturbed rhizosphere soil. The ^{14}C-labelled roots were sampled five times and decomposition rates were calculated assuming first-order decomposition.

Annual pasture production at the site was 16 020 kg DM ha^{-1}, and pasture growth varied with season being highest (75–79 kg ha^{-1} d^{-1}) in spring and lowest (18–20 kg ha^{-1} d^{-1}) in winter. The above- and below-ground partitioning of ^{14}C also varied with the season. The respiratory ^{14}C–CO_2 losses, calculated as the difference between the total amounts of ^{14}C recovered in the soil-plant system at 4 h and 35 days, were high (66–70%) during the summer, autumn and winter season, and low (37–39%) during the spring and late-spring season. Pasture plants partitioned more C below-ground during spring compared with summer, autumn and winter seasons. Overall, at this high fertility dairy pasture site, 18 220 kg C/ha was respired, 6490 kg remained above-ground in the shoot, and 6820 kg was translocated to roots and 1320 kg to soil. Root decomposition rate constant (k) differed widely with the season and were the highest for the autumn roots. The half-life was highest (111 days) for autumn roots and lowest (64 days) for spring roots. About one-third of the root label measured in the spring season disappeared in the first 5 weeks after the initial 35 Day of allocation period. The late spring, summer, late summer and winter roots had intermediate half-lives (88–94 days). These results indicate that seasonal changes in root growth and decomposition should be accounted for to give a better quantification of root turnover.

Abbreviations: C – carbon; DAP – diammonium phosphate; Day 0 – 4 hours after labelling; Day 35 – 35 days after labelling; DM – dry matter yield; first 5 weeks – 5 weeks after the initial 35 Day of allocation period; SOM – soil organic matter

Introduction

Soils, the major sink for carbon (C) in terrestrial ecosystems, account for two-thirds of the total carbon pool (Schimel et al., 1995). Soil organic C is important because of its influence on soil physical, chemical and biological properties and processes. Changes in soil organic C levels also have global impacts on C sequestration and net emissions of CO_2, the major greenhouse gas . Maintenance of soil organic C levels depends on the balance between the annual C inputs to soil and decomposition. Between 20 and 50% of all assimilated C transported below-ground to the root system (Swinnen et al., 1995a; Saggar et al., 1997, 1999) is one of the major factors determining the

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quality and quantity of soil organic matter (SOM) in agroecosystems. Consequently, the C inputs is an important driving variable in SOM simulation models (Bolinder et al., 1997, 1999).

In grazed pasture soils, annual C inputs originate from: C returned in animal excreta; ungrazed plant litter; annual root growth; and from losses of rhizodeposits from the plant root (soluble exudates, secretions and lysates, dead root losses, fresh organic matter). Within a pasture system, Saggar et al. (1997, 1999) showed that C inputs were strongly influenced by phosphorus (P) fertility and slope. These studies provided the data on C fluxes for constructing C budgets for a grazed hill-country ecosystem. However, these estimates were based on the patterns of C distribution during the period of very active pasture growth in spring. Work by Barker et al. (1988) shows that annual root growth rates can vary 3 – 4-fold, being highest in spring and lowest in winter, in proportion to the above-ground biomass accumulation. To what extent these differences in growth rate influence the partitioning of photoassimilated C to the root and to soil has not been measured. Thus, quantification of the rates at which C moves to roots (allocation) in each season, and from roots to soil (exudation and root dynamics), is essential for more accurate and complete understanding of C inputs and fluxes through a pasture ecosystem and to predict accurately soil C balance in temperate pastures.

Earlier New Zealand studies on seasonal changes in new root growth (Caradus and Evans, 1977) found that it coincided with soil moisture availability. Summer was the season of greatest C allocation to roots in a Canadian native grass (Warembourg and Paul, 1977) compared to spring/autumn or spring for ryegrass (*Lolium perenne* L.) (Parsons and Robson, 1981; Stewart and Metherell, 1999). Using biomass sampling, Barker et al. (1988) found that root production was highest during spring and least during winter. Apart from these studies, there is little information available for temperate pastures on the seasonal patterns of root production, and our knowledge about the below-ground annual C inputs is fragmentary. As grasslands cover 20% of the global land area (Mellilo et al., 1993), with 30% of this in the temperate region (Radcliffe and Baars, 1987), better estimates of below-ground inputs in these grassland ecosystems is vital to improve the ability of SOM simulation models to predict soil C balance.

The use of a constant value for root decomposition when calculating root turnover on an annual basis can give misleading results (Andrèn et al., 1992). Quantitative information on seasonal root decomposition rates is also required to improve root production calculations and the estimates of annual root C inputs. The lack of suitable techniques to follow C flows through the plant–root–soil system is probably responsible for lack of knowledge about below-ground seasonal processes. Pulse-labelling with ^{14}C or ^{13}C can be used to provide quantitative information on below-ground C inputs and *in-situ* decomposition rates of this newly formed root material (Van Ginkel et al., 1996). A series of pulse-labellings during different growth periods have been successfully used to estimate below-ground C input and root turnover (Swinnen et al., 1995a, b; Stewart and Metherell, 1999).

This paper reports on the seasonal changes in assimilation and partitioning of photoassimilated C in the plant–root–soil system of a temperate pasture, and root decomposition rates. In our current experiment, the *in situ* field decomposition of newly formed roots during different seasons, also using a series of ^{14}C-labelling, was also studied for 1 year in undisturbed rhizosphere soil. Our objectives were (i) to determine the assimilation and partitioning of photoassimilated ^{14}C at different seasons of pasture growth, (ii) to measure seasonal C fluxes in pastures, and (iii) to determine the seasonal *in situ* root decomposition under field conditions.

Materials and methods

Sites

The ^{14}C pulse labelling experiment and subsequent root decomposition studies were conducted between September 1998 and July 2000 at Massey University Dairy Farm, Dairy Unit I, Palmerston North. The site was a high fertility farm, that had continuously received 90 kg N/ha and 40 kg P/ha as Urea and DAP since 1996, with previous applications of 6.5 kg P/ha and 15 kg K/ha as potash superphosphate each year. Soils are Karapoti fine sandy loams, classified as Weathered Fluvial Recent Soils (Hewitt, 1998) and Dystric Eutrudepts (Soil Survey Staff, 1996). The site has an average rainfall (over the last 30 years) of 962 mm, which is well distributed throughout the year. The annual rainfall during the study period was 891 mm in 1998–1999 (August 1998–July 1999) and 838 mm in 1999–2000 (August 1999–July 2000) and soil temperature at 100 mm depth ranged between 6.5 and

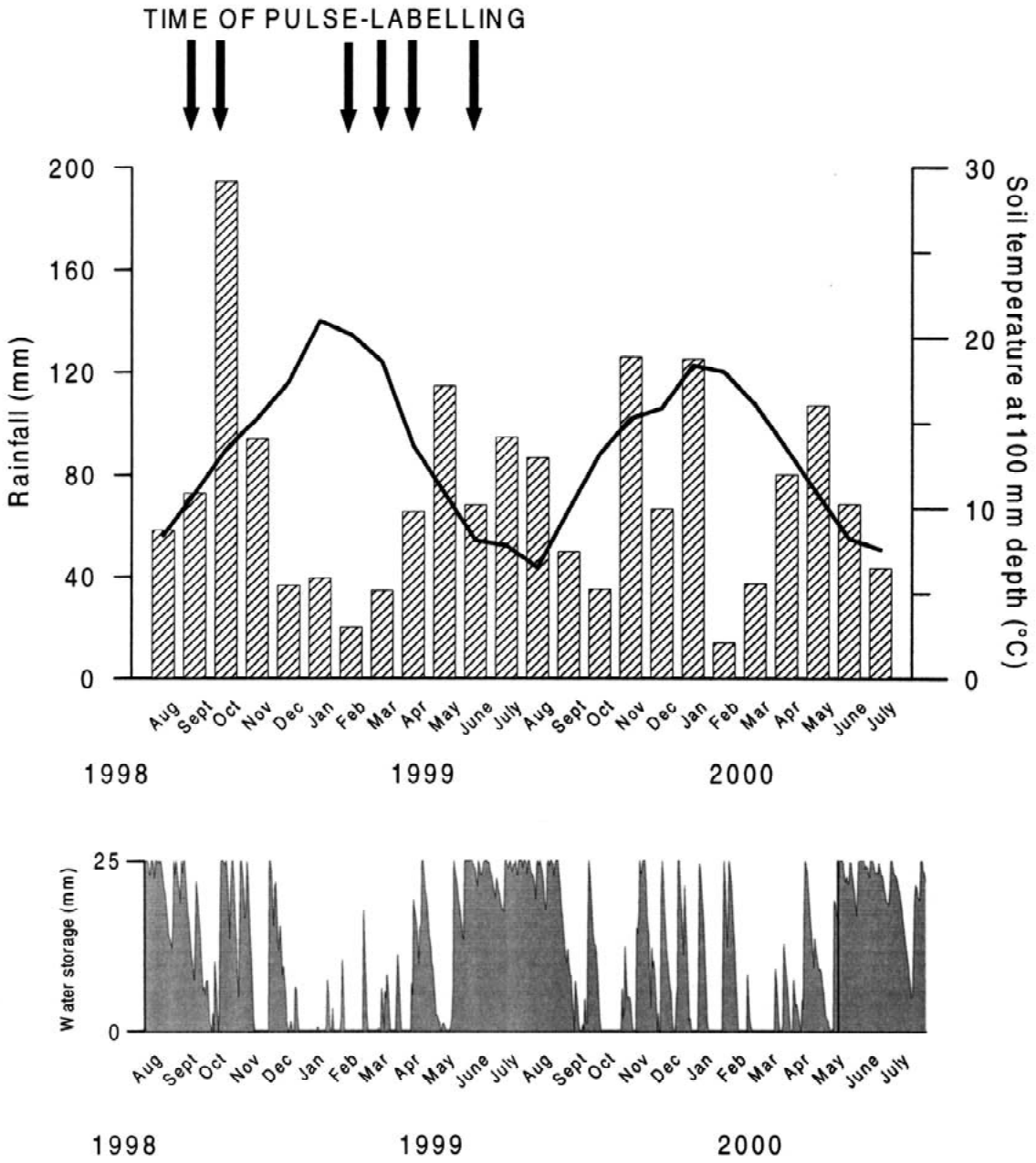

Figure 1. Rainfall and soil temperature distribution, and soil water balance at the pasture site during 1998–2000.

20.2 °C (see Figure 1). A pasture water balance model of Scotter et al. (1979), which takes into account the effect of soil water deficits on evapotranspiration, was used to compute daily soil water balance for the two year period (Figure 1.)

A representative 25 × 25 m section of the farm was fenced 3–4 weeks prior to labelling to exclude grazing and for safe use of radioisotopes. The area was mown to 20 mm height, one week before labelling.

Assessment of pasture production

Six frame exclosures (0.33 × 0.66 m) were located. These exclosures were rotated around six pre-selected points, being moved to a pre-trimmed area at the start

of each measurement period. Pre-trim and harvest cuts were made 10–20 mm above ground level using hand clippers. Intervals between harvest varied from 19 to 84 days, depending upon herbage accumulation. After recording the green weight of the clippings, samples were oven-dried at 65 °C for 24–48 h. DM percentages were calculated and yields converted to total pasture DM ha^{-1} yr^{-1}.

$^{14}CO_2$–C pulse-labelling

Full details of techniques for $^{14}CO_2$–C pulse-labelling, shoot, root and soil sampling, and total C and ^{14}C analyses are presented elsewhere (Saggar and Searle, 1995; Saggar et al., 1997, 1999) and summarised below.

Labelling

Six initial labelling times were established by inserting lysimeters at six different seasons of pasture growth, i.e. spring (14/9/98), late spring (21/10/98), summer (17/2/99), late summer (25/3/99), autumn (28/4/99) and winter (21/6/99) (Table 1). To simulate the grazed conditions above-ground plants were cut to 20 mm height, one week before ^{14}C pulse-labelling. A representative area (250 mm diam.) was pulse-labelled, between 1000 and 1200 h, using a sealed hemispherical chamber made from specially adapted perspex fishbowl and PVC pipe. The ^{14}C–CO_2 gas was injected into the hemisphere, through a rubber septum. Previous work (Saggar and Searle, 1995) has shown that regardless of the time of introduction of the ^{14}C–CO_2 pulse between 900 and 1300 h over a two-day period, within 2 h of injection of ^{14}C–CO_2, the ^{14}C–CO_2 level in the chamber was $\leq 2\%$ of the total added, indicating that the labelled CO_2 had been assimilated by the pasture shoot/root system. Therefore, the chambers were removed (after 2 h) and the labelled sward opened up to the environment. No control was made on total CO_2 and temperature during labelling. Six replicates were labelled at each of the six labelling times.

Sampling

Four soil cores (36 mm diam.) were taken to a depth of 100 mm, from each of the six replicates 4 h after labelling (Day 0), and 35 days after labelling (Day 35). The above-ground parts of the labelled pasture plants were clipped from all four cores. Roots were then separated from two soil cores, by gentle shaking and wet sieving. The remaining two cores were sieved (2 mm) for analysis of the soil.

Total C, ^{14}C, total N, pH and cation exchange capacity were determined on air-dry soil. The moisture content of the field-moist and air-dry soil was determined by oven-drying at 105 °C to a constant weight. All results are expressed on an oven-dry (105 °C) weight basis, unless otherwise stated. Oven-dried (65 °C) samples of the above-ground pasture and root biomass were analysed for total C and N.

Analyses

Soil pH, CEC. Soil pH (1:2.5 water) and cation exchange capacity (CEC) were determined according to Blakemore et al. (1987).

Total C and ^{14}C. Total C in the labelled soils and plant material was determined following oxidation and digestion using a modified digestion-tube apparatus incorporating a CO_2 trap (Sparling et al., 1991). A known aliquot of trapping solution was used for liquid scintillation counting and for estimation of total ^{14}C.

Total C and N. Total C in the non-labelled soil, and total C and N in the plant material were analysed by a combustion method (Induction Furnace, Leco, St Joseph, Mich.). Total soil N was determined using a semi-microkjeldahl digestion and by measuring NH_4^+-N concentrations in the digests (salicylate/nitroprusside) on a Technicon AutoAnalyser II system (Blakemore et al., 1987). Total P was measured on the same Kjeldahl digest (Twine and Williams, 1971).

^{14}C–CO_2 *respiration loss*

A total ^{14}C budget for labelled pools was calculated from the total ^{14}C recovered. The respiratory losses of ^{14}C–CO_2 after 35 days were calculated as the difference between total recoveries of assimilated ^{14}C after these periods and the recoveries after 4 h.

Carbon fluxes

Seasonal estimates of the amounts of C assimilated, translocated to roots and added to soil, were made according to Saggar et al. (1997, 1999) using the seasonal dry matter production measurements from adjacent areas. It was assumed that, at steady state (Day 35), the distribution of net fixed ^{14}C in the pasture–root–soil system represents the average partitioning of

Table 1. ^{14}C-labelling and subsequent sampling schedule for pasture site

Season	Sampling day					
	0	35	156	192	226	350
Spring	14 Sep 98	21 Oct 98	17 Feb 99	25 Mar 99	28 Apr 99	30 Aug 99
	h,r,s	**h,r,s**	**r**	**r**	**r**	**r**
	0	35	119	154	188	389
Late spring	21 Oct 98	25 Nov 98	17 Feb 99	25 Mar 99	28 Apr 99	15 Nov 99
	h,r,s	**h,r,s**	**r**	**r**	**r**	**r**
	0	36	70	194	271	404
Summer	17 Feb 99	25 Mar 99	28 Apr 99	30 Aug 99	15 Nov 99	27 Mar 00
	h,r,s	**h,r,s**	**r**	**r**	**r**	**r**
	0	35	70	89	328	404
Late summer	25 Mar 99	28 Apr 99	2 Jun 99	21 Jun 99	15 Feb 00	1 May 00
	h,r,s	**h,r,s**	**r**	**r**	**r**	**r**
	0	35	54	124	334	397
Autumn	28 Apr 99	2 Jun 99	21 Jun 99	30 Aug 99	27 Mar 00	29 May 00
	h,r,s	**h,r,s**	**r**	**r**	**r**	**r**
	0	35	70	147	315	365
Winter	21 Jun 99	26 Jul 99	30 Aug 99	15 Nov 99	1 May 00	20 Jun 00
	h,r,s	**h,r,s**	**r**	**r**	**r**	**r**

(Sampled: h = herbage; r = roots; s = soil).

assimilate:

$$\text{Estimated assimilated C} = (A_{\text{shoot}} \times \text{C}_{\text{shoot}})/(^{14}\text{C}_{\text{shoot}}) \quad (1)$$

where estimated assimilated C is the seasonal flux (kg C/ha/year); A_{shoot} = seasonal shoot growth (kg C/ha/year); C_{shoot} = shoot C concentration (%); $^{14}\text{C}_{\text{shoot}}$ =% of net assimilated ^{14}C in shoots at day 35, during that season. The estimated assimilated C during each growth season was then divided among plant -soil components based on the % ^{14}C distribution at Day 35. The sum of seasonal estimates of root and soil C inputs provided annual below-ground C inputs.

In situ *root decomposition*

After clipping the pasture plants in each lysimeter on Day 35, the labelled plant–root–soil system was left for up to one year for the plants to grow under field conditions and initiate root decomposition measurements. Thus the Day 35 after pulse-labelling corresponds to Day 0 for the root decomposition. The roots were then sampled periodically (Table 1) to determine the amount of total ^{14}C remaining in the roots as described above. The amount of ^{14}C remaining in the roots was plotted against time, assuming a first-order decomposition rate. The net rate of change of root ^{14}C at any time equals the decomposition rate (V_{dec}), and is proportional to the amount of residual root ^{14}C at that instant. This is expressed by the following first-order differential equation:

$$V_{\text{dec}} = -(\text{dC}/\text{d}t) = k\text{C} \quad (2)$$

where k is the first-order decay rate constant (time^{-1}), and C is concentration of residual root ^{14}C at an instant in time. This equation has the exact solution:

$$\text{C} = \text{C}_0\, \text{e}^{-kt} \quad (3)$$

where C_0 is the initial ^{14}C percentage at Day 35 in the roots (100%). The rate constant k was estimated by a nonlinear least squares method. Other models were tested but did not describe the data as effectively as Equation (2). The goodness-of-fit of each model was measured by R^2 (the coefficient of determination). The root half-life (time taken by the roots to be reduced to half of the initial value) was calculated as:

$$t_{1/2} = 0.693/k \quad (4)$$

Statistical analyses

We used the SYSTAT 7.0 Windows software package for all statistical analyses. Means (n=6) and standard errors of the means were calculated for DM yield during each season. The significance of differences between seasons was assessed by analysis of variance and Fisher's LSD test. The ^{14}C data for each

replicate were expressed as percentages of net assimilated ^{14}C in the plant/soil system. After transformation to arcsine square roots, they were subjected to analysis of variance. Results are reported as statistically significant at the 5% probability level.

Results

Site and climate characteristics

The long-term pasture site used for this study was well-drained, moderately acid (pH_{water} 5.56) with total soil C, N and P contents of 31.50, 2.80 and 1.12 g kg^{-1} soil, respectively. The cumulative rainfall in both years was below the average rainfall received in most years (Figure 1). Rainfall distribution was higher than average in the spring of 1998, with 361 mm of rain compared with the average 248 mm. This was followed by a particularly dry summer (December–February), with only about half the normal rainfall for this season. The rainfall during the remainder of the labelling year was 10–20% lower than the 30 year mean monthly values. In both years, air temperatures were highest in the summer months of December to March; the mean monthly temperatures ranged between 15 °C and 20 °C. Coolest temperatures were recorded in the winter months of June to August (8.4 °C–10.2 °C). The annual fluctuations in soil temperature at 100 mm depth followed similar trends to the air temperatures, and can be considered normal for this region.

The computed daily soil water balance for the surface 0–100 mm depth based on weather-controlled evapotranspiration and rainfall from this pasture site (as described by Scotter et al., 1979) is shown in Figure 1. The New Zealand winter is characterised by, low soil temperatures and periodic high rainfall, resulting in generally increased soil water content. The greatest period of soil moisture deficit was in summer 1998-1999 (December–April). The following spring/summer/autumn season 1999–2000, although characterised by an overall soil moisture deficit, did have some well distributed rainfall events. Over this period the late summer/autumn (February–April 2000) was the driest (Figure 1.).

Pasture production

Above-ground pasture production during the year at this site was 16 020 kg ha^{-1}, and the growth varied with season, being highest in spring (75–79 kg ha^{-1} d^{-1}) and lowest in winter (18–20 kg ha^{-1} d^{-1}) (Figure 2). These seasonal variations in pasture growth rates are typical of New Zealand pastures where, pasture growth is limited by low soil temperatures during winter, despite high soil moisture. Low soil moisture rather than the temperature is the major yield-determining factor in the summer and autumn season (the mean temperatures over the summer and autumn season measured at this site ranged from 15.3 to 20.2 °C). The annual root production was 16 720 kg ha^{-1}, with the highest root growth rate of 95–108 kg ha^{-1} d^{-1} during the spring season, which then declined to 65 kg ha^{-1} d^{-1} in late spring and to 41 kg ha^{-1} d^{-1} in summer seasons. Lowest root growth was obtained during late summer, autumn and winter (Figure 2).

Table 2. Pasture shoot and root nutrient composition during the year. Values represent mean of 6 replicates ± s.e.

Sampling date	Carbon (g kg^{-1})	Nitrogen (g kg^{-1})	Phosphorus (g kg^{-1})	C:N ratio	C:P ratio	N:P ratio
Shoot nutrient composition						
Spring	407.5 ± 5.60	26.7 ± 1.80	4.80 ± 0.10	15.3	85	5.6
Late spring	409.3 ± 2.40	24.6 ± 1.30	5.40 ± 0.10	16.6	76	4.6
Summer	397.1 ± 3.90	16.2 ± 0.70	2.40 ± 0.10	24.6	165	6.7
Late summer	408.7 ± 0.66	23.4 ± 0.90	2.60 ± 0.10	17.5	157	9.0
Autumn	412.6 ± 0.62	27.9 ± 1.00	3.40 ± 0.10	14.8	121	8.2
Winter	407.7 ± 0.54	39.4 ± 0.70	5.20 ± 0.10	10.4	78	7.5
Root nutrient composition						
Spring	410.9 ± 8.00	18.5 ± 0.90	3.00 ± 0.10	22.2	138	6.2
Late spring	427.9 ± 5.00	16.3 ± 0.70	2.60 ± 0.20	26.3	165	6.3
Summer	386.7 ± 6.50	15.4 ± 0.50	2.20 ± 0.10	25.1	178	7.1
Late summer	411.8 ± 7.10	16.7 ± 0.40	2.20 ± 0.20	24.7	186	7.5
Autumn	394.5 ± 6.80	17.7 ± 0.50	2.20 ± 0.10	22.3	180	8.1
Winter	394.2 ± 5.90	18.9 ± 0.50	2.20 ± 0.10	20.9	183	8.8

Mean pasture shoot and root C contents were 410 g kg^{-1} and 400 g kg^{-1}, respectively (Table 2), and varied slightly with season. The N and P contents of shoots were consistently higher than those of roots and varied with season (Table 2). Generally, N and P contents were low during summer and autumn periods. The shoot C:N and C:P ratios varied between 10.4–24.6 and 76-165, respectively, with those of roots varying between 20.9–26.3 and 138–186, respectively. There were more seasonal variations in C:N and C:P ratios of the shoots than of the roots.

^{14}C-distribution

The distribution of ^{14}C expressed as a proportion of net assimilated ^{14}C–CO_2 varied with the length of chase period and season (Table 3). Initially, 84–90% of the ^{14}C was in the shoot biomass (Table 3). This percentage of ^{14}C declined with time during all seasons, with the amount remaining at Day 35 being the

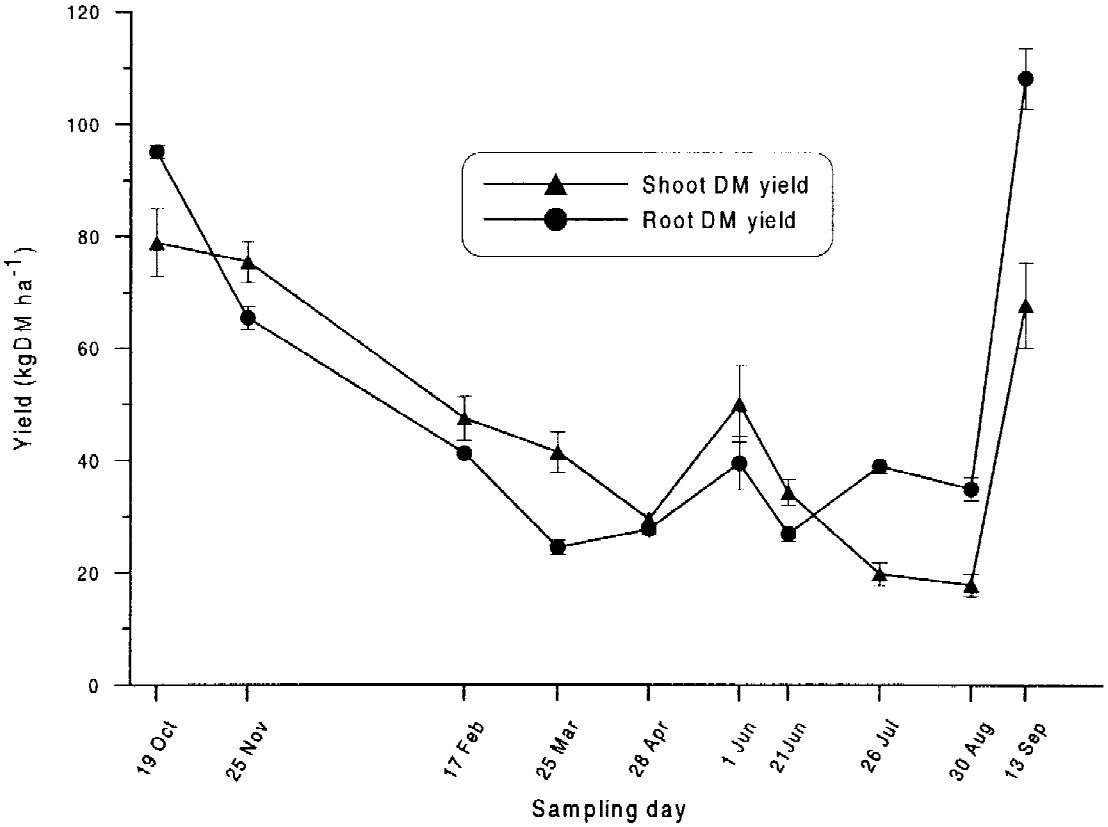

Figure 2. Pasture shoot and root growth at the site at different seasons i.e. spring (September–October), late spring (October–November), summer (January–February), late summer (March–April), autumn (April–May) and winter (June–July) during September 1998–September 1999. Error bars are 1 SEM.

highest during the spring and late spring season (26–31%) and lowest during winter (10%). Within 4 h of pulse application, 7–12% of the ^{14}C was detected in the roots (Table 3), but by Day 35, 27–31% of gross assimilated ^{14}C was present in the root in spring and late spring pasture compared with 10–21% in the summer/autumn and winter seasons. Thus about 10–20% more ^{14}C was partitioned below-ground during spring compared with summer, autumn and winter seasons.

Respiration

At Day 35, depending upon the pasture growth season, 37–70% of the ^{14}C label was not recovered (Table 3) and is assumed to have been lost by shoot, root and soil respiration. A small proportion of the ^{14}C unaccounted for may have been transferred to deeper depths through diffusion or root growth but our below-ground measurements were confined to the 0–100 mm depth. A recent study (Bhupinder-Pal Singh, 2000, unpublished PhD thesis) found that 92% of the pasture root mass is distributed within 0-100 mm. As in our previous studies (Saggar et al., 1997, 1999), it was not possible to distinguish between shoot, root, and soil respiration. The calculated respiratory ^{14}C–CO_2 losses were high (66–70%) during summer, autumn and winter seasons, and low (37–39%) during the spring and late spring season.

Carbon budget

During the spring and autumn, pasture assimilated (respired plus conserved) the highest amounts of C (125 and131 kg C ha^{-1} d^{-1} respectively), and the lowest in the late summer (55 kg C ha^{-1} d^{-1}) (Figure 3). This implied a decline in C assimilation during the drier February–March period (Figure 1). The assimilated C remaining in the above-ground biomass was 30–32 kg C ha^{-1} d^{-1} during the spring season, 20 kg during autumn, 13–16 kg during summer, and only 8 kg during winter (Figure 3). By using the distribution of ^{14}C after 35 days, the amount of C incorporated into the roots was calculated as 26–39, 10–12, 16 and 16 kg C ha^{-1} d^{-1} for the spring, summer, autumn

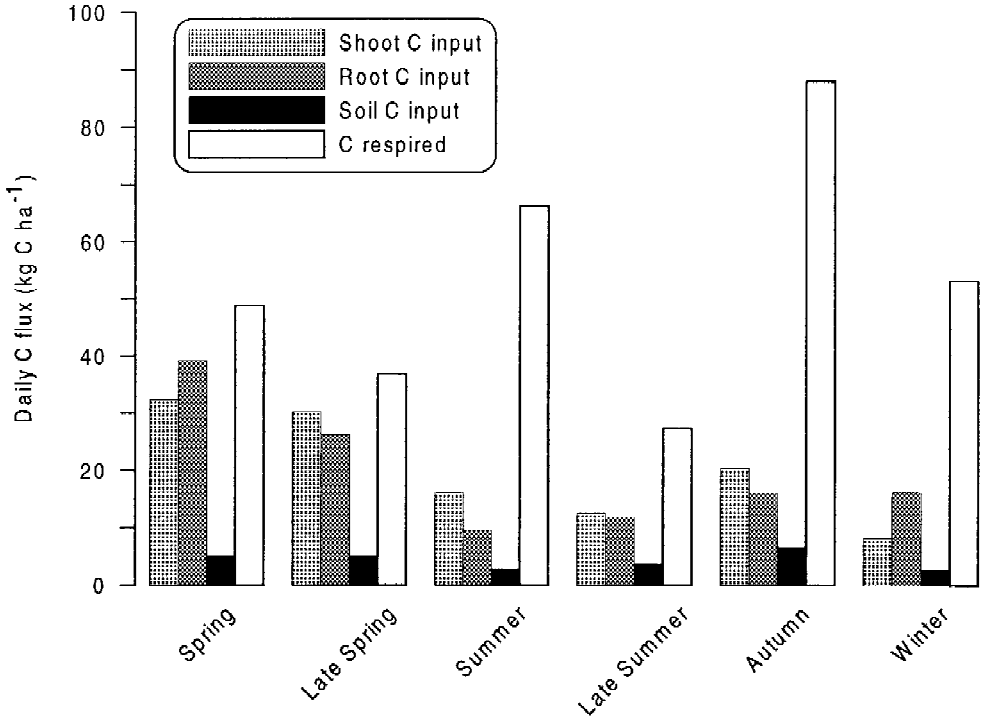

Figure 3. Distribution of assimilated carbon (kg C/ha) in pastures at different seasons estimated from pasture growth rate (Figure 2), C content (Table 2) and ^{14}C distribution at 35 days after labelling (Table 4).

and winter seasons, respectively (Figure 3). Shoot growth was maximal during spring and late spring and C transfer to the roots also reached its maximum during these periods. However, differences existed in the incorporation into the roots between the spring and late spring; the calculated flux being 13 kg C ha^{-1} d^{-1} higher in spring than in late spring. Shoot growth was minimal during winter. There were also, small differences in the incorporation into the roots between summer, autumn and winter seasons. When these seasonal assimilation were accumulated over the year, total assimilation was 32.8 Mg ha^{-1}. The amounts of C respired and incorporated annually into roots and soil were also estimated from the seasonal fluxes. At this regularly fertilised dairy pasture site, 18 220 kg C/ha was respired, 6490 kg remained above-ground in the shoot, and 6820 kg was incorporated into roots, and 1320 kg into the soil.

Root decomposition

Root decomposition rates differed widely with season (Table 4). About one-third of the root label measured in spring disappeared within the first 5 weeks (Figure 4). Less loss was recorded during the first 5 weeks of the autumn season when only one-fifth of the label lost. Over the first 8 weeks, roots were rapidly decomposed in all the seasons (Figure 4) when about 30 – 50% of the labelled root C was lost. The roots labelled during spring decomposed fastest, with 50% of the label disappearing. Subsequent decomposition was slow, and the rate of root loss followed an exponential relationship with time. The root decomposition rate constants (k) were 1.7 times higher for the spring-labelled roots than for the autumn-labelled roots. The rate constants for the winter, summer, late summer and late spring roots were similar, and 1.2–1.3 times higher than for autumn roots. The half-life was, therefore, the highest (111 days) for autumn roots and lowest (64 days) for spring roots (Table 4). The late spring, summer, late summer and winter roots had intermediate half-lives (88–94 days). Only 1 – 8% of the labelled root C remained by the end of the year.

Discussion

In accordance with previous studies (Rattray et al., 1995; Saggar et al., 1997, 1999; Swinnen et al., 1994), we found that the recently assimilated C was rapidly translocated to the roots. The final balanced allocation of ^{14}C in the plant is reached when the metabolic com-

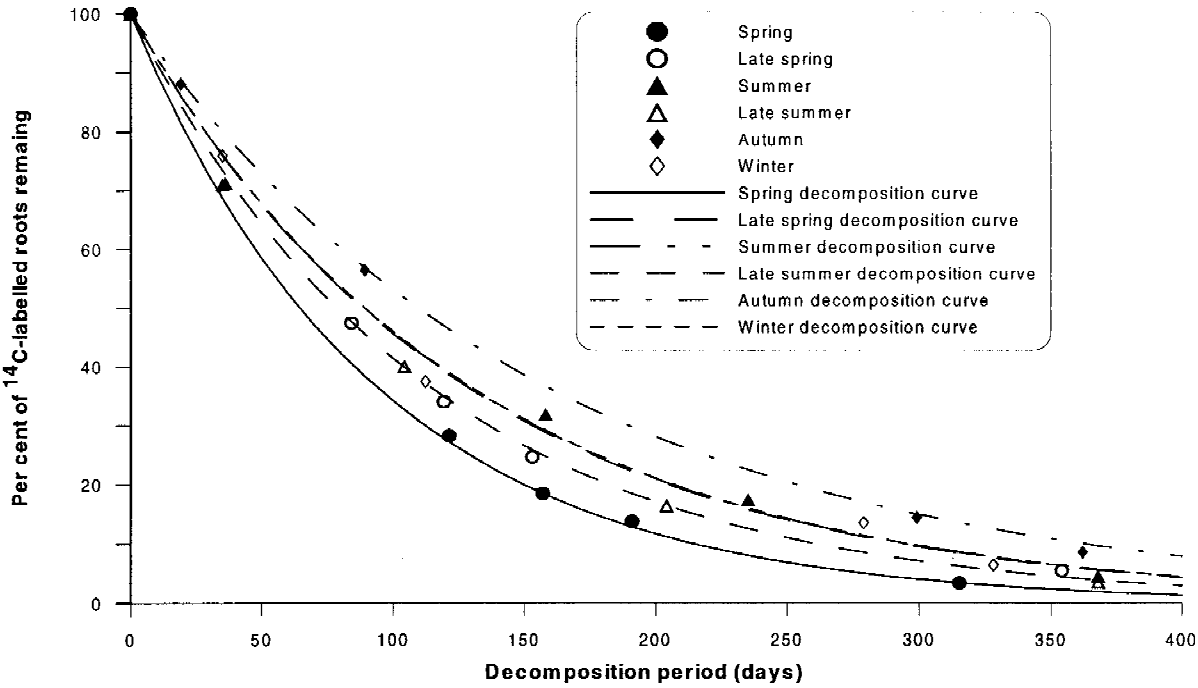

Figure 4. Amount of ^{14}C-labelled roots in different seasons remaining during *in-situ* field decomposition. Data points are means of 3 replicates. First-order decomposition rate curves were fitted to the data. 0 day point on x-axis relates to root-^{14}C 35 days after labelling.

Table 3. Distribution of ^{14}C (per cent) in the shoot, root, and soil of pasture during each season at 4 h and 35 days after pulse labelling. For each property, values followed by the same letter are not significantly different at $P = 0.05$; values for respired $^{14}C–CO_2$ were determined by difference and are not compared statistically

System component	Season					
	Spring	Late spring	Summer	Late summer	Autumn	Winter
			4 h			
Shoot	84c	85c	89a	89a	90a	87b
Root	12c	12c	9c	8c	7c	10c
Soil	4.0ab	3.6b	1.2c	3.3b	2.3b	2.5b
			35 days			
Shoot	26de	31d	17f	23e	16f	10g
Root	31a	27a	10c	21b	12c	20b
Soil	4.1ab	5.2a	3.0b	6.7a	5.1a	3.4b
Respired[A]	39	37	70	49	67	66

[A]Calculated as a difference between amounts of $^{14}C–CO_2$ in standing herbage, root or soil at 4 hours and 35 days; ND, not determined.

ponents of the shoot and root are depleted of ^{14}C and the plant–soil system is at or near steady state. In our previous studies (Saggar and Searle, 1995; Saggar et al., 1997, 1999), based on the dynamics of both the decrease of ^{14}C in shoots and ^{14}C respiration rate, we used an allocation period of 35 days.

The total $^{14}CO_2$ efflux data from the system during the allocation phase (35 days), calculated as a difference between the total amount of ^{14}C recovered in the plant–root–soil system at 4 h and 35 days, suggest that the respiratory loss varied with season (Table 3). This respiratory loss was equivalent to 1–1.1% per day during spring and late spring season, and increased to 1.9–2.0% during the summer, autumn and winter periods. It is likely that root respiration and microbial respiration of root exudates would have

dominated the respiratory loss between allocation and after-labelling phases. Respiration losses are reported to be maximal in the first night after labelling and subsequently decline exponentially with time, and it is estimated that plants with C_3 pathways lose 20–50% of assimilated C by shoot respiration (Kuzyakov et al., 1999; Warembourg and Morral, 1978). Root respiration also predominates in the first few days after labelling. Swinnen et al. (1995a), for example, found ^{14}C soil–root respiration rate peaked 1–3 days after labelling. The microbial respiration of root exudates occurs later than root respiration because it consists of a chain of successive processes: root exudation, microbial uptake and microbial decomposition (Kuzyakov et al. 1999). An initial pulse of ^{14}C appears in the soil from soluble organic root exudates followed by a more constant release from labelled storage and structural material (Prosser and Farrar, 1981). Some of the ^{14}C in root exudates may have moved below our sampling depth of 0–100 mm through diffusion or mass flow. This would only be a concern in time of year when high rainfall was occurring during May – September.

The differences among the seasons in respiratory loss during the allocation phase (35 days), observed in our study (Figure 3), mainly reflect the differences in the rates of depletion of ^{14}C metabolic components of the shoot and root. Although shoot, root and microbial respiration was not measured in this study, it appears that root respiration could have been the dominant loss mechanism for the limited water conditions of summer- and autumn-labelled pastures, resulting in a lower proportion of ^{14}C remaining in roots. This is consistent with the fact that plants respond to a relative shortage of any essential resource by increasing below-ground allocation (Bloom et al., 1985; Hamblin et al., 1990; Mehrag and Killham, 1990; Palta and Gregory, 1997; Saggar et al., 1997, 1999) and a higher proportion of this allocated ^{14}C is used for maintenance. As the rhizosphere activity (root and microbial respiration) is low during the winter season compared with the spring season, shoot respiration could have dominated during winter leaving a higher proportion of ^{14}C below-ground. This increase in the proportion of assimilated ^{14}C lost through shoot respiration indicates that during short days with cold winter temperatures the most recently fixed assimilates in the shoot were used for maintenance and a small proportion contributed to pasture growth.

Our results suggest that the weather conditions during the allocation period had an effect on ^{14}C partitioning. Under spring conditions of non-limiting moisture and optimum growth temperature during active pasture growth, photoassimilated C is more effectively conserved in the shoots and in the roots than the summer, winter and autumn seasons of greater moisture and temperature stress (dry or cold). This is supported by the findings of earlier New Zealand studies on seasonal changes in new root growth (Caradus and Evans, 1977), indicating that root growth coincides with soil moisture availability. Typically, this occurs during winter when soil water contents are generally high, whereas during summer autumn periods we recorded soil water deficits (Figure 1). Similar to our previous studies (Saggar et al., 1997, 1999), 26–31% of the photoassimilate was conserved in the shoot and 27–31% conserved in the roots during the spring season. Conservation of ^{14}C in shoots (10 – 17%), and incorporation into roots (10 – 20%) was much less during summer, winter and autumn seasons (Table 3). Furthermore, a higher proportion of photoassimilated ^{14}C was found in summer and autumn shoots than in winter shoots. Winter roots contained twice as much ^{14}C as the shoots. In New Zealand pastures, despite high soil moisture during winter, low soil temperatures significantly limit the pasture growth. However, low soil moisture rather than temperature was the major growth determining factor over the summer and autumn season as the mean temperatures measured at this site ranged from 15.3 to 20.2 °C. This seasonal ^{14}C data, which are representative of the time of labelling, demonstrate that the response of pasture plants under low temperature and/or limiting moisture conditions is to store more C below-ground e.g. Saggar et al. (1999). Barber and Martin (1976) found that rhizodeposition in wheat was enhanced in situations with low soil moisture content.

The present study also describes the seasonal fluxes of C (amounts of C assimilated, and translocated to roots and to soil) in a temperate pasture. Seasonal C fluxes were estimated by relating the distribution of ^{14}C-labelled photosynthate at steady state

Table 4. Turnover time and half-life of pasture roots labelled during different seasons of the year

Labelling season	Decay equation ($y = C_0 \times e^{-kt}$)	R^2	Half-life (days)	Turnover time (days)
Spring	$y = 100 \times e^{-0.01079t}$	0.990	64	93
Late spring	$y = 100 \times e^{-0.00792t}$	0.968	88	126
Summer	$y = 100 \times e^{-0.00779t}$	0.947	89	128
Late summer	$y = 100 \times e^{-0.00739t}$	0.998	94	135
Autumn	$y = 100 \times e^{-0.00624 \times t}$	0.973	111	160
Winter	$y = 100 \times e^{-0.00779 \times t}$	0.970	89	128

(35 days) to the seasonal measurements of dry matter production. Our net C assimilation tended to be higher in spring and autumn than in summer and winter. However, the shoot C yield was 30–32 kg C ha^{-1} d^{-1} during spring, 20 kg during autumn, 13–16 kg during summer, and only 8 kg during winter (Figure 3). Also, the amount of C incorporated into the roots was 26–39, 10–12, 16 and 16 kg C ha^{-1} d^{-1} for the spring, summer, autumn and winter seasons, respectively (Figure 3). These differences are mainly due to seasonal differences in the above- and below-ground allocation pattern discussed above, e.g. shoot growth was maximal during spring and late spring, but C flux was 13 kg C ha^{-1} d^{-1} higher in spring than in late spring due to a greater conservation in the roots in spring (Table 3). There were four-fold seasonal differences in shoot C yield as well as the C allocated to roots. When these fluxes were integrated over the year at this regularly fertilised dairy pasture site, 6490 kg C remained above-ground in the shoot, 6820 kg C was incorporated into roots, and 1320 kg C to soil. These estimates of C allocated to the root biomass are slightly higher than those reported (4490–5510 kg C ha^{-1} yr^{-1}) for hill pastures (Saggar et al., 1997, 1999). As the productivity of dairy pasture (16 020 kg ha^{-1}) is higher than hill pasture (4918–14 120 kg ha^{-1}) and the climate is milder, it is likely to invest more in root material for the acquisition of nutrients and moisture required for additional production.

This study shows that over the first 8 weeks roots decomposed rapidly in all seasons (Figure 4) when about 30 – 50% of the labelled root C was lost. This rapid initial ^{14}C loss of roots is typical in pasture root decomposition studies, and it is dominated by decomposition of easily-decomposable compounds (Verburg et al., 1998; Van Vuuren et al., 2000). The decomposition of more recalcitrant structural root material dominates the loss in the longer term. Results from a decomposition model constructed for root C fractions (easily decomposable, slowly decomposable, and recalcitrant) showed that the easily and slowly decomposable fractions disappeared in 12 weeks (Kelting et al., 1998). Our root turnover estimates of 93–160 days (13–23 weeks) (Table 4) agrees fairly well with those calculated from a decomposition model for newly formed fine tree roots by Kelting et al. (1998). These values are, however, rather low compared with root turnover values of 60–80 weeks obtained by Stewart and Methrell (1998) for irrigated and non-irrigated pastures, perhaps because their pastures occur in a much drier and cooler climate zone. However, our turnover times are greater than the 40–88 days (6–12 weeks) obtained by Swinnen et al. (1995b) for wheat roots grown at tillering and ear emergence. Our data also suggest that pasture root decomposition rates differed with season. The higher decomposition rate constant (*k)* values, found for spring-labelled root, appear to be related to optimum soil moisture and temperature conditions for root decomposition in this temperate climate. The lower *k* values for summer, winter and autumn seasons are partly due to limited moisture and/or temperature, and partly to change in root nutrient concentrations such as limited N and/or P supply by the root material, caused by an increased C:N and C:P ratios from 22 to 26, and from 138 to 183, respectively (Table 2). Little is known about the effects of the intrinsic N and P status of pasture roots on decomposition. Nevertheless, our recent work (Saggar et al., 2000), showed that P and N supply regulates the turnover of soil organic matter, and when these nutrients are in limited supply, decomposition is retarded. The lowest *k* value for autumn-labelled roots also reflects the end of a significant dry period (Figure 1), with soil moisture having a determining effect on root decomposition.

Conclusions

This study has provided data on the seasonal fluxes and quantities of C partitioned in the plant–root–soil system of a temperate pasture, and on root decomposition rates. The study has highlighted the seasonal differences in assimilation and partitioning of photoassimilated ^{14}C and the quantity and quality (C:N, C:P ratios) of root production and turnover. The amount of root production depends on the relationship between translocation and respiration of photoassimilate during the allocation phase (35 days). Our pulse-labelling experiments have shown remarkable differences between shoot C yield and C transfers to root with season. There were also more seasonal variations in C:N and C:P ratios of the shoots than those of roots. However, the annual quantity of C incorporated into the root (6820 kg C ha^{-1}) was comparable with what was retained in the shoot (6490 kg C ha^{-1}), suggesting that, for each kg of pasture C produced, these perennial pastures incorporate a little more than a kg C below-ground in root material. The partitioning between above- and below-ground will vary depending on the soil fertility and moisture availability as reported previously (Saggar et al., 1997, 1999). Under high fertility and non-limiting moisture conditions, a higher proportion of ^{14}C remains above-ground.

This study also demonstrated that seasonal changes not only affect the amount of C incorporated into the root biomass (root production), but also affect the output through root decomposition. Seasonal differences in root production and turnover are not generally considered in most SOM turnover models. The data provided in this study is an attempt to rectify this deficiency. It is clear from our results that to estimate C budgets accurately for temperate pastures, C turnover models such as Roth-C and CENTURY should account for seasonal changes in below-ground C inputs through root growth and decomposition.

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