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UNIVERSITY OF ALBERTA

TRANSFORMATION AND STABILIZATION OF CARBON IN TWO BARLEY-SOIL ECOSYSTEMS

BY

JINGGANG XU

A THESIS SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

IN

SOIL SCIENCE

DEPARTMENT OF SOIL SCIENCE

EDMONTON, ALBERTA.

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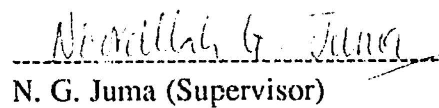
The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled TRANSFORMATION AND STABILIZATION OF CARBON IN THE BARLEY-SOIL ECOSYSTEMS submitted by JINGGANG XU in partial fulfillment of the requirement for the degree of PH. D in SOIL SCIENCE.



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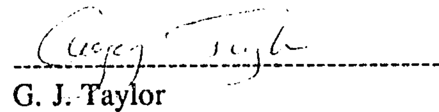

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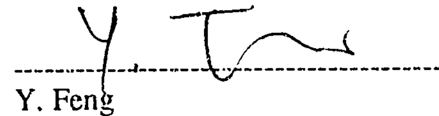

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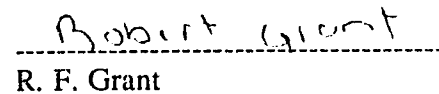

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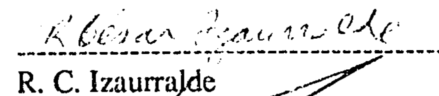

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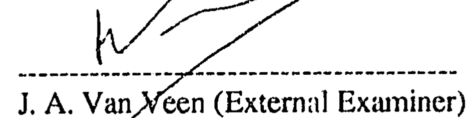

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Abstract

Above- and below-ground primary production is the main source of soil organic C for most ecosystems. This research was conducted with different barley (*Hordeum vulgare L.*) cultivars (cv. Abee, bonanza, Harrington and Samson) to study the transformation and stabilization of C in barley-soil ecosystems under field, greenhouse and laboratory conditions. Shoot mass and root mass of Abee were greater than those of Samson, but there was no difference between other cultivars under field conditions. Root mass increased until the heading stage, while shoot mass kept increasing till the ripening stage. Shoot ^{14}C and root ^{14}C of Samson were greater than those of Abee although the shoot mass and root mass of Abee was greater than those of Samson in ^{14}C-pulse-labelled plants under field conditions. Microbial ^{14}C, water-soluble organic ^{14}C and respired ^{14}C in soil samples under Samson were greater than those under Abee at the stem extension and heading stages during a 10-d incubation.

Under hydroponic conditions, Samson released more C than Abee during 25 d growth. Path analysis showed root length had a greater effect on root-released C than root C and shoot C. The average half life (8.5 d) of the root-released C of Abee in soil was shorter than that (10.9 d) of Samson. Decomposition of roots *in situ* was studied by incubating soil cores of excised the shoots. The proportion of the labile components of the roots under Abee (47.7%) was greater than that under Samson (38.8%), but the half lives of the labile and resistant components of the roots were not significantly different between the two cultivars. A mathematical simulation model describing root decomposition *in situ* confirmed that more C was maintained in soil under Samson than under Abee.

The experiments conducted at three scales and simulation modelling indicated that different barley cultivars may have different patterns of C dynamics in barley-soil ecosystems. Selection of a suitable cultivar of the same plant species may maintain or increase soil organic C.

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Table of Contents

Chapter		
1.	Introduction	1
	References	3
2.	Above- and below-ground net primary production of four barley cultivars in western Canada	5
	Introduction	5
	Materials and Methods	6
	Results	9
	Discussion	16
	References	18
3.	Above- and below-ground transformation of photosynthetically fixed C by two barley cultivars	21
	Introduction	21
	Materials and Methods	23
	Results	26
	Discussion	41
	References	46
4.	Relations between shoot C, root C, root length and root-released C of two barley cultivars and kinetics of root-released C decomposition in soil	49
	Introduction	49
	Materials and Methods	51
	Results and Discussion	55
	References	62
5.	Root decomposition *in situ* of two barley cultivars in soil	66
	Introduction	66
	Materials and Methods	68
	Results	72
	Discussion	78
	References	81
6.	Simulation of root decomposition *in situ* for two barley cultivars	85
	Introduction	85
	Model Descriptions	86

	Results	90
	Discussion	97
	References	99
7.	Synthesis	101
	Future research	104
	References	105
	Appendix 1	107
	Appendix 2	113

List of Tables

Table		Page
II.1	Properties of soil used in the experiment	7
II.2	ANOVA of root mass and root length in 0-10 cm and 0-40 cm depth of four barley cultivars in 1989 and 1990	9
II.3	Shoot mass and shoot mass/root mass ratios of four barley cultivars in 1989 and 1990	15
III.1	Total C budget in two barley-soil ecosystems	28
III.2	Respired C during 10-d incubation from unfumigated soil samples, soil microbial C and water-soluble organic C of two barley-soil ecosystems	29
III.3	^{14}C budget of two barley-soil ecosystems	32
III.4	^{14}C in Respired C during 10-d incubation, soil microbial C and water-soluble organic C of two barley-soil ecosystems	34
III.5	Specific activity of ^{14}C in shoot C, root C and in soil of two barley-soil ecosystems	36
III.6	Specific activity of ^{14}C in respired C during 10-d incubation, soil microbial C and water-soluble organic C of two barley-soil ecosystems	38
III.7	^{14}C stabilized in soil in two barley-soil ecosystems.	45
IV.1	Shoot C, root C, root length , released C and ratios of shoot C/root C, shoot C/released C and root C/released C of two barley cultivars	55
IV.2	The correlation coefficients of three characteristics and root exudations	58
IV.3	Direct and indirect effect of shoot C, root C and root length on root exudation	59
V.1	Distribution and kinetics of C in different soil pools of two barley-soil ecosystems	73
V.2	Distribution and kinetics of ^{14}C in different soil pools of two barley-soil ecosystems	74
V.3	Specific activity of ^{14}C in different soil pools of two barley-soil ecosystems	75

VI.1 Initial pool sizes of total C and ^{14}C in the simulation model for two barley cultivars 88

VI.2 Parameters used in the simulation model 91

VI.3 Simulated inputs and outputs of C between Day 0 and Day 15 and between Day 15 and Day 80 for Abee 95

VI.4 Simulated inputs and outputs of ^{14}C between Day 0 and Day 15 and between Day 15 and Day 80 for Samson 97

VI.5 Model simulation of ^{14}C distribution on Day 15 and Day 80 for two barley cultivars 98

VII.1 Distribution of root translocated C over different root processes 101

List of Figures

Figure		Page
I.1	Carbon flow chart in barley-soil ecosystem	2
II.1	Average total root mass and root length of four barley cultivars at various growth stages over 1989 and 1990	10
II.2	Average total root mass and root length of four barley cultivars at various depths over 1989 and 1990	12
II.3	Average total root mass and root length of four barley cultivars at various depths and growth stages over 1989 and 1990	13
III.1	Conceptual model of C flow in plant-soil ecosystem.	22
III.2	The ratios of shoot ^{14}C/root ^{14}C for two barley cultivars over growing season	31
III.3.	Linear model of the total soil ^{14}C with root ^{14}C	42
III.4	Linear models of the stabilized soil ^{14}C and respired ^{14}C by soil microorganisms during 10-d incubation with water-soluble organic ^{14}C in soil	43
IV.1	A path diagram to describe the direct and indirect effects shoot C, root C and root length on root-released C	53
IV.2	Kinetics of root-released C remaining in soil of the two barley cultivars	61
V.1	Amount of ^{14}C remaining in soil and roots over time in undisturbed soil cores containing roots of two different barley cultivars	77
VI.1	Flow chart of C in the simulation model.	86
VI.2	Model outputs and experimental data for CO_2-C, water-soluble organic C, microbial C, CO_2-^{14}C, water-soluble organic ^{14}C and microbial ^{14}C during the incubation period for Abee	92
VI.3	Model outputs and experimental data for CO_2-C, water-soluble organic C, microbial C, CO_2-^{14}C, water-soluble organic ^{14}C and microbial ^{14}C during the incubation period for Samson	93

VII.1 The flow chart of C cycling in barley-soil ecosystem 102

Chapter 1. Introduction

Above-ground primary production is the main source of organic C for most ecosystems. Photosynthetically fixed C is transferred from the above-ground parts of living plants to roots and from roots to the surrounding soils. Below-ground plant C is present as live roots, dead roots, soluble root exudates and mucilage. Root-released organic materials are utilized by microorganisms for biosynthesis, energy production and microbial products which are further transformed in soil. Soil organic C is also utilized by soil microorganisms and fauna. Root derived C and the C added into soil as plant residues are major C input mechanisms and their utilization by microbes and fauna are key issues in the functioning of soil ecosystems (Van Veen et al. 1991). The change of soil C in an ecosystem is a function of soil C inputs (plant residues, dead roots and exudates) and outputs (mainly root and microbial respiration). It is necessary to study the dynamics of C transformations and stabilization in plant-soil ecosystems in order to understand soil organic matter changes (Fig. I.1).

The ^{14}C pulse labelling and mathematical simulation techniques present new ways and give further insights into studying C transformation and cycling in plant-soil ecosystems. In field conditions it is difficult to carry out continuous ^{14}C-labelling, the alternative approach, pulse labelling, remains the most practical technique for ^{14}C studies in the field conditions (Whipps and Lynch 1983). The use of ^{12}C and ^{14}C data together can give information on both long term accumulation and temporary changes of C. Mechanistic dynamic simulation models help to integrate the fragmentary knowledge about the processes involved and therefore to develop a better understanding of the behavior of the ecosystem as a whole. They are also useful in formulating and testing hypotheses and in establishing the relative importance of parameters (Verberne et al. 1990).

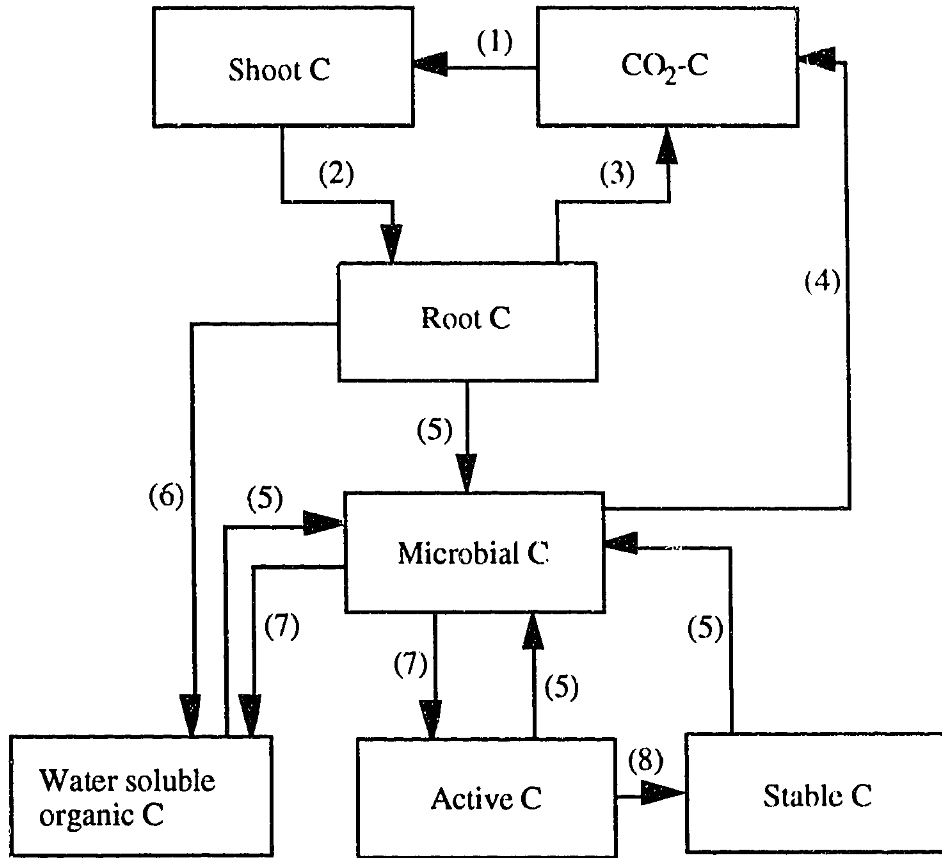

Fig. I.1. Carbon flow chart in barley-soil ecosystem. The processes are (1) photosynthesis, (2) translocation, (3) root respiration, (4) microbial respiration, (5) microbial uptake of different substrates, (6) root exudation, (7) microbial death and (8) chemical stabilization of active C into stable C.

Agronomic studies of crops concentrate almost exclusively on production of plant parts with direct economical interest, e.g. grain or hay. Thus, there is ample information on the above-ground primary production for a wide range of agroecosystems (Milchunas et al. 1985). In contrast, the information on below-ground primary production, especially for different cultivars of the same plant species, is

limited. At present, there is a great need to understand C cycling in the agroecosystems, especially in below-ground portions of these ecosystems.

The selection of plant species is influenced by many factors such as climate, soil type and needs of people. Although different plant species have different rates of photosynthesis and translocation, it is not always feasible to substitute plant species in agroecosystems. The selection of different cultivars of the same plant species in agroecosystems may be a viable alternative from a management point of view. However, the knowledge on the rates of photosynthesis, translocation and stabilization of root-released C from different cultivars of the same species in soil is limited.

Barley is an important crop grown in western Canada. Recently, several new barley cultivars were introduced into this region. The above-ground primary production and its response to the environmental factors, such as fertilizer applications, soil fertility status and soil moisture conditions on these cultivars have been studied (Briggs 1991; Grant et al. 1991). However, there is a lack of information on the below-ground primary production.

This project was initiated to study: (1) Above- and below-ground primary production of four barley cultivars in western Canada; (2) Above- and below-ground transformation of photosynthetically fixed C by two barley cultivars; (3) Relations between shoot C, root C, root length and root-released C of two barley cultivars and the decomposition of root-released C in soil; (4) *In situ* root decomposition of two barley cultivars and (5) Simulation of *in situ* root decomposition for two barley cultivars.

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Chapter 2. Above- and below-ground primary production of four barley cultivars in western Canada

Introduction

Crop studies concentrate almost exclusively on production of plant parts of direct economical interest. Thus, there is much more information on the above-ground than on below-ground primary production for a wide range of agroecosystems (Milchunas et al. 1985). Roots are important for plant anchorage, water and nutrient uptake, storage of carbohydrates, synthesis of growth regulators and input of organic C into the soil. An understanding of these functions and processes are critical for improving plant performance and soil quality.

Plant shoots and roots have specialized to exploit different facets of their environment -- shoots entrap solar radiation and, through photosynthesis, elaborate the metabolites on which all growth depends; roots anchor the plant in soil and absorb water and nutrients. Therefore, there is a dynamic interplay between shoots and roots (Russell 1977). Plant shoots and roots constantly are exposed to changing conditions. Sometimes, the shoot environment limits growth while at other times, root related stresses reduce growth. Examples of shoot stresses are: low light intensity, excessive low or high aerial temperatures, leaf eating insects, aerial pollutants, and wind damage. Examples of root stresses are: mechanical impedance, water stress, nutrient stress, oxygen stress due to excessive water, pathogen effects, temperature stress, aluminum toxicity and salinity stress (Taylor and Arkin 1981). Although plant breeding and development of new cultivars of grains and oil seeds have markedly improved crop yields, the root systems of these crops have only been studied incidentally. More work is needed to understand the dynamics of root systems of these crops.

Barley is seeded on approximately 2.5 million hectares in Alberta (Alberta Agriculture Statistics Branch 1991). Most of the studies on new cultivars have focused

on the above-ground primary production and the responses to the environmental factors, such as fertilizer application rates, soil fertility status, and soil moisture conditions (Briggs 1991; Grant et al. 1991). Selection criteria for new cultivars should include more information on below-ground production because a greater allocation of C below-ground is a possible strategy to build soil organic matter. Also, the continuous input of C through roots over the growing season enhances the activity of microorganisms and fauna which in turn affect nutrient cycling (Juma and McGill 1986) and soil structure formation (Berg and Pawluk 1984). The intimate contact of roots with soil peds, microflora, and fauna may improve soil structure because activity occurs over the growing season. In the long term, barley cultivars that produce more dry matter above- and below-ground may ensure sustainability of the soil resource.

This experiment was initiated to investigate the dynamics of standing shoot mass and root mass, shoot mass/root mass ratios, and root lengths of four barley cultivars grown on a Black Chernozem in western Canada.

Materials and Methods

Experimental Design and Analyses

Field experiments were conducted on a Black Chernozem (Typic Cryoboroll) at the Ellerslie Research Station (53° 25' N, 113° 33' W). Average annual precipitation at Ellerslie is 452 mm, of which 339 mm occurs as rain and 113 mm as snow. It receives the greatest rainfall in June, July and August, and the greatest snowfall in December and January. July is the warmest month with an average minimum temperature of 9.6 °C and a maximum of 22.4 °C. January is the coldest month with average minimum temperatures of -21.7 °C and average maximum temperatures of -11.5 °C. Ellerslie has an average of 109 frost free days per year (Atmospheric Environmental Service 1982). The basic soil properties are shown in Table II.1.

Four barley cultivars (Abee, Bonanza, Harrington, and Samson), representing a broad spectrum in above-ground production (Dr. J. Helm, personal communication), were seeded on June 1, 1989 and 1990. Abee is a two-rowed medium height feed cultivar; Bonanza is a six-rowed standard height malting cultivar; Harrington is a two-rowed medium height malting cultivar; and Samson is a six-rowed semi-dwarf feed cultivar. The experiment consisted of four barley cultivars grown on 10 m x 1 m plots in three replicate blocks (10 m x 4 m each) using a split-plot design. Barley grain was drilled at 90 kg ha^{-1} (equivalent to 200 seeds m^{-2}) in rows 23 cm apart using a seed drill equipped with narrow hoe-openers following running coulters. Urea (75 kg N ha^{-1}) and superphosphate (20 kg P ha^{-1}) fertilizers were placed 3 cm below the seeds at the time of seeding.

Table II.1. Properties of Black Chernozem (Typic Cryoboroll) at Ellerslie (Dinwoodie and Juma 1988)

Depth (cm)	Total C (%)	Total N (%)	pH (1:2 soil:H_2O) (mass:volume)	Bulk density (Mg m^{-3})	Texture
0-10	6.46	0.53	6.1	0.86	SiCL
10-20	6.32	0.49	6.0	1.06	SiCL
20-30	5.23	0.41	6.0	1.17	SiC
30-40	2.67	0.23	6.2	1.34	SiC
40-50	1.26	0.11	6.2	1.39	SiC

Shoots were sampled from 0.1 m^2 area in each plot during the tillering (Zadoks growth stage 26), stem extension (Zadoks growth stage 32), heading (Zadoks growth stage 52), and ripening (Zadoks growth stage 85) stages to determine shoot mass. Shoots were excised at the surface of the soil, dried at 75 °C for 12 h and weighed. Two soil cores (8 cm diameter) were taken from within and between rows at 10 cm intervals to a depth of 70 cm from each plot at each growth stage. The intact soil cores were frozen immediately after sampling and kept at -20 °C until further processing.

Samples were thawed and roots were separated from the soil using the hydropneumatic elutriation method (Smucker et al. 1982). Organic debris was separated from roots by hand. Washed root samples were kept frozen at -20°C until further analysis. Root lengths were determined on all samples by the line-intersect method of Tennant (1975) using digitized microcomputer images (Zoon and Von Tienderen 1990). The data for root mass and root lengths obtained from two cores from each plot were averaged. The experiment was repeated in 1990. As there were no significant differences in root mass and root lengths amongst the layers below 40 cm in 1989, the soil cores were taken only within 40 cm depth in 1990.

Statistical Analyses

The experiment was a three replicate split-plot design. The root mass and root length data obtained in the 0 - 10 cm and 0 - 40 cm during 1989 and 1990 seasons were analyzed separately using the GLM procedure of the SAS package (SAS Institute Inc. 1987). The model used was:

$$y_{ijkl} = \mu + B_i + Y_j + BY_{ij} + C_k + YC_{jk} + BYC_{ijk} + S_l + YS_{jl} + CS_{kl} + YCS_{jkl} + BYCS_{ijkl}$$

where μ is the population mean; B_i is a random effect of the ith block (i =1, 2, 3); Y_j is a random effect of the jth year (j =1, 2); C_k is a fixed effect of the kth cultivar (k =1, 2, ..., 4); S_l is a fixed effect of the lth growth stage (l =1, 2, ..., 4). Shoot mass and shoot mass/root mass ratios for 1989 and 1990 was analyzed using the same model.

Differences between means were tested using the Student-Newman-Keuls (SNK) test, at 0.05 probability level. Best fit linear regression equation for the diameter of root and the depth of soil layers were formulated using the REG procedure of the SAS package.

Results

Preliminary analysis of the 1989 data showed that root mass and root length of four barley cultivars were significantly different amongst the 0-10, 10-20, 20-30, and 30-40 cm soil depth. There were no differences in root mass and root length amongst soil depth increments below 40 cm. Roots below 40 cm accounted for <5% of the total root mass and length. The ANOVA for 1989 and 1990 root mass and root lengths obtained in 0-10 cm and 0-40 cm are presented in Table II.2.

Table II. 2. ANOVA of root mass and root length in 0 -10 cm and 0 - 40 cm soil depths of four barley cultivars in 1989 and 1990[z]

Source of Variation	DF	Root mass		Root length	
		0-10 cm	0-40 cm	0-10 cm	0-40 cm
Block (B)	2	ns	ns	ns	ns
Year (Y)	1	ns	ns	ns	ns
Error I	2				
Cultivar (C)	3	**	**	*	**
Y x C	3	ns	ns	ns	ns
Error II	12				
Growth Stage (S)	3	***	***	***	***
Y x S	3	ns	ns	ns	ns
C x S	9	ns	ns	*	*
Y x C x S	9	ns	ns	ns	ns
Error III	48				

[z] The difference between means is significant at: *, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$; ns, not significant.

Overall, the root mass of Abee was greater than that of Samson, but there was no significant difference between other cultivars. The root mass at the heading and ripening stages was greater than that at the stem extension stage. The root mass at the stem extension was greater than that the tillering stage (Fig. II.1).

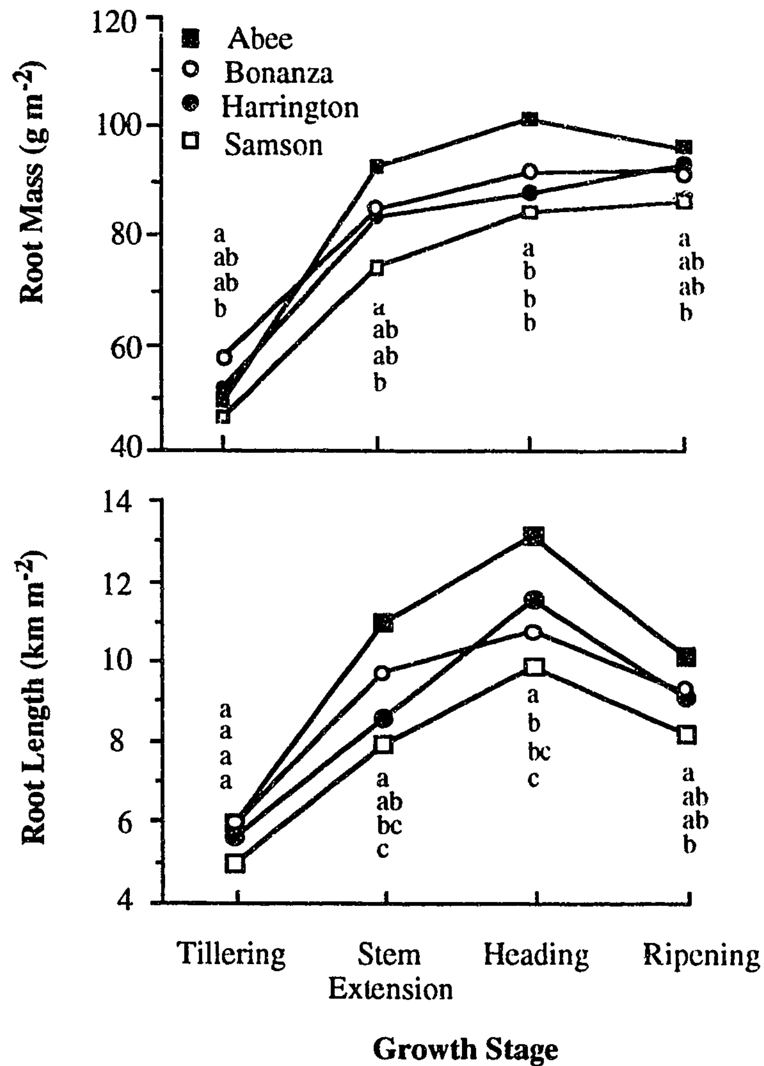

Fig. II.1. Average total root mass and root length of four barley cultivars at various growth stages over 1989 and 1990. The means of the cultivars bearing the different letters are significantly different in root mass or root length at the given growth stage ($p<0.05$) and refer to the magnitude of these variables from the lowest to the highest.

There were no significant differences in root length amongst the four barley cultivars at the tillering stage. At the stem extension stage, root length of Abee was significantly greater than that of Harrington and Samson. The root length of Bonanza was significantly greater than that of Samson. At the heading stage, the order of root length was Abee > Harrington > Bonanza > Samson. At the ripening stage, the order of root length from high to low was the same as that for the root mass. The differences in root mass and root length from 0 to 40 cm between the four cultivars may be mainly because of the differences in the surface layer (Fig II.2).

The root mass and root length decreased with depth for all four barley cultivars used in the experiment (Fig. II.2). The equations of root mass and root length with depth [$y = a + b*\ln(D)$ where y is root mass or root length and D is depth] for each cultivar at the heading and ripening growth stages were obtained individually and compared (Bates and Watts 1988). The results showed that there were no significant differences among these equations. This indicated that the four barley cultivars have the similar vertical distribution trends.

Roots proliferated into deeper soil layers as the growing season progressed, but the surface layer still accounted for >80% of total root mass and total root length in the soil profile over the growing season. Over the whole growing season, the vertical distributions of root mass and root length followed the same trend. Root mass and root length of the four cultivars decreased at greater depth. Total root mass and root length increased as the growth cycle progressed. There was no significant difference in the root mass between the heading and ripening stages, but the root length was significantly higher at the heading than at the ripening stage (Fig. II.3). Overall, the ratio of root length at the 30-40 cm depth to the total root length in the profile (4%) was twice the value of the corresponding value for root mass (2%).

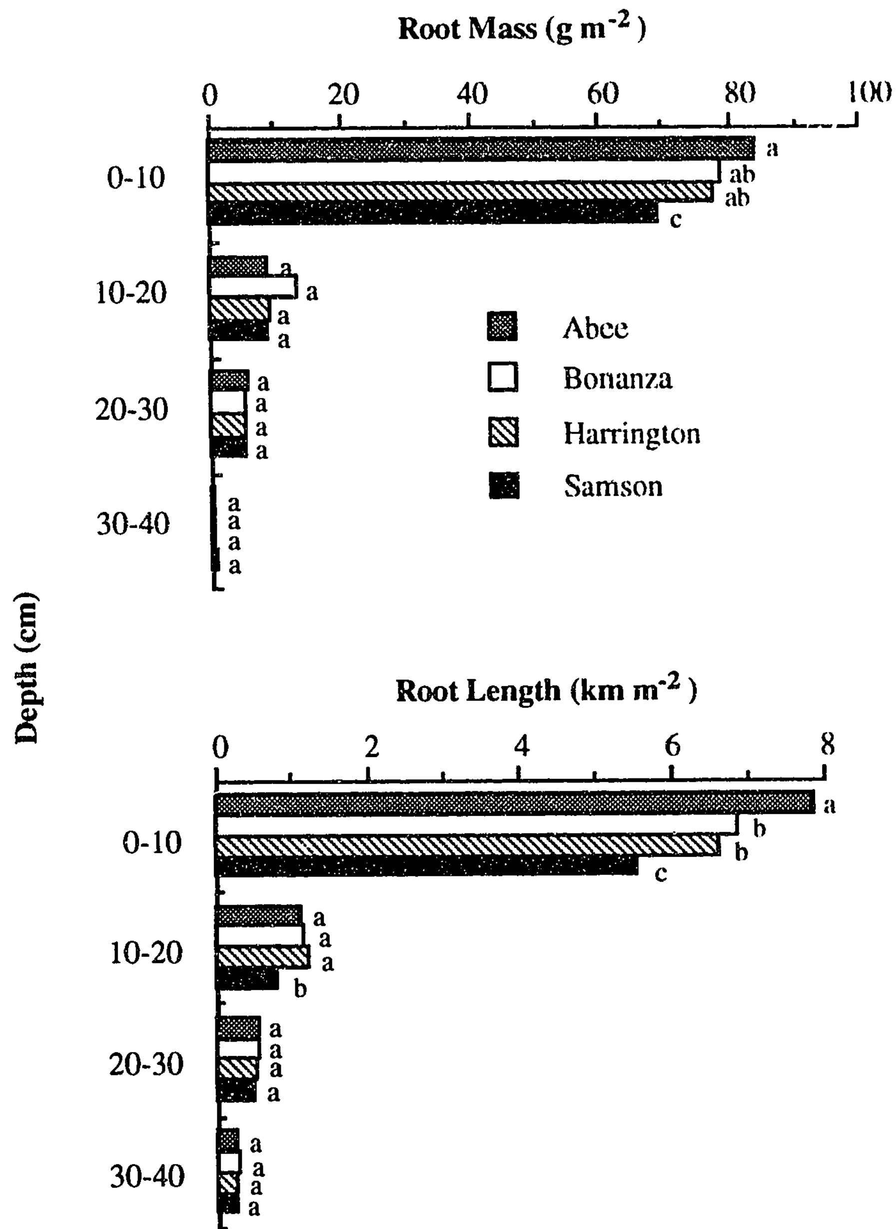

Fig. II.2. Average root mass and root length of four barley cultivars at various depths over 1989 and 1990. The means of the cultivars bearing the different lower-case letters are significantly different in root mass or root length over whole growing season at the given depth ($p<0.05$).

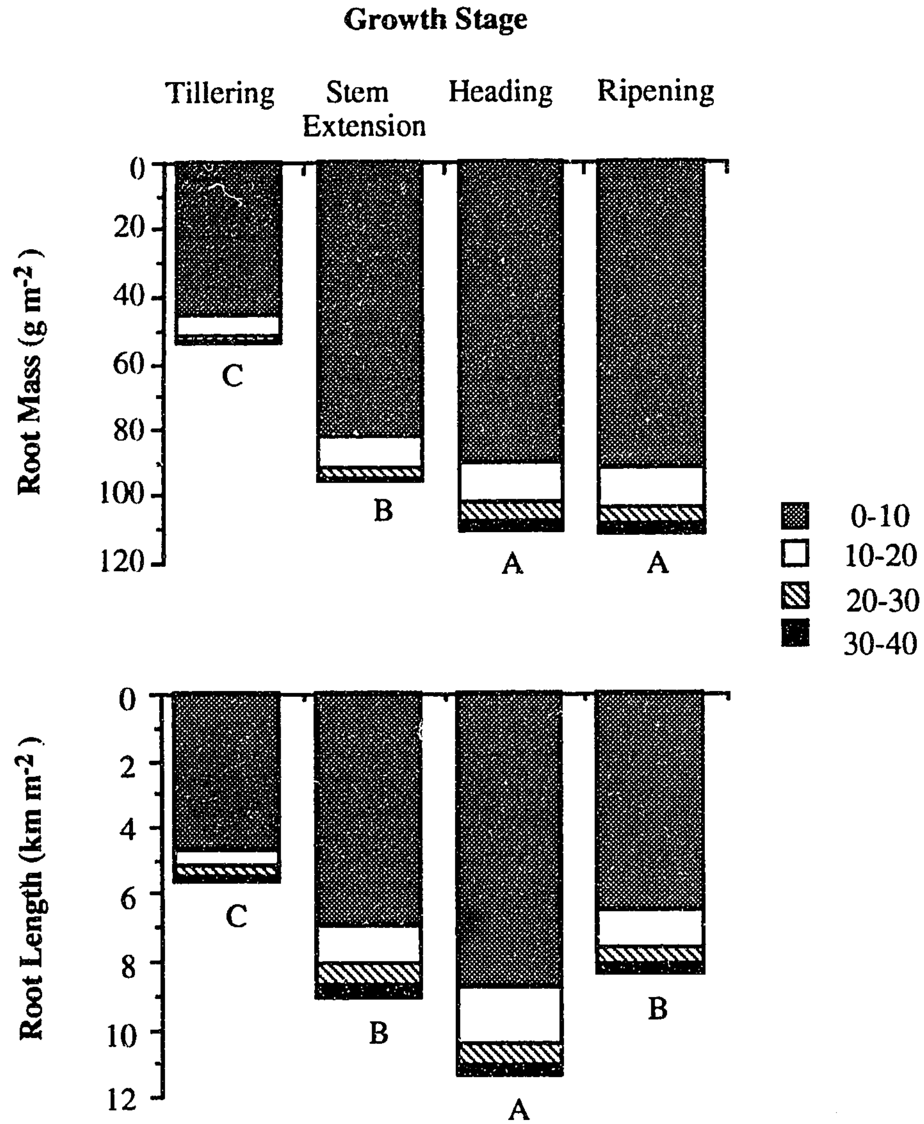

Fig. II.3. Average root mass and root length of four barley cultivars at various growth stages over four growth stages in 1989 and 1990. The means of four cultivars of growth stages bearing the different upper-case letters are significantly different in root mass or root length ($p < 0.05$).

Shoot mass in 1989 was significantly greater than that in 1990 (Table II.3). During the tillering stage, the shoot mass of Bonanza was significantly greater than that of Samson. There were no differences amongst other barley cultivars. During the stem extension stage, the ranking of cultivars for shoot mass was Abee and Bonanza > Harrington > Samson. During the heading stage, the ranking of cultivars for shoot mass was Abee > Bonanza and Harrington > Samson. During the ripening stage, the shoot mass of Abee was significantly greater than the shoot mass of Harrington and Samson and the shoot mass of Bonanza was significantly greater than that of Samson. The differences amongst other cultivars were not significant. In contrast to root mass, shoot mass of barley increased continuously over the four growth stages (Table II.3).

The shoot mass/root mass ratio increased over the growing season, because shoot mass increased at a greater rate than root mass during the growing season, especially after the heading stage. During the tillering stage, the ranking of cultivars for shoot mass/root mass ratios was Samson > Abee > Bonanza and Harrington. The shoot mass/root mass ratio of Samson declined by the stem extension stage and then increased steadily until the ripening stage. In contrast, shoot mass/root mass ratios of the other three cultivars increased slightly between the tillering and stem extension stages and rapidly from the stem extension to the ripening stage. During the ripening stage the ranking of cultivars for shoot mass/root mass ratios was Abee > Harrington > Samson. The ratios of Abee and Bonanza, and Bonanza and Harrington were not significantly different. The shoot mass/root mass ratios were lower in 1990 than in 1989 (Table II.3). The differences were mainly due to the difference in shoot mass because the root mass was similar for the two years (Table II.2).

Table II.3. Shoot mass (g m^{-2}) and shoot mass/root mass ratios of four barley cultivars in 1989 and 1990

		Shoot mass			Shoot/root ratio		
Growth Stage	Cultivars	1989	1990	Means[z]	1989	1990	Means[z]
Tillering	Abee	276	289	283ab	6.2	5.1	5.6b
	Bonanza	337	283	310a	4.8	4.7	4.8c
	Harrington	281	276	279ab	4.7	4.7	4.7c
	Samson	260	180	220b	6.4	6.5	6.5a
Stem Extension	Abee	604	576	590a	6.3	5.4	5.9a
	Bonanza	659	526	592a	6.6	5.3	6.0a
	Harrington	630	470	550b	7.6	4.9	6.3ab
	Samson	485	424	454c	5.1	4.7	4.9b
Heading	Abee	1122	1056	1089a	8.7	9.1	8.9a
	Bonanza	1112	959	1035b	9.7	8.3	9.0a
	Harrington	963	948	956b	9.7	8.3	9.0a
	Samson	858	862	860c	8.0	7.6	7.8b
Ripening	Abee	1379	1223	1301a	11.8	12.5	12.1a
	Bonanza	1278	1206	1242ab	11.5	10.7	11.1ab
	Harrington	1210	1193	1201bc	11.3	10.4	10.8b
	Samson	1175	1170	1172c	10.3	9.4	9.8c

ANOVA[y] of shoot mass and shoot mass/root mass ratios

Source of Variance	DF	Shoot Mass	Shoot mass/root mass ratio
Block (B)	2	ns	ns
Year (Y)	1	**	**
Error I	2		
Cultivar (C)	3	***	**
Y x C	3	ns	ns
Error II	12		
Growth Stage (S)	3	***	***
Y x S	3	ns	ns
C x S	9	ns	***
Y x C x S	9	ns	ns
Error III	48		

[z] The means of shoot mass and the ratios of shoot mass/root mass for the cultivars bearing different letters are significantly different in given growth stage ($p<0.05$).

[y] The difference between means is significant at: *, $p\leq0.05$; **, $p\leq0.01$; ***, $p\leq0.001$; ns, not significant.

Discussion

Measurements of barley root mass indicated that root growth generally increased up to the heading stage during the growing season. Similar trends have been observed in cotton (Klepper et al. 1973), and spring and winter wheat (Gross et al. 1987; Kopke et al. 1982). The differences in root mass between four barley cultivars were relatively small at early growing stages, greatest at the heading stage and declined between the heading and ripening stages. More than 80% of barley roots were concentrated in the surface layer (Fig II.2). The vertical distribution pattern was similar to those of spring and winter wheat grown on a Black Chernozem in Saskatchewan (Gross et al. 1987). The results obtained in the experiment showed that the shoot mass in 1989 was higher than that in 1990 but there was no significant difference in root mass between the two years. This may be because 1989 was wetter than 1990 during the growing season. Also, the significant difference in root mass between four barley cultivars was due to the difference in root mass in the surface layer (Fig. II.3). In the surface layer, the root mass trend was Abee > Bonanza > Harrington > Samson, and the total root mass trend was the same as the trend of the surface layer.

Root length dynamics did not follow similar trend as root mass dynamics through the whole growing season. Root length at ripening stage was significantly lower than root length at heading stage but there was no significant difference between heading and ripening stages in root mass. Perhaps this was mainly due to the decomposition of fine roots later during the growing season, reducing root length more than root mass. Soon (1988) found maximum root lengths of barley were attained approximately 73 to 80 d after seeding in a Black Solod depending on cultivar and soil moisture conditions. My results also showed that the root mass and root length peaked at the heading stage. The total root length estimated in the experiment were within the range (9-15 km m^{-2}) reported by Soon (1988). The specific root length (m g^{-1} dry mass) were also within the range reported by Atkinson (1989).

The proportion of the fine roots increased with soil depth. The losses of fine roots may be proportionally higher in the lower soil layers because the root washing technique used in this study did not recover all the fine roots (Grzebisz et al. 1989). Therefore, the proportion of the root mass present in 0-10 and 10-20 cm layers may have been overestimated (Floris and Noordwijk, 1984). However, the loss of fine roots may not affect the overall root mass very much but it may significantly reduce the estimates of root lengths at lower layers. Soil texture and bulk density influence root distribution. Bulk density and clay content increased with depth in the soil profile of this study. For example, the soil contained >55% clay and soil bulk density was about 1.4 Mg m^{-3} at 40 cm depth and this may have restricted root penetration and reduced the root growth in the lower layers.

The standing root mass represents a C input which will decompose in subsequent years. This study showed that there was a difference in the dynamics of the standing root mass of different cultivars of barley. I concluded that: (1) shoot and root mass of Abee was significantly greater than that of Samson. This means that the below-ground input of organic matter is a function of cultivar types; (2) more than 90% of barley root mass are concentrated in the 0-20 cm layer, which makes barley susceptible to temperature and water regimes in the 0-20 cm soil layers; (3) root mass increased rapidly until the heading stage, while the shoot mass increased at a higher rate than roots between heading and ripening stages. This resulted in a widening of shoot/root ratios; and (4) decomposition of very small roots may have contributed to a more rapid decrease in root length than in root mass after heading stage. In order to assess the complete impact of root inputs into soil ecosystem, more information is needed for other types of root-released organic materials such as root exudates, sloughed-off root cells and mucilage.

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Chapter 3. Above- and below-ground transformation of photosynthetically fixed C by two barley cultivars

Introduction

Management of inputs of shoot and root C affects the amount of organic matter in soil and its turnover rate (Juma and McGill 1986). Crop residue management has generally focussed on manipulation of straw in the fall or in the spring. However, straw management does not reveal an accurate picture of C inputs into soil because root C is ignored. Although the standing root mass at ripening may be only 10% of the shoot mass, a quantity equal to about three to four folds of maximum standing root mass is released into the soil over the growing season in form of root material and exudates (Biondini et al. 1988; Sauerbeck and Johnen 1977). Thus up to 33% of the total C fixed by photosynthesis may be used to build and maintain the root system. Davenport and Thomas (1988) compared C partitioning in corn and brome grass using ^{14}C-labelled CO_2 and found that 90% of the labelled C was allocated to shoots and 10% to roots for corn, but 60% was allocated to shoots and 40% to roots for brome grass at harvest. The deposition of labelled C to soil under brome grass was twice as much as that under corn. Milchunas et al. (1985) studied blue grama and wheat with the ^{14}C labelling method and found blue grama fixed about four times as much ^{14}C as wheat but the proportion of ^{14}C translocated below-ground was about 15% less than wheat. Van Veen et al. (1991) reported that 60 to 90% of the total C assimilated by arable crops was stabilized in different pools of the plant-soil ecosystem and 10 to 40% of that was released from the roots into the soil. Estimations of annual input of C into soil by growing crops ranged from 900 to 3000 kg ha^{-1}. Large variations exist with plant species, cultivars, development stages and environmental conditions (Enoch and Hurd 1977; Van Veen et al. 1989; Van Veen et al. 1991).

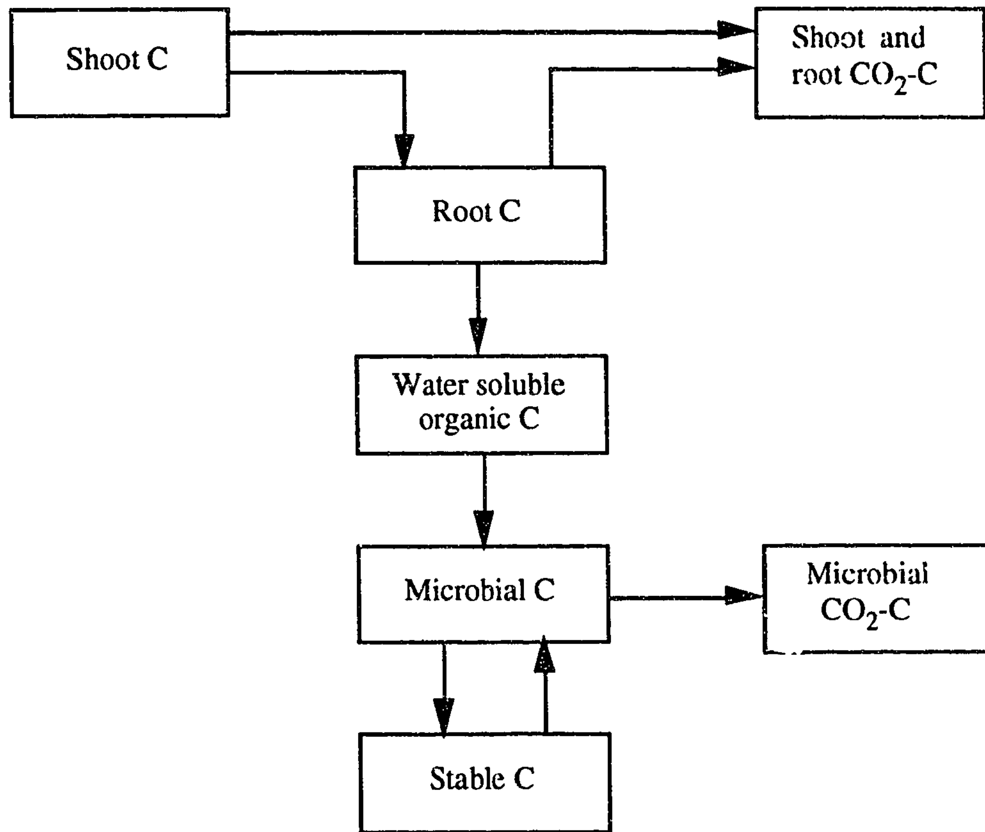

Fig.III.1. Conceptual model of C flow in plant-soil ecosystem.

Campbell et al. (1991) found no significant difference in soil organic matter content between the treatments where the straw was left on the surface or baled off in a 30 year old wheat-wheat-fallow rotation. They suggested that root inputs may be more important than straw inputs in maintaining the amount of organic matter present in soil. Also, the continuous input of root over the growing season is responsible for the activity of microorganisms and fauna which in turn affect nutrient cycling (Beck and Glimore 1983; Juma and McGill 1986) and soil structure formation (Berg and Pawluk 1984), since the intimate contact of roots with soil peds, microflora and fauna occurs over the growing season.

In chapter 2 using four barley cultivars (Abee, Bonanza, Harrington and Samson) grown in a Black Chernozem, I found that shoot and root mass of Abee was

significantly greater than that of Samson, indicating that the below-ground input of organic matter could be a function of a specific cultivar. However, the amount of standing root C represents only a part of C translocated below-ground. The root-released C enters the soluble C pool, which is utilized by microorganisms for growth, respiration and production of metabolites. Cultivars which release more of the translocated C may be responsible for partial stabilization of added C in soil organic matter (Fig. III.1). Further studies are needed to evaluate the dynamics of above- and below-ground materials during the growing season and their contribution to maintaining soil organic matter. I hypothesized that cultivars which release more C into soils rather than produce more standing root mass could stabilize more C in microbial biomass and soil organic matter. I studied the above- and below-ground C dynamics in two barley-soil ecosystems using pulse ^{14}C-labelling technique under field conditions.

Materials and Methods

Site description and experimental design

A field experiment was conducted on a Black Chernozem at the Ellerslie Research Station (53° 25' N, 113° 33' W) in 1990. This soil is naturally endowed with a thick Ah horizon which has good structure, high nutrient and base status, and neutral pH, and is important for cereal production in Alberta. Ellerslie receives 452 mm of precipitation annually. The average maximum and minimum temperatures in the growing season (June to September) are 22.4 and 5.6 °C, respectively.

The experiment consisted of two barley cultivars (Abee and Samson) grown on 10 m x 1 m plots in three replicate blocks (10 m x [illegible] m each) using a factorial split-plot design. Abee is a two-rowed medium height feed cultivar and Samson is a six-rowed semi-dwarf feed cultivar. Barley grains were drilled at 90 kg ha^{-1} (equivalent to 200 seeds m^{-2}) in rows 23 cm apart using a seed drill equipped with narrow hoe-openers

following running coulters. Urea (75 kg N ha^{-1}) and superphosphate (20 kg P ha^{-1}) fertilizers were placed 3 cm below the seeds at the time of seeding.

Twenty four microplots were established for pulse labelling the barley plants at four growth stages (3 blocks x 2 cultivars x 4 growth stages). Each microplot consisted of an open ended cylinder (20 cm internal diameter, 30 cm long) which was pressed into each experimental plot after crop emergence. Six microplots (3 blocks x 2 cultivars) were pulse labeled with $^{14}CO_2$ at each of the four growing stages: tillering (Zadoks growth stage 26), stem extension (Zadoks growth stage 32), heading (Zadoks growth stage 52), and ripening (Zadoks growth stage 85).

^{14}C labelling procedure

On each labelling date clear plastic canopies were sealed over the top of the cylinders with a strip of rubber tire tube. The ^{14}C labelling was carried out on a sunny day and each microplot was labelled with a total of 60 MBq $^{14}CO_2$. The temperature within the canopies ranged from 25 to 29 °C during the labelling period. A test tube containing 1 ml of a 0.01 M solution of $Na_2{}^{14}CO_3$ with a specific activity of 6000 MBq/mmol was sealed in a hole on top of each of the plastic canopies. The test tube had two small holes drilled in the side which were within the plastic canopies. The mouth of the test tube was outside the plastic canopy and sealed with a rubber seal. One ml of 0.05 M H_2SO_4 was injected through the rubber seal, releasing $^{14}CO_2$ which escaped into the canopy through the holes on the side of the test tube. Ten ml of air was bubbled through the solution in the test tube using a syringe with a long needle attached in order to release some of the trapped $^{14}CO_2$. A small battery operated fan was enclosed in the canopy to mix the $^{14}CO_2$ throughout the plastic canopy atmosphere. The plants within each of the plastic canopies were exposed to the $^{14}CO_2$ for two h. Midway through the labelling, 3 ml $^{12}CO_2$ was injected into the plastic canopy in order to maintain CO_2 level and photosynthetic rates as described by

Dinwoodie and Juma (1988). After two h labelling period 15 ml of 0.25 M NaOH was injected through a rubber seal into a beaker held within the canopy in order to absorb any remaining $^{14}CO_2$ before the plastic canopies were removed. The plastic canopies were removed 30 min after NaOH was injected. The NaOH solution in the beaker was saved for the measurement of residual $^{14}CO_2$ as was the $Na_2{}^{14}CO_3$ solution in the test tube after the addition of 1 ml of 0.25 M NaOH to trap any unreleased $^{14}CO_2$. This procedure was undertaken to meet the safety requirement of the use of radioactive materials.

Sampling procedure

Fifteen days after each labelling, shoots were harvested close to the soil surface from a cylinder in each replicate and the cylinders were excavated. The soil in the cylinder was separated into three 10 cm layers. Below the 30 cm, two soil cores (8 cm diameter, 10 cm long) were taken to a depth of 50 cm. Roots were manually separated from soil. Shoot and root material was dried at 70 °C and weighed. Soil samples were stored moist at 4 °C over night and analyzed as described below.

Analyses

Total C was determined on ground plant and soil subsamples by dry combustion using a Leco Carbon Determinator CR-12. The quantity of ^{14}C in shoots, roots, and soil was determined after oxidation in Harvey Biological Oxidizer, Model OX300. The ^{14}C released during oxidation was trapped in Harvey's ^{14}C Cocktail and measured with a Minaxiß Tri-Carb 4000 series scintillation counter.

Microbial respiration and microbial C were measured in the laboratory on 25-g samples of moist, sieved soil by the chloroform fumigation technique (Jenkinson and Powlson 1976). Microbial C was calculated by dividing the flush of CO_2-C by a Kc factor of 0.411 (Anderson and Domsch 1978). The quantity of CO_2-C released by the

unfumigated samples during the 10-d incubation was used as a measure of microbial respiration. Aliquots of NaOH (1 ml) containing trapped CO_2 from both the fumigated and unfumigated treatments were added to Scintiverse 1 (10 ml) and analyzed for ^{14}C with a Minaxiß Tri-Carb 4000 series scintillation counter.

Water-soluble organic C was determined using the method of McGill et al. (1986). A 10-g sample of field moist soil was shaken in 20 ml of water for one h, centrifuged, and filtered through a 0.45 µm Millipore filter. The extract was frozen until analysis on a Beckman Total Organic Carbon Analyzer, Model 915-B. The analysis of ^{14}C in water-soluble organic C was the same as the analysis of ^{14}C in microbial C and respired C.

Statistical Analyses

The data of root C, respired C, microbial C, water-soluble organic C, soil C, root ^{14}C, respired ^{14}C, microbial ^{14}C, water-soluble organic ^{14}C, and soil ^{14}C were analyzed using split-plot design consisting of three factors (cultivar, growth stage, soil depth) with three replicates using GLM procedure of the SAS package (SAS Institute Inc. 1987). The data of shoot C, shoot ^{14}C and the ratio of shoot ^{14}C/root ^{14}C were analyzed using the same design consisting of two factors (cultivar and growth stage). Student-Newman-Keuls (SNK) procedure was used for multiple comparison of main factors.

Results

Total C budget of two barley-soil ecosystems

The average contents of shoot C and root C of Abee over the growing season were significantly greater than those of Samson (Table III.1). The total shoot C increased over the four growth stages for both barley cultivars. In contrast, root C increased up to the heading stage and then decreased. Root C of Abee decreased faster than that of

Samson. Root C of Abee was higher than that of Samson in the 0-10 and 10-20 cm depths but they were not significantly different at lower depths. Root C increased up to the heading stage and then decreased in the 0-10 cm depth, however root C was similar at other depths over the growing season. Total C in soil decreased with depth, but did not significantly change over the growing season.

Influence of barley cultivars on respired C during 10-d incubation, microbial C and water-soluble organic C

The quantity of CO_2-C respired from unfumigated soil samples varied over the 4 growth stages (Table III.2). Soil respiration under the two barley cultivars at the first two growing stages was similar but the soil respiration of Abee was higher than that of Samson at the heading and ripening stages. Soil respiration of Abee was higher than that of Samson in the 0-10 cm depth, but the reverse was true at the 10-20 cm depth. There was no significant difference in soil respiration between the two cultivars at lower depths.

Soil microbial C, as determined by the chloroform fumigation technique, was not significantly different between the two barley cultivars, but significantly decreased linearly with depth. The soil microbial C under Samson increased steadily over the four growth stages, but that under Abee increased from tillering to the stem extension and remained relatively constant up to the heading stage and increased during the heading to the ripening stage.

Water-soluble organic C in soil under Abee decreased with time, but it increased in soil under Samson from tillering to the stem extension stage and then decreased until the ripening stage (Table III.2). Water-soluble organic C in soil under Samson was higher than that under Abee at the stem extension and heading stages. Water-soluble organic C decreased significantly with soil depth for both cultivars.

Table III.1. Total C budget (g C m^{-2}) in two barley-soil ecosystems

	Depth (cm)	Growth Stage			
		Tillering	Stem Extension	Heading	Ripening
		Abee			
Shoot C		39.5	126.1	221.0	257.2
Root C	0 - 10	6.7	9.6	13.8	10.7
	10 - 20	2.8	3.5	3.7	3.2
	20 - 30	1.2	1.4	1.4	0.9
	30 - 40	0.2	1.0	0.5	0.1
	40 - 50	0.1	0.3	0.2	0.1
		Samson			
Shoot C		30.9	81.2	176.4	206.4
Root C	0 - 10	5.9	9.1	10.1	8.4
	10 - 20	1.9	1.4	2.0	1.9
	20 - 30	0.5	1.8	1.2	1.2
	30 - 40	0.1	0.9	0.4	0.8
	40 - 50	0.0	0.4	0.3	0.2
Soil C	0 - 10	5624	5146	5377	5254
	10 - 20	6070	5719	5613	5395
	20 - 30	4643	4464	4468	4782
	30 - 40	2050	1987	2022	2044
	40 - 50	1028	1038	1044	1041

Summary of ANOVA[z]

Source of Variation	DF	shoot C	Root C	Soil C
Block	2			
Cultivar (C)	1	***	*	
Error I	2			
Growth Stage (S)	3	***	***	ns
C x S	3	ns	*	
Error II	12			
Depth (D)	4		***	***
C x D	4		***	
S x D	12		***	ns
C x S x D	12		*	
Error III	64			

[z] In this and all subsequent tables the difference between means is significant at: *, p≤0.05; **, p≤0.01; ***, p≤0.001; ns, not significant.

Table III.2. Respired C during 10 -d incubation from unfumigated soil samples, soil microbial C and water-soluble organic C of two barley-soil ecosystems (g C m^{-2}).

	Growth Stage				
	Depth (cm)	Tillering	Stem Extension	Heading	Ripening
			Respired C		
Abee	0 - 10	15.7	14.0	33.6	20.7
	10 - 20	11.9	8.9	20.6	18.4
	20 - 30	8.9	3.9	11.5	4.5
	30 - 40	2.7	1.9	6.6	1.1
	40 - 50	3.0	1.7	2.8	0.4
Samson	0 - 10	15.0	15.4	52.9	19.6
	10 - 20	18.2	7.3	19.2	10.4
	20 - 30	11.1	3.0	13.3	3.1
	30 - 40	2.5	1.1	10.9	1.9
	40 - 50	0.7	0.9	6.0	1.7
			Microbial C		
Abee	0 - 10	31.9	32.8	34.4	37.3
	10 - 20	32.8	36.4	26.7	43.7
	20 - 30	21.0	26.6	28.9	31.6
	30 - 40	11.5	13.2	14.2	12.7
	40 - 50	5.0	10.3	15.2	11.4
Samson	0 - 10	35.5	31.6	49.9	51.8
	10 - 20	30.7	38.3	31.7	44.7
	20 - 30	22.5	29.8	26.4	39.4
	30 - 40	7.9	21.6	18.6	27.3
	40 - 50	5.2	11.4	13.2	17.2
			Water-soluble organic C		
Abee	0 - 10	12.0	10.0	9.7	7.2
	10 - 20	3.2	3.1	3.2	2.2
	20 - 30	2.7	2.8	2.5	1.6
	30 - 40	1.8	1.5	1.5	1.3
	40 - 50	1.2	1.2	1.3	1.2
Samson	0 - 10	12.2	17.2	15.1	6.9
	10 - 20	2.9	3.5	3.5	2.4
	20 - 30	2.1	2.3	1.9	1.9
	30 - 40	1.5	1.9	1.6	1.6
	40 - 50	1.3	1.3	1.2	1.2

Table III.2. Respired C during 10 -d incubation from unfumigated soil samples, soil microbial C and water-soluble organic C of two barley-soil ecosystems (g C m^{-2}) (continued).

Summary of ANOVA

Source of Variation	Respired C	Microbial C	WSOC
Block			
Cultivar (C)	ns	ns	*
Error I			
Growth Stage (S)	*	*	*
C x S	*	*	*
Error II			
Depth (D)	**	***	**
C x D	**	ns	ns
S x D	ns	ns	ns
C x S x D	***	ns	ns
Error III			

^{14}C budget of two barley-soil ecosystems.

Shoot ^{14}C of Abee increased quickly between the tillering and heading stages. After the heading, the increase rate slowed down (Table III.3). Shoot ^{14}C of Samson increased more slowly between the tillering and stem extension stages. After the stem extension, it increased at a faster rate. The shoot ^{14}C of Samson was significantly higher than that of Abee only at the stem extension stage.

For Abee, root ^{14}C decreased significantly with time over the growing season, but for Samson it increased from tillering to the stem extension stage, and then decreased till the ripening stage (Table III.3). At the stem extension and heading stages, the root ^{14}C of Samson was significantly higher than that of Abee. The root ^{14}C of Samson was higher than that of Abee in the 0-10 cm depth, but a reverse trend was observed in the 10-20 cm depth. There was no significant difference at the 20-30 cm depth (Table III.3). In the 0-10 cm depth, the root ^{14}C at the ripening stage was significantly lower than that at other growth stages. There was no significant difference in root ^{14}C between growth stages at lower depths.

The ratios of shoot ^{14}C/root ^{14}C increased significantly with time over the growing season for both barley cultivars, but the rate of increase was significantly higher for Abee than for Samson. At tillering, the ratios of shoot ^{14}C/root ^{14}C for the two cultivars were similar, but from the stem extension stage, it increased faster for Abee than for Samson (Fig. III.2). At the ripening, the ratio of shoot ^{14}C/root ^{14}C of Abee was almost twice as much as that of Samson.

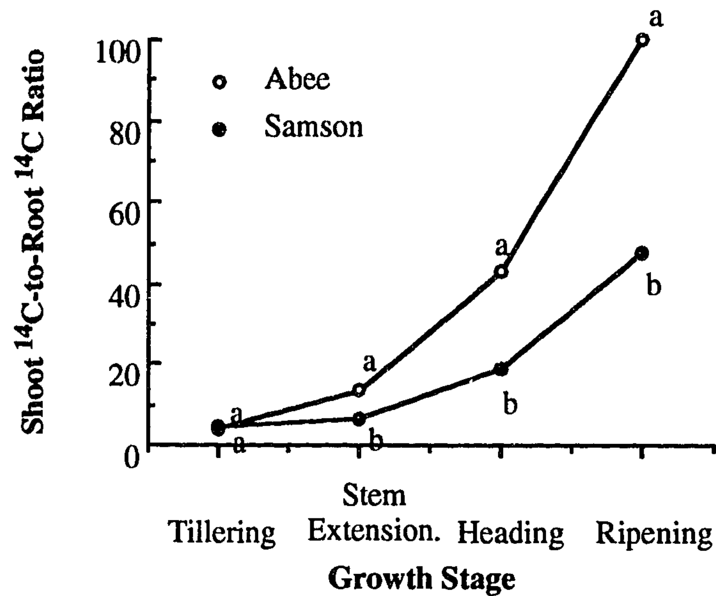

Fig. III.2. Shoot ^{14}C/root ^{14}C for two barley cultivars over growing season. The means of the cultivar bearing the different letters are significantly different at the definite stage ($p < 0.05$).

Table III.3. ^{14}C budget of two barley-soil ecosystems (MBq m^{-2})

	Depth (cm)	Tillering	Stem Extension	Heading	Ripening
		Growth Stage			
		Abee			
Shoot ^{14}C		41.0	57.1	137.7	220.8
Root ^{14}C	0 - 10	3.3	2.1	2.3	1.4
	10 - 20	0.5	0.3	0.4	0.4
	20 - 30	0.1	0.1	0.1	0.1
	30 - 40	-	-	-	-
	40 - 50	-	-	-	-
Soil ^{14}C	0 - 10	17.3	7.0	5.9	4.3
	10 - 20	7.8	3.0	3.5	4.9
	20 - 30	2.0	1.3	1.6	2.0
	30 - 40	0.7	0.8	1.2	1.7
	40 - 50	0.6	0.8	0.9	1.3
	Total	73.3	72.5	153.6	236.9
Recovery 15 d after labelling (%)		3.8	3.8	8.0	12.4
		Samson			
Shoot ^{14}C		62.8	83.9	164.4	186.5
Root ^{14}C	0 - 10	2.8	3.5	4.2	2.7
	10 - 20	0.4	0.2	0.3	0.2
	20 - 30	0.1	0.1	0.1	0.1
	30 - 40	-	-	-	-
	40 - 50	-	-	-	-
Soil ^{14}C	0 - 10	16.4	12.2	14.8	4.7
	10 - 20	10.5	7.3	4.9	2.6
	20 - 30	1.9	1.5	1.7	3.2
	30 - 40	0.7	1.3	1.4	1.4
	40 - 50	0.7	0.9	1.1	1.3
	Total	96.3	110.9	192.9	202.7
Recovery 15 d after labelling (%)		5.0	5.8	10.1	10.6

Table III.3. ^{14}C budget of two barley-soil ecosystems (MBq m^{-2}) (continued).

Summary of ANOVA

Source of Variation	Shoot ^{14}C	Root ^{14}C	Soil ^{14}C
Block			
Cultivar (C)	ns	*	*
Error I			
Growth Stage (S)	***	*	**
C x S	**	*	*
Error II			
Depth (D)		***	***
C x D		*	ns
S x D		**	**
C x S x D		*	***
Error III			

Soil ^{14}C under Abee was significantly lower than that under Samson at the stem extension and heading stages but there were no significant differences at the tillering and ripening stages. Soil ^{14}C decreased from tillering to the stem extension stage for both cultivars, but the decrease under Abee was greater than that under Samson. The soil ^{14}C under Abee increased steadily from stem extension till the ripening stage, but it increased from stem extension to the heading stage and then decreased from heading to the ripening stage under Samson. Multiple comparison analysis showed that soil ^{14}C at various depths followed the following trend: 0-10 cm > 10-20 cm depth > 20-30 cm, but there was no significant difference amongst the depths below 30 cm. In the 0-10 cm depth, the trend of the soil ^{14}C at various growth stages was: stem extension > heading and ripening stages > tillering stage. In 10-20 cm depth, the soil ^{14}C at the stem extension stage was significantly higher than that at other three growth stages. In the below 20 cm depths, there was no significant difference over the growing season.

Table III.4. Respired ^{14}C during 10-d incubation, soil microbial ^{14}C and water-soluble organic ^{14}C of two barley-soil ecosystems (kBq m^{-2}).

	Depth (cm)	Tillering	Stem Extension	Heading	Ripening
		Growth Stage			
		Respired ^{14}C			
Abee	0 - 10	1551.5	814.8	712.2	464.2
	10 - 20	446.8	253.8	287.6	607.6
	20 - 30	194.5	78.6	91.8	142.5
	30 - 40	50.8	55.8	54.9	69.4
	40 - 50	44.4	53.7	61.7	63.4
Samson	0 - 10	1412.3	2143.2	2056.6	357.9
	10 - 20	314.7	625.2	352.7	176.6
	20 - 30	108.1	203.7	124.7	81.1
	30 - 40	81.9	78.6	114.0	55.3
	40 - 50	47.7	64.0	83.7	58.7
		Microbial ^{14}C			
Abee	0 - 10	479.2	399.3	244.8	331.4
	10 - 20	358.3	113.2	86.5	233.8
	20 - 30	77.7	63.7	20.8	82.7
	30 - 40	15.9	14.8	20.4	63.3
	40 - 50	1.6	2.4	4.3	35.4
Samson	0 - 10	666.2	1554.7	247.4	405.5
	10 - 20	149.7	129.5	108.3	166.7
	20 - 30	172.5	67.6	51.8	44.9
	30 - 40	11.2	24.5	21.6	28.5
	40 - 50	2.3	1.9	2.2	8.4
		Water-soluble Organic ^{14}C			
Abee	0 - 10	46.5	24.9	34.3	32.0
	10 - 20	24.6	17.8	23.9	21.0
	20 - 30	19.4	17.9	14.4	16.1
	30 - 40	18.9	15.5	15.8	15.2
	40 - 50	14.8	15.6	11.0	14.0
Samson	0 - 10	49.6	74.7	70.5	30.3
	10 - 20	21.5	28.6	29.2	25.2
	20 - 30	16.0	22.2	19.4	16.4
	30 - 40	15.9	15.5	15.0	16.1
	40 - 50	15.1	14.9	16.6	15.2

Table III.4. Respired ^{14}C during 10-d incubation, soil microbial ^{14}C and water-soluble organic ^{14}C of two barley-soil ecosystems (kBq m^{-2}) (continued).

Summary of ANOVA

Source of Variation	Respired ^{14}C	Microbial ^{14}C	WSO ^{14}C
Block			
Cultivar (C)	*	*	*
Error I			
Growth Stage (S)	*	*	*
C x S	*	*	*
Error II			
Depth (D)	**	***	***
C x D	ns	ns	**
S x D	ns	ns	ns
C x S x D	ns	ns	***
Error III			

Influence of barley cultivars on respired ^{14}C during 10-d incubation, and ^{14}C present in microbial C and water-soluble organic C pools

Respired ^{14}C during the 10-d laboratory incubation from the unfumigated soil samples under Abee decreased with time over the growing season. But it peaked at the stem extension and heading stages under Samson (Table III.4). Respired ^{14}C during the 10-d incubation from the unfumigated soil samples under Samson was significantly higher than that under Abee at the stem extension and heading stages, but there was no significant difference at the tillering and ripening stages. Respired ^{14}C during the 10-d incubation from unfumigated soil samples decreased with depth for both barley cultivars.

Microbial ^{14}C under Samson was significantly higher than that under Abee at the stem extension stage. The differences at the tillering, heading and ripening stages were not significant (Table III.4). Microbial ^{14}C under Abee decreased from tillering to the heading stage then increased till the ripening stage, but it increased from tillering to the stem extension stage, decreased till the heading stage, and then increased again

Table III.5. Specific activity of ^{14}C in shoot C, root C and in soil of two barley-soil ecosystems (kBq g^{-1} C)

Depth (cm)		Tillering	Stem Extension	Heading	Ripening
		Abee			
Shoot		1037.4	453.3	623.6	859.4
Root					
	0 - 10	498.5	222.4	167.8	127.1
	10 - 20	174.1	72.9	84.0	123.9
	20 - 30	57.6	39.2	46.1	54.8
	30 - 40	24.7	25.6	41.6	56.4
	40 - 50	19.5	24.2	35.2	42.6
Soil					
	0 - 10	3.08	1.37	1.03	0.78
	10 - 20	1.10	0.45	0.53	0.77
	20 - 30	0.43	0.30	0.35	0.41
	30 - 40	0.36	0.38	0.61	0.84
	40 - 50	0.61	0.76	0.93	1.30
		Samson			
Shoot		2028.4	1304.6	932.8	904.4
Root					
	0 - 10	472.5	383.3	413.5	136.2
	10 - 20	232.7	172.5	118.4	66.7
	20 - 30	53.6	55.1	49.8	84.9
	30 - 40	23.1	43.3	76.8	45.6
	40 - 50	21.9	30.2	45.7	39.2
Soil					
	0 - 10	2.9	2.3	2.5	0.8
	10 - 20	1.4	1.0	0.7	0.4
	20 - 30	0.4	0.3	0.3	0.6
	30 - 40	0.3	0.6	0.6	0.6
	40 - 50	0.6	0.8	1.0	1.3

Summary of ANOVA

Source of Variation	Shoot ^{14}C	Root ^{14}C	Soil ^{14}C
Block			
Cultivar (C)	***	**	*
Error I			
Growth Stage (S)	***	**	*
C x S	**	**	*
Error II			
Depth (D)		***	***
C x D		*	***
S x D		**	**
C x S x D		*	***
Error III			

till the ripening stage under Samson. Microbial ^{14}C decreased linearly with depth for both cultivars.

Water-soluble organic ^{14}C in soil under Abee first decreased from tillering to the stem extension stage, then increased to the heading and finally decreased slowly for the rest of the season. Under Samson, it first increased from tillering to the stem extension stage, then slowly decreased to the heading stage and decreased rapidly from heading to the ripening stage. Water-soluble organic ^{14}C under Samson was significantly higher than that under Abee at the stem extension and heading stages, but there was no significant difference at the tillering and ripening stages. Water-soluble organic ^{14}C in the 0-10 cm depth was significantly higher than that in the depths below 10 cm for both barley cultivars.

Influence of barley cultivars on specific activity (kBq/g C) in shoot C, root C and soil C

The specific activity (kBq g^{-1} C) of ^{14}C in shoots of Samson was significantly higher than that of Abee (Table III.5). For Abee, it decreased from tillering to the stem extension stage and then increased till the ripening stage, but for Samson, it decreased steadily over the growing season.

The specific activity of ^{14}C in root of Abee decreased sharply from tillering to the stem extension stage and remained almost constant till the ripening stage. In contrast, the specific activity of ^{14}C in roots of Samson was almost constant until the heading stage and then decreased. The specific activity of ^{14}C in roots of Samson was significantly higher than that of Abee at the stem extension and heading stages. In the 0-10, 10-20 and 20-30 cm depths, the specific activity of root ^{14}C of Samson was higher than that of Abee. In the depths below 30 cm there was no difference. The ranking of the specific activity of ^{14}C in roots in the 0-10 cm depth over the growing

Table III.6. Specific activity of ^{14}C in Respired C during 10 -d incubation, soil microbial C and water-soluble organic C of two barley-soil ecosystems (kBq g^{-1} C).

	Growth Stage				
	Depth (cm)	Tillering	Stem Extension	Heading	Ripening
			Respired C		
Abee	0 - 10	98.8	58.2	21.2	22.4
	10 - 20	37.5	28.5	7.1	33.0
	20 - 30	21.9	20.2	8.6	31.7
	30 - 40	18.8	29.4	8.3	63.1
	40 - 50	14.8	31.6	22.0	70.4
Samson	0 - 10	94.1	139.2	38.8	18.3
	10 - 20	17.3	85.6	38.3	16.9
	20 - 30	9.7	67.9	9.4	26.2
	30 - 40	32.7	71.4	10.4	29.3
	40 - 50	68.1	71.1	13.95	34.5
			Microbial C		
Abee	0 - 10	15.0	12.2	7.2	8.9
	10 - 20	10.9	3.1	[illegible]	5.4
	20 - 30	3.7	2.4	[illegible]	2.6
	30 - 40	1.4	1.1	1.4	4.9
	40 - 50	0.3	0.2	0.3	3.1
Samson	0 - 10	18.7	49.2	4.9	7.8
	10 - 20	4.9	3.4	1.7	3.7
	20 - 30	7.7	2.3	2.0	1.1
	30 - 40	1.4	1.1	1.2	1.0
	40 - 50	0.4	0.2	0.2	0.5
			Water-soluble Organic C		
Abee	0 - 10	3.9	2.5	3.5	4.4
	10 - 20	7.7	5.7	7.5	9.5
	20 - 30	7.2	6.3	5.8	10.1
	30 - 40	10.5	10.3	10.5	11.7
	40 - 50	12.3	13.0	8.5	11.7
Samson	0 - 10	4.1	4.3	4.7	4.4
	10 - 20	7.4	8.2	8.3	10.5
	20 - 30	7.6	9.6	10.2	8.6
	30 - 40	10.6	8.2	9.4	10.1
	40 - 50	11.6	11.4	13.8	12.7

Table III.6. Specific activity of ^{14}C in Respired C during 10 -d incubation, soil microbial C and water-soluble organic C of two barley-soil ecosystems (kBq g^{-1} C) (continued).

Summary of ANOVA

Source of Variation	WSO C	Microbial C	Respired C
Block			
Cultivar (C)	ns	ns	*
Error I			
Growth Stage (S)	ns	**	ns
C x S	*	**	*
Error II			
Depth (D)	*	***	*
C x D	ns	*	ns
S x D	ns	*	*
C x S x D	*	ns	ns
Error III			

season was tillering > stem extension and heading > ripening. In the 10-20 cm depth it was tillering > stem extension > heading and ripening. There was no difference below the 20 cm depths.

The specific activity of ^{14}C in soil under Abee decreased from tillering to the stem extension stage, then increased till the ripening stage but under Samson it decreased steadily over the growing season. The specific activity of ^{14}C in soil under Samson was higher than that under Abee at the stem extension and heading stages, but it was not significantly different at the tillering and ripening stages. At the 0-10 and 10-20 cm depths, the specific activity of ^{14}C in soil under Samson was higher than that under Abee, but below 30 cm there was no difference between the two barley cultivars. The ranking of the specific activity of ^{14}C in soil in the 0-10 cm depth over the growing season was tillering > stem extension and heading > ripening. In the 10-20 cm depth it was tillering > stem extension > heading > ripening. There was no difference below the 20 cm depths.

Influence of barley cultivars on specific activity (kBq/g C) in respired [illegible]uring 10-d incubation, microbial C and water-soluble organic C

The specific activity of respired ^{14}C during 10-d incubation under Abee decreased from tillering to the heading stage, then increased till the ripening stage. It increased from tillering to the stem extension stage, decreased to the heading stage, then increased slowly to the ripening stage for Samson. The specific activity of respired ^{14}C during 10-d incubation under Samson was higher than that under Abee at the stem extension and heading stage, but there was no significant difference at the tillering stage. At ripening stage, the specific activity of respired ^{14}C during 10-d incubation under Abee was higher than that under Samson. In the 0-10 cm depth, the order of the specific activity in respired ^{14}C during 10-d incubation amongst the growth stages was tillering and stem extension > heading and ripening. In the 10-20 cm depth, the order was stem extension > tillering , heading and ripening. In the 20-30 cm depth, the order was stem extension > ripening > tillering and heading. In the 30-40 and 40-50 cm depths, the order was stem extension and ripening > tillering and heading.

The specific activity of microbial ^{14}C decreased from tillering to the heading stage and then increased till the ripening stage under Abee. Under Samson, it increased from tillering to stem extension stage, decreased to heading stage and then increased till ripening stage. The specific activity of microbial ^{14}C under Samson was higher than that under Abee at the stem extension and heading stage, but there was no significant difference at the tillering and ripening stages. In the 0-10 cm depth, the specific activity of microbial ^{14}C under Samson was higher than that under Abee, but the reverse trend was obtained in the 10-20 cm depth. There was no significant difference in below 20 cm depths between the two barley cultivars. In the 0-10 cm depth, the order of the specific activity of microbial ^{14}C amongst the growth stages was: stem extension and heading stages > tillering and ripening stages. In the 10-20 cm depth, the order of the

specific activity of microbial ^{14}C was: tillering > ripening > stem extension and heading. Below 20 cm, there was no significant difference amongst the growth stages.

The specific activity of water-soluble organic ^{14}C decreased from tillering to the heading stage and then increased till ripening stage under Abee. Under Samson, it remained constant from tillering to stem extension stage, increased to heading stage and then remained constant till ripening stage. Overall, the specific activity of water-soluble organic ^{14}C increased with the depth over growing season.

Discussion

Milchunas et al. (1985) found that after pulse labelling wheat, the allocation of ^{14}C in shoots, roots and soil was essentially complete after 5 d. The ^{14}C in soil was the highest 3.5 h after labelling and then declined after 5 d to an amount which remained constant for the remaining 62 d. The steady state value may be due to ^{14}C entering the soil from different C pools within the plant. After pulse labelling a living plant, an initial pulse of ^{14}C appears in the soil from soluble organic root exudates followed by a more constant release of ^{14}C from labelled storage and structural material, both of which have lower turnover rates within the plants than soluble C (Prosser and Farrar 1981). My result of ^{14}C activity in soil was obtained 15 d after labelling and it could be assumed to be the root-released C at a steady state (Milchunas et al. 1985).

The distribution of the ^{14}C in soil 15 d after pulse labelling was 1-2% in water-soluble organic C, 8-9% in microbial C and about 90% was in the soil organic matter including very fine roots which could not be removed from soil. However, the major portion of soil ^{14}C can be described as the C stabilized in the soil. There was a significant correlation ($r=0.796^{***}$, $n=24$) between root ^{14}C and soil ^{14}C (Fig. III.3). This implied that the photosynthetically fixed C stabilized in soil was controlled mainly by the amount of root-released C within 15 d after labelling. The amount of ^{14}C stabilized in soil was higher under Samson than under Abee (Table III.7), although

Samson had a lower root C than Abee (Table III.1). The specific activity of roots of Samson were higher than that of Abee (Table III.5). This implied that at the stem extension and heading stages, more ^{14}C was released by roots of Samson than Abee (Table III.3). Therefore, the amount of ^{14}C released to the soil showed a different trend than that for root C in soil.

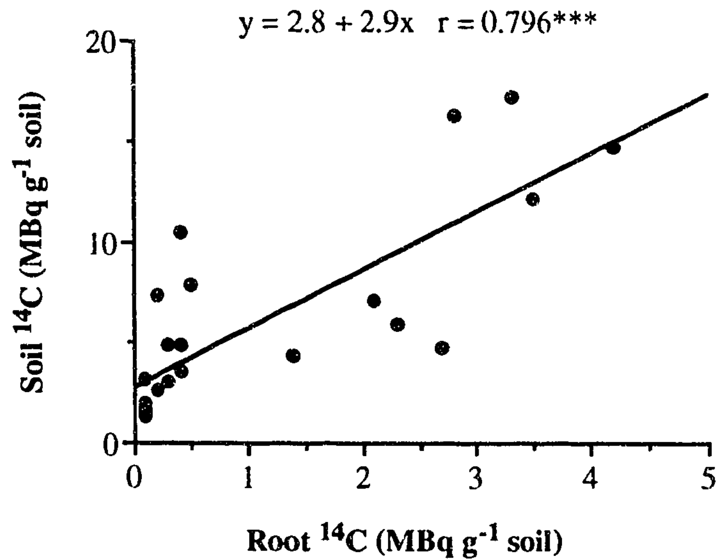

Fig.III.3. Linear model of the total soil ^{14}C with root ^{14}C.

Water-soluble organic C is used by microorganisms for biomass and energy production. There was a significant correlation between the water-soluble organic ^{14}C and stabilized soil ^{14}C (Fig. III.4, Table III.7), but there was no correlation between stabilized soil ^{14}C and soil microbial ^{14}C. This implied that the photosynthetically fixed C stabilized in soil was controlled mainly by the amount of C released by roots. The microbial biomass in the soil was relatively stable and the substrate available to the microorganisms was the key factor controlling the C transformation and cycling. A significant linear relationship between water-soluble organic ^{14}C in soil and ^{14}C respired by microorganisms during a 10-d incubation was obtained in this experiment

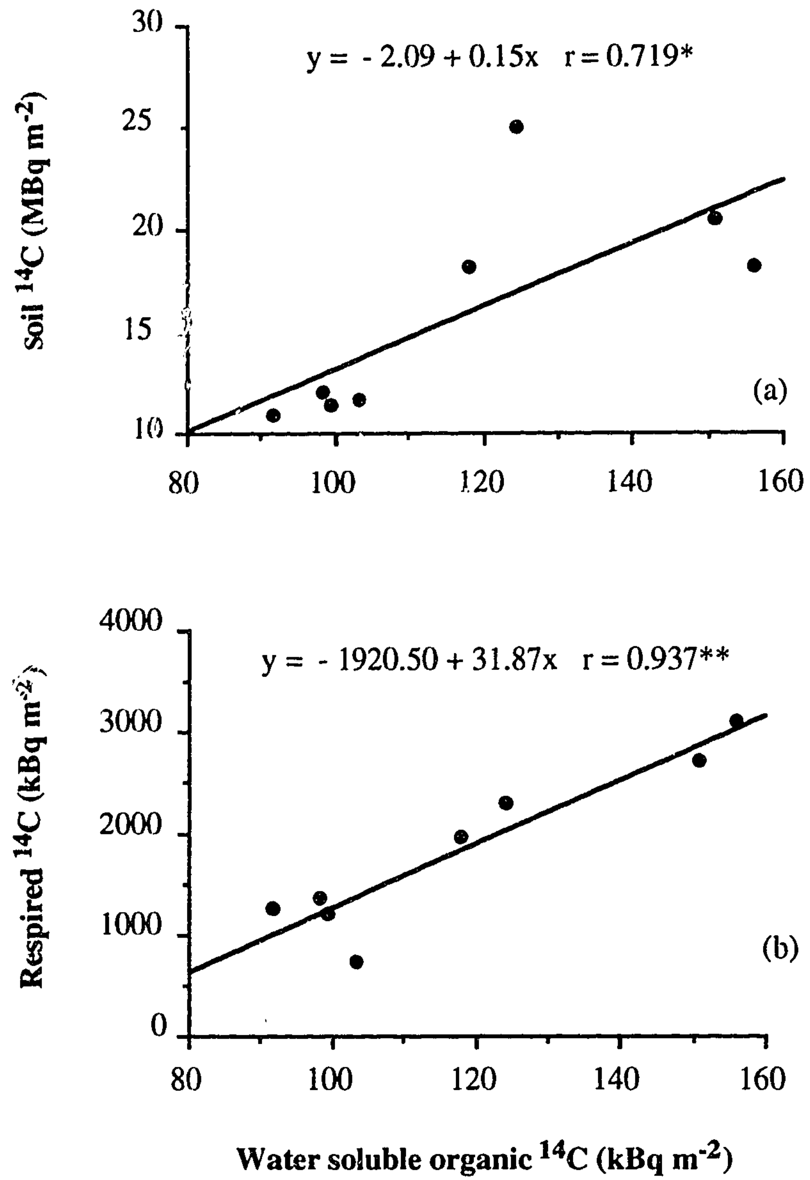

Fig.III.4. Linear models of the stabilized soil ^{14}C and respired ^{14}C by soil microorganisms during 10 -d incubation with water-soluble organic ^{14}C in soil.

(Fig. III.4). This indicated that water-soluble organic C was rapidly taken up by microorganisms and transformed into microbial biomass, microbial products and CO_2.

Water-soluble organic C in soil originates from two sources: root-released C and soil organic C. The specific activity of ^{14}C in the water-soluble organic C in soil was the result of the mixture of C from the two sources and their ^{14}C enrichments. Under Samson, the specific activity of ^{14}C in water-soluble soil organic C was higher than that under Abee at the stem extension and heading stages, indicating that at these growth stages, the proportion of root-released materials in water-soluble soil organic C was higher under Samson than under Abee. This implied that Samson released more water-soluble organic C into the soil than Abee as the soil originated water-soluble C should be similar under both cultivars grown in the same type of soil.

Martin and Kemp (1986) found that the proportion of C transloca[illegible] into root changed with the growth of the crops. I found that the age of plants had a strong effect on C partitioning. As the plants became older, the proportion of C translocated into below-ground decreased. This effect was greater for Abee than for Samson as the ratio of shoot ^{14}C/root ^{14}C increased (Fig. III.2 and Table III.3). The difference between the two barley cultivars mainly occurred in the middle of the growing season indicating the need to measure the dynamics of C over the growing season.

The specific activity of shoot C > root C >> respired C > microbial C > water-soluble organic C > soil organic C (Tables III.5 and III.6). The water-soluble organic C is derived from roots and stable soil C. Soil microorganisms can use water-soluble organic C and stable soil organic C as C sources (Fig. III.1). My results showed that the specific activity of respired ^{14}C was higher than that in water-soluble organic C at all growth stages for both barley cultivars. This implied that the root-released water-soluble organic C was more readily available as the energy source for soil microorganisms than the water-soluble organic C originating from soil.

Table III.7. ^{14}C stabilized in soil in two barley-soil ecosystems (MBq m^{-2})

Depth (cm)	Growth Stage			
	Tillering	Stem Extension	Heading	Ripening
	Abee			
0 - 10	15.2	5.8	4.9	3.5
10 - 20	7.0	2.6	3.1	4.0
20 - 30	1.7	1.1	1.5	1.8
30 - 40	0.6	0.7	1.1	1.6
40 - 50	0.5	0.7	0.8	1.2
Total	25.0	10.9	11.4	12.1
	Samson			
0 - 10	14.3	8.4	12.4	3.9
10 - 20	1.0	6.5	4.4	3.1
20 - 30	1.6	1.2	1.5	2.2
30 - 40	0.6	1.2	1.2	1.3
40 - 50	0.6	0.8	1.0	1.2
Total	18.1	18.1	20.5	11.7

Summary of ANOVA

Source of Variation	Soil ^{14}C
Block	
Cultivar (C)	*
Error I	
Growth Stage (S)	**
C x S	**
Error II	
Depth (D)	**
C x D	ns
S x D	ns
C x S x D	*
Error III	

The specific activity of microbial ^{14}C was higher than that in water-soluble organic C but was lower than respired C under both barley cultivars. This also supports the argument that microbes preferred to use root derived organic C. However, the stable C was also enriched with ^{14}C. Assuming that the C from water-soluble organic C is used at an efficiency of 30 to 50% (McGill et al. 1981), a portion of root and soil derived C is concurrently stabilized in soil. The throughput through the roots was more important

than the standing root mass. My results showed that ^{14}C stabilized in soil under Samson was 9% higher than under Abee. The amount of C fixed by different plant species varies but it is not always possible to substitute one species with another in Chernozemic regions. However, it is easier to substitute plant cultivars. The amount of C stabilized by different cultivars may be a possible solution in increasing soil organic matter content.

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Chapter 4. Relations of shoot C, root C, root length with root-released C of two barley cultivars and decomposition of root-released C in soil

Introduction

The production and utilization of shoot C, root C and root-released C are fundamental to the functioning of soil ecosystems (Ingrid et al. 1984). Campbell et al. (1991) found no significant difference in soil organic matter content in wheat-wheat-fallow rotation over a period of 30 years amongst treatments where the straw was left on the surface or baled off. They suggested that root inputs may be more important than straw inputs in maintaining the amount of organic matter in soil. Davenport and Thomas (1988) compared C partitioning in corn and brome grass using ^{14}C labelled CO_2 and found that labelled root-released C to soil by brome grass was twice as much as by corn.

In Chapter 2, I measured the primary production of shoots and roots of four barley cultivars and found more root mass under Abee than under Samson at the stem extension, heading and ripening stages in field experiments. Using ^{14}C labelling technique in Chapter 3, I also found that the total ^{14}C activity in shoots and roots of Samson were significantly higher than that of Abee over the growing season. The ^{14}C remaining in soil, in microbial C and in water-soluble organic C were significantly higher under Samson than under Abee at the stem extension and heading stages but there were no differences at the tillering and ripening stages. Root ^{14}C was correlated with soil ^{14}C. A greater proportion of photosynthetically fixed C was stabilized in soil under Samson than under Abee. The root-released C entered the water-soluble organic C pool and was utilized by microorganisms and resulted in the formation of soil organic matter.

Van Veen et al. (1991) reviewed information of various processes of C cycling in agroecosystems and concluded that the root exudation had the lowest degree of certainty compared to other root processes. Root-released C is estimated to account for 20-40% of the photosynthetically fixed C by plants (Van Veen et al. 1991). Although some information is available on the effect of environmental factors such as CO_2 levels (Van Veen et al. 1989) and nutrient availability (Beck and Gilmore 1983; Laheurte and Berthelin 1988), and the effect of microorganisms on root exudations (Martin 1977; Merckx et al. 1987; Prikryl and Vancura 1980), very little is known about the internal relations between shoot C, root C, root length and root-released C. Therefore, an experiment was conducted to identify these relations under controlled sterile conditions.

The root-released C is readily available to microorganisms. Using ^{14}C labelling technique, I found that most of ^{14}C respired by soil microorganisms during 10-d incubation were from water-soluble organic ^{14}C. The uptake of C also results in the formation of microbial biomass and microbially derived products which have a lower rate of decomposition (Juma and McGill 1986). In order to determine the kinetics of the transformation of root-released material, an experiment was conducted to study the decomposition of root-released materials in soil. This information is needed to describe the transformation of root-released materials in models describing the dynamics of soil organic matter.

The objectives of this experiment were: (1) to quantify the amount of root-released C produced by two barley cultivars; (2) to evaluate the direct and indirect effects of shoot C, root C and root length on the root-released C; and (3) to quantify the kinetics of decomposition in soil of the root-released C from the two barley cultivars.

Materials and Methods

Measurements of Shoot C, Root C, Root Length and Root-released C

Two barley cultivars, Abee and Samson, were used in this study. Abee is a two-rowed medium height feed cultivar and Samson is a six-rowed semi-dwarf feed cultivar. The seeds of approximately similar size for each cultivar were soaked in water for 1 h and surface sterilized with 2% $AgNO_3$ for 20 min. The excess $AgNO_3$ was removed with 1% NaCl. Thereafter, the seeds were rinsed once with 1% NaCl and then five times with sterile distilled water (Liljeroth et al. 1990). The seeds were allowed to germinate on 1:10 strength tryptone soy agar. Sterile seedlings were selected after three days and each seedling was transferred to a 75-ml plastic bottle containing 50 ml of sterile Hoagland and Arnon's nutrient solution No. 2 with pH of 6.5 (Hoagland and Arnon 1950). The solution contains 6.0 mM of KNO_3, 4.0 mM of $Ca(NO_3)_2{\cdot}4H_2O$, 1.0 mM of $NH_4{\cdot}H_2PO_4$, 2.0 mM of $MgSO_4{\cdot}7H_2O$, 0.009 mM of $MnCl_2{\cdot}4H_2O$, 0.046 mM of H_3BO_3, 0.0008 mM of $ZnSO_4{\cdot}7H_2O$, 0.0003 mM of $CuSO_4{\cdot}5H_2O$, 0.0001 mM of $H_2MoO_4{\cdot}H_2O$ and 2 ml of Fe-Chelate with concentration of 5 g Fe kg^{-1} solution. The experiment consisted of two treatments (barley cultivars) with eight replicates (bottles or seedlings). The cultures were placed in a growth chamber which was maintained at 80% relative humidity, 16-h day cycle at 20°C and 8-h night cycle at 12°C in natural light. The solutions were changed every 5 d and kept frozen at -20 °C till further analysis.

Plants were removed from the bottle after 25 d growth. The plate counting method was used to check the sterility of the solutions. In order to assess the cumulative root-released C, all the solutions obtained over the 25-d period were thawed and mixed. Total C in shoots and roots was determined by dry combustion. Root lengths were measured using line-intersect method of Tennant (1975) with a digitized microcomputer image analyzer. Total water-soluble organic C, determined with a Total Organic

Carbon Analyzer, Model 915-B, was assumed to be the root-released or root-derived C.

Path Analysis

The variances of shoot C, root C, root length and root-released C of the two barley cultivars were analyzed using the ANOVA procedure of the SAS package (SAS institute Inc. 1987).

Path analysis method was used to determine the direct and indirect effects of shoot C, root C and root length on root-released C (Sokal and Rohlf 1981). By using standardized variables, a set of normal equations in linear regression analysis can be represented by the following form (assuming there were three independent variables):

$$Pyx_1 + Pyx_2 * Rx_1x_2 + Pyx_3 * Rx_1x_3 = Ryx_1$$

$$Pyx_1 * Rx_2x_1 + Pyx_2 + Pyx_3 * Rx_2x_3 = Ryx_2$$

$$Pyx_1 * Rx_3x_1 + Pyx_2 * Rx_3x_2 + Pyx_3 = Ryx_3$$

where Pyx_i is the path coefficient. Rx_ix_j is the correlation coefficient between independent variables and Ryx_i is the correlation coefficient between dependent and independent variables. Therefore, the correlation coefficient between any independent variables and the dependent variable can be decomposed into several components: the direct effects (Pyx_i) and the indirect effects ($Pyx_i * Rx_ix_j$). Thus the effects of the individual independent variables on the dependent variable and their effects via other independent variables can be further investigated. The set of structural normal equations relating the variables under the study can be represented by a path diagram (Fig. IV.1). In my study, y was root-released C, x_1 was shoot C, x_2 was root C, and x_3 was root length. This diagram shows that there are nine round-trip routes from x to y (corresponding to the left-handed part of the set of normal equations). Three are direct round-trips (corresponding to the direct effects, x_i to y) and six are indirect round-trips through two x's (corresponding to the indirect effects x_i to x_j to y).

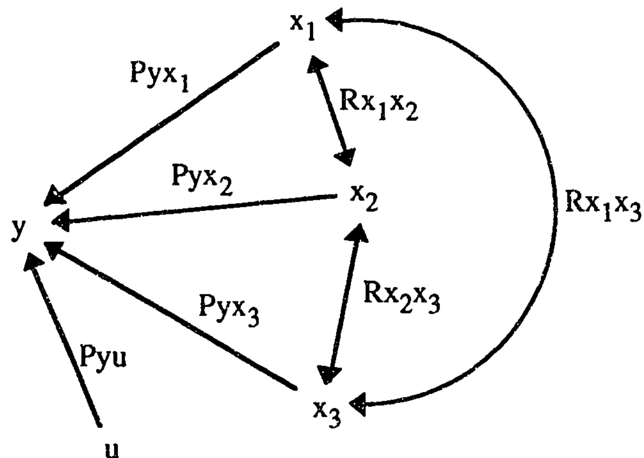

Fig. IV.1. A path diagram to describe the direct and indirect effects shoot C, root C and root length on root-released C. y is root-released C, x_1 is shoot C, x_2 is root C, x_3 is root length and u is the uncorrelated residues.

Decomposition of Root-Released C in Soil

Labelling of root-released C

All the seedlings of each cultivar were placed on a plastic sheet and covered with a clear plastic canopy (20 cm in diameter and 30 cm in height) and sealed in the growth chamber when the plant seedlings were 20 d old. They were pulse-labelled with a total of 60 MBq $^{14}CO_2$ over a period of 5 d to obtain labelled root-released materials for the decomposition study described below. All other conditions and procedures were similar to those described in Chapter 3.

After the 5-day labelling period, 15 ml of 0.25 M NaOH were injected through a rubber seal into a beaker held within the canopy in order to absorb any $^{14}CO_2$ remaining in the canopy. The canopy was removed 1 h after NaOH was injected. The NaOH solution was saved for the measurement of residual $^{14}CO_2$. For the measurement of ^{14}C-activity in the solution, an aliquot (5 ml) of the nutrient solution

from each bottle was added to 10 ml of Harvey's ^{14}C cocktail and then counted with a liquid scintillation analyzer.

Decomposition of labelled root-released C in soil

Surface (0-10 cm) soil samples of a Black Chernozem (Typic Cryoboroll) were obtained from the Ellerslie Research Station located 10 km south of the University of Alberta, Edmonton. The surface horizon has a granular structure, high nutrient and base status, SiCL texture and neutral pH. The total organic C and N contents were 64.9 g C kg^{-1} soil and 5.30 g N kg^{-1}, respectively.

For the measurement of the decomposition rates of root-released C in soil, 5-ml aliquot of the composite solution from each seedling was added to a 25-g soil sample. The experiment consisted of two treatments (root-released C from two barley cultivars) replicated eight times. After amending the soil with root-released material, the soil moisture content was adjusted to 60% of the maximum water holding capacity (29% W/W). Then, the soil samples were placed in 2 l glass jars and incubated at 20 °C. Twenty five ml of 0.1 M NaOH was used to absorb the CO_2 evolved from the soil. On the day 3, 10, 18, 26, 39, 55, 81, the NaOH was changed and the ^{14}C in NaOH solution was determined by a liquid scintillation analyzer. The procedures of the determination of ^{14}C-activity in NaOH solution was the same as that of the determination of ^{14}C-activity in the nutrient solution.

Kinetic analysis of the decomposition of labelled root-released C in soil

The double exponential model was used to describe the decomposition of labelled root-released C added to the soil. The equation used was:

$$^{14}C \text{ remaining} = Le^{-kt} + Re^{-ht}$$

where L is the proportion of the labile root-released C (%), R is the proportion of the resistant root-released C (%), k and h are the first order decomposition rate constants (d^{-1}) for these components, respectively. The sum of L and R is 100%. The fitting of the experimental data to the model was conducted using the least square method by NLIN procedure of SAS (SAS Institute Inc. 1987).

Results and Discussion

Shoot C, Root C, Root Length and Root-Released C of Two Barley Cultivars

There were no significant differences in shoot C and root C between the two barley cultivars 25 d after germination (Table IV.1) but the root length of Abee was greater than that of Samson. The root-released C of Abee was significantly less than of Samson. The shoot C and root C of the two barley cultivars were similar because the growth rates of the two barley cultivars were similar during the early growth stages. This is consistent with the observations under field conditions that the shoot mass and root mass of Abee were similar to those of Samson before the tillering stage but at the later growth stages they were greater for Abee than for Samson (Chapter 2).

Table IV.1. Shoot C, root C, root length , released C and ratios of shoot C/root C, shoot C/root-released C and root C/root-released C of two barley cultivars[z]

	Abee	**Samson**
Shoot C (mg/plant)	101.8 a	91.8 a
Root C (mg/plant)	52.9 a	48.3 a
Root Length (cm/plant)	216.2 a	177.4 b
Released C (mg/plant)	13.3 b	14.9 a
Shoot C/Root C	1.9 a	1.8 a
Shoot C/Root-released C	7.6 a	6.2 b
Root C/Root-released C	3.9 a	3.2 b

[z] The means with different letters are significantly different ($p \leq 0.05$).

The values of root lengths obtained in this experiment (177.4 and 216.2 cm plant^{-1}) were similar to those of seminal barley roots (253.2 cm plant^{-1}) grown in sterile nutrient solutions for 21 d but lower than the total root length (1251 cm plant^{-1}) (Barber and Gunn 1974). Root length is affected by a number of factors such as nutrient concentrations, plant species, type of cultivars and growth conditions. Liljeroth et al. (1990) found that root length of barley decreased by more than 50% when the N concentrations in the nutrient solution were increased from 200 to 400 mg l^{-1}. The N concentration in my experiment (210 mg l^{-1}) was higher than that (182 mg l^{-1}) of Barber and Gunn (1974). The nutrient solution was changed every 5 days therefore the concentration of N in my experiment was higher over the entire growth period compared to that of Barber and Gunn (1974). This may be one of the reasons that my estimates are lower than those of Barber and Gunn (1974). The values of the root lengths obtained in this experiment were shorter than the results obtained in the field conditions (Soon 1988; Chapter 2). The average root mass (34.4-39.0 mg plant^{-1}) of barley cultured in nutrient solution for 21 d (Barber and Gunn 1974) was only about 10% of the average root mass of wheat (254- 436 mg plant^{-1}) grown in soil for the same period (Barber and Martin 1976). This may be due to the differences in root environment between nutrient and soils.

The ratio of shoot C to root C is one of the important indices for studying C partitioning and cycling in plant-soil ecosystem (Johansson 1991). In this experiment, the ratios of shoot C to root C of the two barley cultivars were not significantly different, which indicated the standing above-ground and below-ground components were similar for the two barley cultivars at this growth stage. The ratios of shoot C to root C in this experiment (1.8 - 1.9 for 25 d growth) were also similar to the results (1.4 - 1.8 for 21 d growth) obtained by Barber and Gunn (1974). The shoot to root ratios of barley cultivars used in this experiment increase over the growing season under field conditions (Chapter 2).

The ratio of shoot C to root-released C and the ratio of root C to root-released C are also important parameters used in studying C partitioning and cycling. The proportions of the root-released C over total root C (26 - 31%) obtained in this experiment were similar to those (6 - 33%) obtained by Liljeroth et al. (1990). However, Newman (1985) reported that the root exudate C lies in the range of 10 - 100 mg C per gram dry weight root which is equivalent to 25 - 250 mg C per g root C (2.5 - 25%) assuming 40% C content in root dry matter. The ratio of shoot C to root-released C and the ratio of root C to root-released C of Abee were both significantly greater than those of Samson. This indicated that Samson released more C per unit shoot C or per unit root C than Abee (Table IV.1).

Previous studies with $^{14}CO_2$ labelling techniques demonstrated that different proportions of photosynthates were transported to roots and released into the rhizosphere by different plants (McDougall 1970; Davenport and Thomas 1988). In this experiment, Abee and Samson are two cultivars of the same species, but the differences in root-released C, the ratio of shoot C to root-released C and the ratio of root C to root-released C were significant. This indicated that the amount of root-released C is the function of the cultivars of the same plant species. In the field experiment, the ^{14}C stabilized in soil under Samson was greater than that under Abee at the stem extension and heading stages, which implies that the Samson released more ^{14}C from roots into soil than Abee at these two stages (Chapter 3). This experiment confirmed the trend observed in the field experiment.

Direct and Indirect Effects of Shoot C, Root C and Root Length on Root-Released C

Shoot C was significantly correlated to root C for Abee but not for Samson (Table IV.2). Root C was significantly correlated to root length for both barley cultivars. Among the three crop characteristics tested in the experiment (shoot C, root C and root length), root length had the highest correlation with root-released C for both barley

cultivars. The below-ground characteristics (root C and root length) of the two barley cultivars were more correlated with root-released C than the above-ground characteristic (shoot C).

The correlation coefficient is the expression of how dependent two variables are on each other. It also can be seen as the effect of one on the other (Sokal and Rohlf 1981). Through path analysis, the effect of the independent variables on the dependent variable (correlation coefficients between the independent variables and the dependent variable)

Table IV.2. The correlation coefficients of three characteristics and root-released C[z]

	Shoot C	Root C	Root length	Root-released C
			Abee	
Shoot C (x_1)	1.00	0.74*	0.55	0.53
Root C (x_2)		1.00	0.89	0.73
Root Length (x_3)			1.00	0.95***
Released C (y)				1.00
			Samson	
Shoot C (x_1)	1.00	0.69*	0.38	0.49
Root C (x_2)		1.00	0.72	0.77*
Root Length (x_3)			1.00	0.85*
Released C (y)				1.00

[z]The correlation coefficient is significant at *, $p<0.1$; **, $p<0.05$; ***, $p<0.01$.

can be divided into two parts: direct effect and indirect effects (Fig. IV.1). In the experiment, the correlation coefficients of the three independent variables (shoot C, root C and root length) with dependent variable (root-released C) were decomposed into three parts for each independent variable: one direct effect and two indirect effects (Fig IV.1). It was found that all the three direct effects of Samson were positive (Table IV.3), which may mean that any increase of the three variables would increase the root-released C. For Abee, the direct effect of root C was negative which meant that the

increase of root C reduced the root-released C. This may be due to the competition of the photosynthates between root growth and root exudation. Overall, the ranking of the direct effects of the three independent variables (absolute value) on the root-released C for both barley cultivars was root length > root C > shoot C.

Table IV.3. Direct and indirect effect of shoot C, root C and root length on root exudation

	Abee	Samson
	Direct effects	
Shoot C (x_1)	0.37	0.07
Root C (x_2)	-1.01	0.27
Root Length (x_3)	1.64	0.63
	Indirect effects	
$x_1 \rightarrow x_2 \rightarrow y^z$	-0.75	0.19
$x_1 \rightarrow x_3 \rightarrow y$	0.91	0.24
$x_2 \rightarrow x_1 \rightarrow y$	0.28	0.05
$x_2 \rightarrow x_3 \rightarrow y$	1.46	0.45
$x_3 \rightarrow x_1 \rightarrow y$	0.21	0.03
$x_3 \rightarrow x_2 \rightarrow y$	-0.89	0.21

$^z x_1 \rightarrow x_2 \rightarrow y$ means the indirect effect of x_1 through x_2 on y.

All the indirect effects for Samson were positive. This indicated that the increase of any one of the three characteristics would indirectly increase the root-released C through other two characteristics. However for Abee, the indirect effects of root C and root length through shoot C and the indirect effects of shoot C and root C through root length were positive, but the indirect effects of shoot C and root length through root C were negative. This may mean that the increase of the shoot C or root length may make the root itself increase and reduce the root-released C as discussed above for Abee . These analyses suggest that the competition of the photosynthates between different

pools of Abee was more serious than between those of Samson, and this may be one of the reasons that the root-released C of Abee was less than that of Samson.

The direct and indirect effects obtained through path analysis provided further insight into the interrelationships of plant characteristics. In some cases, the correlation coefficient was positive, but some of the direct or indirect effects were negative. In other cases, the direct effect was positive or negative, but the indirect effects were opposite. For example, shoot C of Abee was positively correlated with root-released C ($r = 0.53$); its direct effect was positive (0.37), and the indirect effect of it through root length was positive ($x_1 \rightarrow x_3 \rightarrow y = 0.91$), but its indirect effect through root C was negative ($x_1 \rightarrow x_2 \rightarrow y = -0.75$). Because the direct and indirect effects were counteracting each other to some extent, the correlation coefficient was the sum of the direct and indirect effects ($0.37 - 0.75 + 0.91 = 0.53$). These analyses provided further insight into the interrelationship among the different characteristics and gave clearer and more detailed picture of the influence of the shoot C, root C and root length on root-released C, but not the mechanisms which caused these results.

Kinetics of Decomposition of Root-Released C in Soil

Root-released materials are a complex mixture of organic compounds. They contain not only simple compounds which decompose rapidly, but also complex compounds which decompose slowly (McDougall, 1970). In addition, microbial transformation of root-released C results in the formation of complex organic compounds which have a slower decomposition rate. The double exponential model significantly fit the data obtained on the decomposition of root-released C (^{14}C remaining in the soil) in the experiment (Fig. IV.2) and the further analysis (Izaurralde et al. 1986; Bates and Watts 1988) showed that the two equations obtained from the two barely cultivars were different ($p < 0.05$). The proportion of the labile components (L) of the root-released C of Abee was estimated to be 87.3% and that of Samson was

74.4%. This indicated between 74 to 87% of the root-released materials are labile and readily available to the soil microorganisms. The half lives of the labile components was estimated 4.3 d for Abee and 4.5 d for Samson. The proportion of the resistant components of the root-released C was estimated 12.7% for Abee and 25.6 % for Samson. The half lives of the resistant components of the root-released C were estimated 37.7 d for Abee and 29.6 d for Samson, respectively.

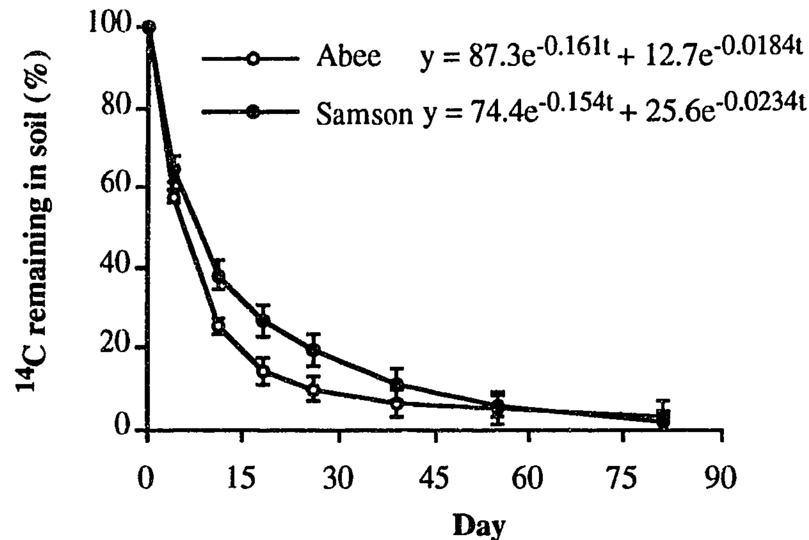

Fig. IV.2. Kinetics of root-released C (represented by ^{14}C) remaining in soil of the two barley cultivars. In the equations y is the ^{14}C remaining in soil (%) and t is time (d).

The half lives of the labile root-released C obtained in the experiment were shorter than that of the water-soluble organic C (half life of 8.9 d) obtained in soil (McGill et al. 1986). This suggested that the composition of the labile root-released C may be less complex than that of the water-soluble organic C obtained in soil. In this experiment, a large proportion of the root-released C was readily decomposable and transformable for the microorganisms in soil. The half lives of the resistant root-released C obtained in the experiment were longer than that of the water-soluble organic C obtained in soil.

This suggested that the composition of the resistant root-released C may be more complex than that of the water-soluble organic C in soil. The average half life of the root-released C of Abee was 8.5 d (87.3% x 4.32 + 12.7% x 37.7) and the half life of the root-released C of Samson was 10.9 d (74.4% x 4.49 + 25.6% x 29.6). Both of those were similar to that of the water-soluble organic C obtained from soil. This suggests that the water-soluble organic C in soil is mainly composed of root-released materials and the microbial products which originate from the root-released materials.

The resistant portion of the root-released C obtained in this analysis contained the resistant portion of the released C and microbially synthesized materials originating from the decomposition of labile components of the root-released C (Fig. IV.2). Therefore, the data have to be further analyzed with a simulation model to understand more about the C transformation and cycling among the different pools in the plant-soil ecosystem.

The present experiment was performed with relatively young plants and for a relatively short time. Keith et al. (1986) found that there was a different distribution pattern of the assimilated C in wheat at different stages of development under field conditions. In younger plants a higher proportion of the assimilated C was translocated below-ground than in older plants. This must influence the root exudations of the plants at different ages. Estimate of total C released by barley roots must be extrapolated to field conditions with caution. The chemical composition of the root-released C of different crops at different stages and its impact on microbial activity needs further investigation.

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Chapter 5. *In situ* root decomposition of two barley cultivars

Introduction

Root C and root-released materials are the main source of soil organic matter for a wide variety of ecosystems. Although the standing root mass at harvest is typically only about 10% of the shoot mass, about three to four times as much C as contained in maximum standing root mass is released to the soil over the growing season in forms of sloughed root materials and root exudates (Sauerbeck and Johnen 1977). Thus up to one third of the C fixed by photosynthesis is used to build and maintain the root system. The decomposition and transformation of root C through microbial and faunal activity are important processes for the formation of soil organic matter (Ulrich 1987).

Below-ground production may be seriously underestimated if calculated as the difference in standing biomass between two sampling dates because roots are continuously growing, dying and decomposing. Total root production could be calculated more accurately if root decomposition rates in field are known (Hansson and Steen 1984; Chapter 2). Most studies of the root decomposition have been conducted with extracted or excised roots added to disturbed soil samples that do not represent field conditions where roots have intimate contact with soil peds, even in plowed fields. Also, previous studies may be biased by the absence of fine roots which have higher turnover rate. In Chapter 2, it was found that the root length of different barley cultivars at the ripening stage was significantly lower than that at the heading stage but there was no significant difference in root mass between these growth stages. These observations suggested that there was a rapid turnover of fine roots because fine roots contribute more to root length than to root mass. Moreover, root sample preparation techniques such as drying, grinding and mixing may also bias the estimation of root decomposition rates. Therefore, it is important to study the root decomposition *in situ* to estimate the decomposition of roots in field conditions.

Studying the decomposition of roots *in situ* is difficult because it is not possible to distinguish fine root from soil organic matter. If continuous ^{14}C labelling technique is used, a large amount of ^{14}C is released into soil and is present as root ^{14}C, root-released ^{14}C, microbial ^{14}C and soil organic matter ^{14}C. Van Veen et al. (1989) found that root-released C accounted for about 30% of the total photosynthetically fixed C and young plants released even more than older plants. If ^{14}C pulse labelling technique is used for a very short interval, root-released ^{14}C would be reduced but the ^{14}C will be more concentrated in labile components than in resistant components of the roots. Thus, the roots would not be uniformly labelled. Milchunas et al. (1985) found that 3.5 h after the beginning of the pulse labelling, about 20% of the ^{14}C was found in cell wall components of the roots, and 5 days after the beginning of the pulse labelling, there was more than 50% of ^{14}C in the cell wall components. Therefore, C translocated to roots is rapidly transformed in structural components. The third problem encountered with ^{14}C pulse labelling technique is the separation of root respiration from microbial respiration. Even if the shoots are excised after pulse-labelling, the roots do not die instantaneously. They may continue to grow for a short period after excision of shoots and may continue to respire. Meharg and Killham (1988) found that roots respired more than 40% of the total ^{14}C fixed by plant in the first two days after the beginning of the pulse labelling. After that, the respired ^{14}C from roots was stable and accounted for less than 2% of the total ^{14}C fixed by the plant. In spite of these difficulties, it may still be possible to use the ^{14}C pulse labelling technique to study root decomposition *in situ* by choosing a short pulse labelling period, excising the shoots, and measuring the decomposition of roots from microbial respiration of ^{14}C after the flush of root respired ^{14}C.

An experiment was designed to study the decomposition of roots *in situ* and quantify different forms of C in a Black Chernozem (Typic Cryoboroll) under two barley cultivars (Abee and Samson) using pulse labelling and incubation techniques.

The hypothesis for this study was that the cultivar which translocates more C into roots will respire more C and also stabilize more C into soil organic matter, because a small proportion of the added C remains in the soil after being partially and wholly transformed by microorganisms..

Materials and Methods

Description of barley cultivars, soil type and environmental conditions

Two barley cultivars (Abee, a two-rowed medium height feed cultivar, and Samson, a six-rowed semi-dwarf feed cultivar) were used because previous studies showed that total ^{14}C-activity in shoot and root of Samson was significantly higher than in Abee over the growing season, and a greater proportion of photosynthetically fixed C was stabilized in soil under Samson than Abee (Chapter 3). The soil used in the experiment was Black Chernozem (Typic Cryoboroll) with a thick Ah horizon. The surface horizon has a granular structure, high nutrient and base status, and favorable pH. The total organic C content was 64.3 g kg^{-1} soil, total N content was 5.3 g kg^{-1} soil and soil texture was SiCL. This soil is important for cereal production in Alberta.

The surface soil (0-10 cm) of Black Chernozem at Ellerslie Research Station was sieved and packed in 16 steel cylinders (20 cm in diameter and 10 cm in height) to a bulk density of 1.0 Mg m^{-3}. Eight cylinders were used for each barley cultivar. Seven barley seeds of similar size were seeded in each cylinder. Urea (75 kg N ha^{-1}) and superphosphate (20 kg P ha^{-1}) fertilizers were placed 3 cm below the seeds at the time of seeding. The plants were grown at 21 °C in a greenhouse without artificial lighting at Edmonton (53°N,113°W) in June and July, 1992. The day length was between 15 to 16 h. The 30-year (1951-1980) monthly radiation during June and July ranges between 18 to 22 MJ m^{-2} (Atmospheric Environmental Service, 1982). During the growth period, soil moisture was maintained at 90% of field capacity. Additionally,

two unplanted cylinders were used as blanks to correct for ^{14}C absorption by soil during the labelling period.

^{14}C labeling Procedure

On the 25th d after emergence, the plants were labeled with $^{14}CO_2$. A clear plastic canopy was sealed over top of each cylinder with a strip of rubber tire tube. The ^{14}C labeling was carried out at 8:00 am on a sunny day and the plants in each cylinder were labelled with a total of 60 MBq $^{14}CO_2$. The temperature within the canopies ranged from 25 to 29 °C during the labeling period. The procedures for the labelling was similar to those described in Chapter 3 except that the plants within the canopy were exposed to the $^{14}CO_2$ for 24 h. Two control cylinders (only soils without plants) were also labelled under the same conditions.

Sample preparation for laboratory experiment and experimental design

After the 24 h period, the shoots were excised on the surface of the soil to stop translocation. A soil corer was placed over the center of each plant and 7 soil cores (5 cm in diameter and 10 cm in height) were taken from each cylinder. The cores from two of the eight cylinders for each cultivar were used to assess the variance of root C and root ^{14}C within and between cylinders. The rest were used in the incubation experiment.

In order to determine the *in situ* root decomposition rate in soil, the remaining undisturbed soil cores taken from each of the 6 cylinders for each cultivar (2 cultivars x 6 cylinders x 7 cores/cylinder) were incubated in the incubation jars at 20 °C and 60% of the maximum water holding capacity 24 h after excision of shoot. The experimental design was 2 barley cultivars x 6 replications (one core from each cylinder) x 6 sampling dates (Day 0, 5, 10, 25, 40 and 80). Fifty ml of 1.0 M NaOH solution was used to absorb the CO_2 evolved from each of the soil core during the incubation. The

NaOH solution was changed every 5 d. On Day 0, 5, 10, 25, 40 and 80, 6 replicates selected at random were used to measure the water-soluble organic C, microbial C, water-soluble organic ^{14}C and microbial ^{14}C as described below. The results reported for each date in the experiment are means of six replicates.

Chemical and biological analysis:

Roots were separated by hand from soil cores sampled at Day 0 and the ^{14}C in the root tissue and soil were analyzed separately. Water-soluble organic ^{14}C, and soil microbial ^{14}C were also measured at Day 0 as described below. The water-soluble organic ^{14}C was considered to be the root-released ^{14}C. The ^{14}C in roots separated by hand plus ^{14}C in fine roots which could not be separated from soil by hand [calculated by (total soil ^{14}C) - (water-soluble organic ^{14}C + microbial ^{14}C)] was considered to be the total root ^{14}C in the soil core. This was assumed to be the initial value of the root ^{14}C for the root decomposition study.

Total root C was calculated based on the following assumption: the chemical composition of the roots separated by hand was similar to that of the whole root system; ^{14}C distribution in the roots separated by hand was similar to that in the whole root system. Therefore,

Separated root C / Total root C = Separated root ^{14}C / Total root ^{14}C

The total root C was calculated as follows:

Total root C = (separated root C) x (Total root ^{14}C) / (Separated root ^{14}C)

For determination of ^{14}C in soil cores obtained at Day 0, 20 mg of ground (<100 mesh) root samples or 50 mg of ground (<100 mesh) soil samples (including fine roots) were oxidized with a Harvey Biological Oxidizer, Model OX-300. The ^{14}C released during oxidation was trapped in ^{14}C cocktail and measured with a 2000CA TRI-CARB Liquid Scintillation Analyzer.

Total CO_2 evolved by the soil core during the incubation was determined by titrating a 5 ml aliquot of NaOH with 100 mM HCl after precipitation of carbonate with 2 M $BaCl_2$ solution. The $^{14}CO_2$ evolved from each soil core was analyzed by adding an aliquot of NaOH (2 ml) containing trapped $^{14}CO_2$ to Harvey's ^{14}C Cocktail (10 ml) and counting with a 2000CA TRI-CARB Liquid Scintillation Analyzer.

Microbial C was measured in the laboratory on 25-g soil samples by the chloroform fumigation technique (Jenkinson and Powlson, 1976) and calculated by the method of Voroney and Paul (1983). Microbial ^{14}C was calculated from the ^{14}C evolved from fumigated sample. The ^{14}C evolved from unfumigated samples was not subtracted (Voroney and Paul 1983).

Water-soluble organic C was determined using the method of McGill et al. (1986). A 10-g sample of field moist soil was shaken in 20 ml of water for 1 h, centrifuged, and filtered through a 0.45 μm Millipore filter. The extract was frozen until analysis on a Beckman Total Organic Carbon Analyzer, Model 915-B. The water-soluble organic ^{14}C was determined as described for analysis of ^{14}C evolved from the soil core.

Statistical Analysis

The variance of root C and root ^{14}C within cylinders was assessed using coefficient of variance (CV) and between cylinders using t test (SAS Institute Inc. 1987). The variance of water-soluble organic C, soil microbial biomass C and soil respired C, and water-soluble organic ^{14}C, soil microbial biomass ^{14}C and soil respired ^{14}C were analyzed using ANOVA procedure of the SAS package (SAS Institute Inc. 1987). The regressions of the double exponential equations for the kinetics of the root decomposition *in situ* were calculated with the NLIN procedure of the SAS package.

Results

Variance of initial root C and root ^{14}C

The CVs of the initial root ^{14}C values in the different soil cores within a cylinder for Abee and Samson were 4.6% and 5.3%, respectively. There was no significant difference between cylinders within a given cultivars. Therefore, I assumed that after labeling the amount of root C and root ^{14}C in each soil core within the treatment (cultivar) in the experiment was not significantly different.

Kinetics of C in different soil pools during root decomposition

The amount of total root C added to the soil under Abee (369 mg C kg^{-1} soil) was significantly greater than that under Samson (332 mg C kg^{-1} soil). The rate of soil respired C increased rapidly from Day 0 to Day 10 and then decreased (Table V.1). Cumulative soil respired C was not significantly different between the two barley cultivars. Water-soluble organic C peaked at Day 5 then decreased with time. Water-soluble organic C under Samson was higher than that under Abee at Day 0 and Day 5 but lower at the remaining dates (Table V.1). Microbial C in soil decreased over time during the incubation period for the two barley cultivars and there was no significant difference between the two barley cultivars. Root C + Soil C was not significantly different over time and between the two barley cultivars.

Kinetics of ^{14}C in different soil pools during root decomposition

In contrast to root C, the amount of root ^{14}C added to the soil by Samson (4167 kBq kg^{-1} soil) was significantly greater than that by Abee (3414 kBq kg^{-1} soil). As the laboratory incubation period started 24 h after labelling, I assumed that the contribution of root respiration to the total soil respiration would be minimal. The cumulative respired ^{14}C of Samson was higher than that of Abee over the incubation period.

Table V.1. Distribution of C in different soil pools of two barley-soil ecosystems (mg C kg^{-1} soil)

	Incubation time (d)					
	0	5	10	25	40	80
	Cumulative Respired C					
Abee	0	247	319	482	655	1076
Samson	0	204	277	438	631	1027
	Water-soluble organic C					
Abee	75	120	80	75	65	60
Samson	83	125	75	65	63	54
	Microbial C					
Abee	510	470	430	390	340	320
Samson	627	550	540	370	310	330
	Root C + Soil C (mg C g^{-1} soil)					
Abee	64.4	64.1	64.1	64.0	63.9	63.5
Samson	64.3	64.2	64.1	64.0	64.0	63.6

Summary of ANOVA

Source of Variation	Cumulative respired C	WSOC	Microbial C	Root C + Soil C
Cultivar (C)	ns	ns	ns	ns
Time (T)	*	*	***	ns
C x T	ns	*	ns	ns

The amount of ^{14}C respired between Day 0 and Day 5 accounted for approximately 60% of the total respired ^{14}C during the incubation period.

Water-soluble organic ^{14}C under Abee increased from Day 0 to Day 5, decreased up to Day 25, and then increased till Day 80. For Samson, it increased from Day 0 to Day 5, then decreased till Day 80. Microbial ^{14}C decreased over the incubation period for both barley cultivars. The difference ^{14}C between the two barley cultivars was not

significant. The root ^{14}C + soil ^{14}C under Samson was significantly greater than that under Abee over the incubation period. It decreased with time over the incubation period for both cultivars .

Table V.2. Distribution of ^{14}C in different soil pools of two barley-soil ecosystems (kBq kg^{-1} soil)

	Incubation time (d)					
	0	5	10	25	40	80
	Cumulative respired ^{14}C					
Abee	0	1519	1958	2162	2300	2402
Samson	0	1635	2113	2364	2595	2792
	Water-soluble organic ^{14}C					
Abee	3.5	8.8	6.9	4.3	4.9	5.4
Samson	4.9	6.8	5.8	4.6	4.0	3.7
	Microbial ^{14}C					
Abee	512	356	223	152	143	119
Samson	650	334	263	154	141	111
	Root ^{14}C + Soil ^{14}C					
Abee	3414	2046	1742	1611	1481	1403
Samson	4167	2846	2440	2299	2082	1915

Summary of ANOVA

Source of Variation	Cumulative respired ^{14}C	WSO^{14}C	Microbial ^{14}C	Root ^{14}C + Soil ^{14}C
Cultivar (C)	*	ns	ns	**
Time (T)	***	*	*	***
C x T	ns	*	ns	ns

Specific activity of ^{14}C in different soil pools during the root decomposition

The specific activity of root ^{14}C of Samson (12.6 kBq mg^{-1} C) was significantly higher than that of Abee (9.3 kBq mg^{-1} C). The specific activity of cumulative respired ^{14}C of Samson was significantly higher than that of Abee over the incubation period, but it decreased with time for both barley cultivars.

Table V.3. Specific activity of ^{14}C in different soil pools of two barley-soil ecosystems (kBq g^{-1} C)

	Incubation time (d)					
	0	5	10	25	40	80
	Cumulative respired ^{14}C					
Abee	0	6149	6138	4485	3511	2232
Samson	0	8015	7628	5397	4112	2718
	Water-soluble organic ^{14}C					
Abee	47	73	86	57	75	90
Samson	52	54	77	71	64	69
	Microbial ^{14}C					
Abee	1003	757	519	389	421	372
Samson	1233	607	487	416	455	336
	Root ^{14}C + Soil ^{14}C					
Abee	53	29	23	20	18	16
Samson	65	40	33	29	26	23

Summary of ANOVA

Source of Variation	Cumulative respired ^{14}C	WSO^{14}C	Microbial ^{14}C	Root ^{14}C + Soil ^{14}C
Cultivar (C)	***	ns	ns	**
Time (T)	*	*	**	**
C x T	ns	*	ns	ns

The specific activity of water-soluble organic ^{14}C of Abee increased from Day 0 to Day 10, then decreased to Day 25 and thereafter increased again till Day 80. For Samson it increased from Day 0 to Day 10, decreased till Day 40, then increased till Day 80 (Table V.3). There was no significant difference in the specific activity of water-soluble organic ^{14}C between the two barley cultivars.

The specific activity of microbial ^{14}C decreased over the incubation period for both barley cultivars. The difference between the two barley cultivars was not significant. The specific activity of root ^{14}C + soil ^{14}C of Samson was significantly greater than that of Abee over the incubation period. It decreased with time over the incubation period for both cultivars .

Kinetics of root decomposition in situ for two barley cultivars

Roots are composed of smaller molecular weight compounds (labile components such as glucose and amino acids) which decompose relatively fast and larger molecular weight compounds (resistant components such as lignin) which decompose relatively slowly. In addition, microbial transformation of simple compounds derived from roots results in the formation of new complex organic compounds which have slower decomposition rates. Therefore, a double exponential model was used to describe the kinetics of root decompositions *in situ* for the two barley cultivars in the experiment. The double exponential model used was:

$$^{14}C \text{ remaining} = Le^{-kt} + Re^{-ht}$$

where L is the proportion of the labile components (%), R is the proportion of the resistant components (%). The sum of the L and R is 100%, and k and h are the first order decomposition rate constants (d^{-1}) for labile and resistant components, respectively.

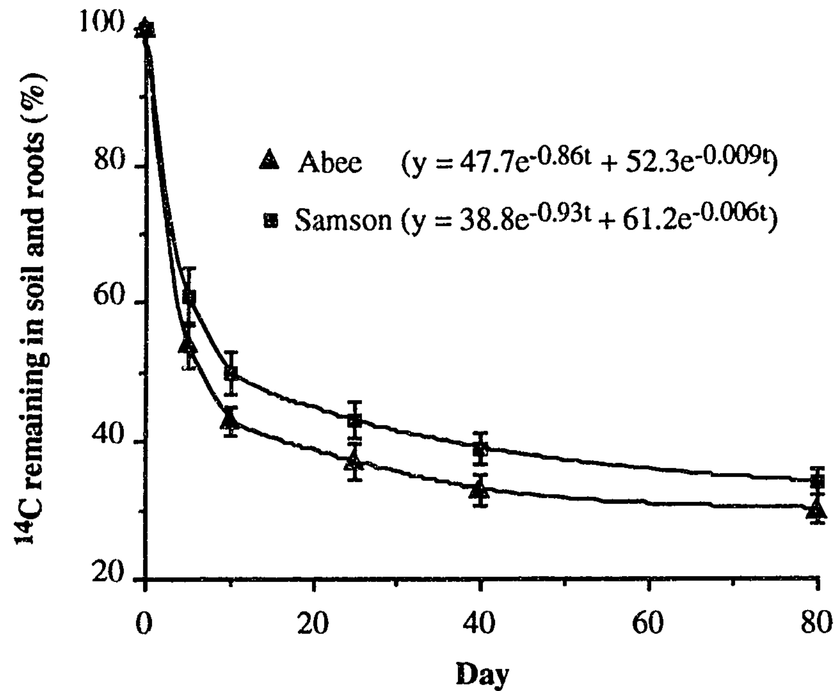

Fig. V.1. Amount of ^{14}C remaining in soil and roots (y) over time (t) in undisturbed soil cores containing roots of two different barley cultivars

The model was significantly fitted for the data obtained in the experiment for both barley cultivars ($p<0.001$). Further analysis (Mo 1984; Bates and Watts 1988) showed that the proportion of the labile components (L) in the roots of Abee (47.7%) was significantly greater than that of Samson (38.8%), but the half lives of the labile components (0.693/k) of the roots were not significantly different between the two barley cultivars (Fig. V.1). The decomposition rate constants for the resistant components of the roots (h) were not significantly different between the two barley cultivars either. This implied that the difference between the two barley cultivars in the root decomposition rate was mainly because of the difference in the ratios of the labile components to the resistant components. The average half lives of the roots was 41 d for Abee and 71 d for Samson. The half life of the roots was longer than that of the root-released C. In the first 15 days of the incubation the root-released C was

decomposed by 70 to 80% but root C was decomposed by only 50 to 60% in the same period.

Discussion

In this experiment, one day labelling was used and the incubation started two days after the beginning of the labelling or one day after the excision of the shoots. Based on the results reported by Milchunas et al. (1985) and Meharg and Killham (1988) one can assume that at least 20% of the ^{14}C in the roots was in the cell wall components when the laboratory incubation started. Furthermore, as the roots may not have died instantaneously after the excision of the shoots, there still may be metabolism occurring in the roots. Some ^{14}C in the labile forms in root may still be transformed into resistant forms but no more ^{14}C was being translocated to roots after excision of shoots. Three days after the beginning of the incubation or 5 d after the beginning of the pulse labelling, more than 50% of the ^{14}C in the roots could be in the cell wall components (Milchunas et al. 1985).

Meharg and Killham (1988) found that roots respired more than 40% of the total ^{14}C fixed by the plant in the first two days after the beginning of the pulse labelling. After that, the respired ^{14}C was stable and accounted for less than 2% of the total ^{14}C fixed by the plant. The incubation in this experiment was started two days after pulse labelling. Therefore, the root respiration was not measured because the laboratory experiment was started 48 h after pulse labelling period ended. Therefore, the proportion of ^{14}C respired by roots would be negligible over the 80 d incubation period.

The decomposition rate of roots *in situ* is different from that of the roots mixed with bulk soil because there is intimate contact of the roots with soil and a greater diversity, quantity and activity of the soil microorganisms in the rhizosphere. The high microbial activity in rhizosphere may increase the decomposition rate of roots *in situ,*

however, the intimate contact of roots with soil peds may increase the stabilization of the organic matter in the mineral soil stratum (Scheu and Wolters 1991). In the experiment, Samson had higher concentration of ^{14}C in roots, and ^{14}C remained in soil under Samson longer than under Abee. This indicated the cultivar which translocated more C (represented by ^{14}C in the experiment) into the roots could stabilize more C into soil organic matter. Campbell et al. (1991) found no difference in soil organic matter content in treatments in which straw was left in the field or baled off over a period of 30 years and suggested that roots may be a key factor influencing soil organic matter for a long term. My results support this idea and showed that the root decomposition not only had short term effect on microbial activity, but also had effect on long term soil organic matter balance.

Overall, water-soluble organic C, water-soluble organic ^{14}C, and microbial C and microbial ^{14}C of Samson were higher than those of Abee on Day 0, but they showed a reverse trend on the subsequent dates. This suggests that the roots of Samson released more C into soil than those of Abee when they were alive, but after excising the shoots, the roots of Abee decomposed faster than those of Samson and more C was transformed into the water-soluble organic C and microbial C. This indicated that the C input through roots and the dynamics of root-released C could be different with the root status. It also could differ not only between plant species (Milchunas et al. 1985) but also between different cultivars of the same species.

Kissim et al. (1981) demonstrated that the more readily biodegradable an organic substrate, the greater the amount of residual C present in the microbial biomass at times soon after rapid microbial activity had ceased. Studies by Ladd et al. (1977) and Amato and Ladd (1980) showed that maximum amounts of microbial C were formed from glucose decomposition within a few days of commencement of incubation, whereas maximal concentrations of microbial C from decomposing plant residues were not achieved until after several months. This reflected the greater complexity of the

turnover process with multicomponent substrates of varying biological stabilities. Nevertheless, my results showed that the microbial ^{14}C was higher on Day 0 and Day 5 and then decreased. This peak of ^{14}C in microbial biomass may be from the labile components of roots. After Day 40, there was a small increase in microbial ^{14}C which may be from the decomposition of resistant components of roots and newly formed resistant compounds derived from microbial turnover in soil. These results are in agreement with those reported by Kissim et al. (1981), Ladd et al. (1977) and Amato and Ladd (1980). The double component exponential model provides a greater insight into the decomposition of roots than a single component exponential model.

In Chapter 3 and Chapter 4, I used the ^{14}C labelling technique to study the C transformation and root-released C decomposition in two barley-soil ecosystems and found that the total ^{14}C in shoot and root of Samson was significantly higher than that of Abee. ^{14}C remaining in soil, in microbial C and water-soluble organic C pools was also significantly higher for Samson than for Abee. A greater proportion of the photosynthetically fixed C was stabilized in soil under Samson than under Abee. The root-released C from Samson remained in soil longer than that of Abee. This experiment provided further information on C transformation and stabilization in soil by different barley cultivars. The initial ^{14}C values in roots under Samson were greater than those under Abee. The ^{14}C remaining in soil and roots under Samson was higher than that under Abee during the incubation but was not significantly different at the end of the experiment. The half life of ^{14}C remaining in soil and roots under Samson was longer than that under Abee but the proportion of labile component was much greater in root-released C than that in root tissues (Fig. V.1). The results obtained using this method yielded an estimate of the decomposition of the total root system *in situ* and the transformation of root derived C in soil, instead of only coarse roots.

In order to extrapolate the results of this study into field conditions, a number of other factors such as the flux of material from roots to soil organisms over the growing

season, chemical properties of the roots, such as non-structural carbohydrate content (Tamura 1985; Steen and Larsson 1986; Andrén 1987), lignin content (Waksman and Tenney 1927; Herman et al. 1977), nitrogen content (Tenney and Waksman 1929; Knapp et al. 1983), water-soluble components (Waksman and Tenney 1928; Hunt 1977; Chrestensen 1985 Andrén 1987) or combinations thereof (Berendse et al. 1987; Taylor et al. 1989); and physical properties such as particle size in a wide sense (root thickness, mean length of root); and soil and weather data would be needed. Simulation modelling of root decomposition *in situ* may provide further insight into the C transformation and cycling in the plant soil ecosystem.

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Chapter 6. Simulation of *in situ* root decomposition of two barley cultivars

Introduction

Root C and root-released C are the main source of soil organic matter for plant-soil ecosystems. Through the process of the decomposition, energy is provided to microorganisms, nutrients are released for uptake by both microorganisms and plants, and a proportion of the photosynthetically fixed C is stabilized into soil. However, the techniques used for the analyses of the decomposition of roots and root-released C in soil are limited. The decomposition of the root materials in soil may be assessed only through the determination of the end products such as CO_2 because simple chemical analysis of the intermediate products of C decomposition can not be always possible (Paul and Van Veen 1978). However, the intermediate processes are evenly important as the end products to understanding the decomposition of the roots and plant debris in soil.

At present, most studies on root decomposition have been conducted with extracted or excised roots added to disturbed soil samples that do not represent field conditions. Also, previous studies may be biased by the absence of fine roots which have higher turnover rate. Moreover, root sample preparation techniques such as drying, grinding and mixing may also bias the estimation of root decomposition rates. Therefore, it is important to study the root decomposition *in situ* to estimate the decomposition of roots in field conditions.

Mechanistic simulation models have proven to be useful for the study of root and soil organic C dynamics. They help to integrate the fragmentary knowledge about the processes involved and therefore to develop a better understanding of the behavior of the soil ecosystem as a whole. They are also useful in formulating and testing

hypotheses and in establishing the relative importance of parameters (Verberne et al. 1990).

A computer model was designed to simulate the dynamics of root decomposition *in situ* and the dynamics of different forms of C in soil under two barley cultivars (Abee and Samson).

Model Descriptions

The model was run on a Mac II si microcomputer using Stella II software. A simplified flow chart of the simulation model is presented in Fig. VI.1. The model consisted of two submodels: C submodel and ^{14}C submodel.

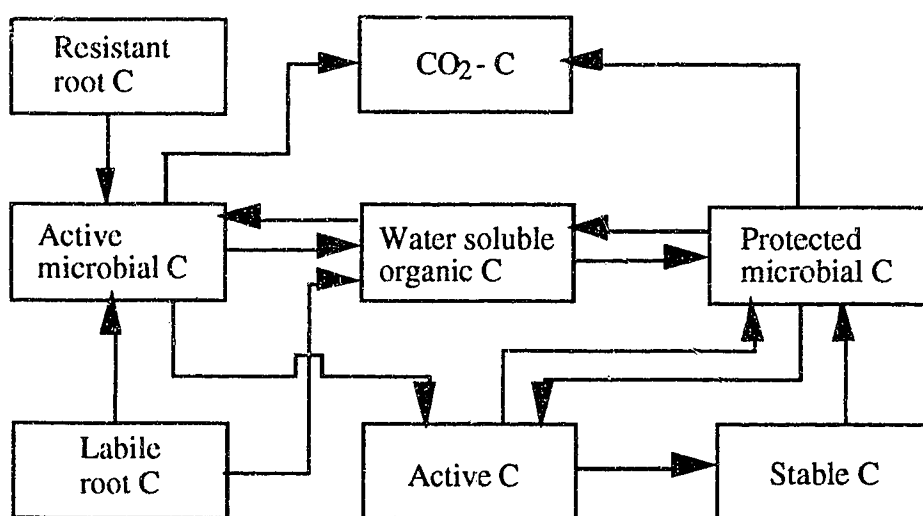

Fig. VI.1. Flow chart of C in the simulation model.

C state variables

The C state variables in the model includes labile root C, resistant root C, water-soluble organic C, active microbial C and protected microbial C, active C, stable C and CO_2-C. Labile root C mainly represents the labile materials in the roots such as

sucrose, polysacchride and amino acids. Resistant root C is mainly composed of structural components of the root tissues such as cellulose, semi-cellulose and lignin. Root C was measured directly in the experiment and the initial pool sizes of the labile root C and resistant root C were estimated by a double exponential equation (Chapter 5). Water-soluble organic C represents a small, very rapid cycling pool consisting of labile organic C materials such as metabolites and cytoplasmic materials of dead organisms. Water-soluble organic C was measured with 10-g fresh soil using the method of McGill et al. (1986). Active microbial C represents the microorganisms in the soil, which could easily access into the roots and grow fast on the root C. Without root C as substrate their biomass would decrease quickly. They accounted for about 17-19% (18% was used here) of the total microbial C (Dinwoodie and Juma 1988). Protected microbial C represents the microorganisms which mainly live in soil aggregates and feed on the soil organic C (Verberne et al. 1990). They are much more stable than the active microorganisms. The protected microbial C was calculated by subtracting the active microbial C from the total microbial C measured on 25-g soil samples by the chloroform fumigation technique (Jenkinson and Powlson 1976). Active C represents rapid cycling insoluble organic C pool consisting of microbial metabolic products and recently stabilized materials (Paul and Juma 1981). Campbell and Souster (1982) determined the active N fraction of a cultivated Black Chernozemic soil from Saskatchewan to be 5.2% of total soil N from a clay loam. This percentage was used to calculate the initial pool size of active C in the present model. Fifty percent of soil organic C consists of chemically recalcitrant materials with a half life of greater than 600 years (Campbell et al. 1967). This phase classified as old C was not simulated in the model because it is very stable in the time period (80 d) of the model simulation. The remainder of the soil organic C was partitioned into microbial C, water-soluble organic C, active C and stable C. The initial pool size of the stable C was

calculated by difference. The initial pool sizes of different C pools in the model are presented in Table VI.1.

Table VI.1. Initial pool sizes of total C (mg C kg^{-1} soil) and ^{14}C (kBq kg^{-1} soil) in the model for two barley cultivars.

State	Abee		Samson	
	C	^{14}C	C	^{14}C
CO_2-C	0	0	0	0
Labile root C	177	2219	129	2292
Resistant root C	192	1195	203	1875
Soluble C	75	4	83	5
Active microbial C	100	512	120	650
Protected microbial C	410	0	507	0
Active C	3028	0	3028	0
Stable C	28777	0	28777	0

^{14}C state variables

The ^{14}C submodel was analogous to the C submodel. ^{14}C pools consisted of ^{14}C activity (kBq kg^{-1} soil). The initial pool sizes of root ^{14}C, water-soluble organic ^{14}C and microbial ^{14}C were measured in the laboratory. The initial pool sizes of the other pools was initialized to 0 (Table VI.1). Further details were given in Chapter 5.

C flows between state variables

The flows within the C submodel directly or indirectly control the flows within the ^{14}C submodel. The uptake of substrate by microbial organisms in the model was calculated by the following equation:

$$Usi = dSi / dt = Ki \times Si$$

where Usi is the uptake rate of the specific substrate i by microbial C (either active microbial C or protected microbial C) (mg C kg^{-1} soil d^{-1}); Ki is the first order rate

constant for the specific substrate i (d^{-1}); Si is the concentration of the specific substrate i (mg C kg^{-1} soil) and t is time (d).

Rate of microbial CO_2-C evolution (R_{CO2}) was calculated using growth and maintenance components (Hunt et al. 1984):

$$R_{CO2} = \Sigma((1-Ymi) \times Usi) + Mi \times Mm$$

where Ymi is the maximum possible yield of the microbial C for consumption of specific substrate i (unitless); Usi is the microbial uptake rate of specific substrate i (mg kg^{-1} soil d^{-1}) and Mm is the microbial maintenance rate (d^{-1}) and Mi is the microbial C (either active microbial C or protected microbial C) (mg C kg^{-1} soil).

Microbial death rate (Dm) was proportional to the amount of the microbial C present respectively:

$$Dm = dMi / dt = -Kd \times Mi$$

where Dm is the microbial death rate (mg C kg^{-1} soil d^{-1}); Kd is the microbial death rate constant (d^{-1}). Mi is the microbial C. Forty five percent (1 - fr) of this material was assumed to be water-soluble and entered the water-soluble organic C fraction. The remaining 55% (fr) was assumed to be insoluble or chemically stable and entered the active C pool (Hunt et al. 1984).

Active C was transferred to the stable C pool by a first order kinetic reaction that was dependent on the size of the active C pool. This simulates the chemical stabilization of active organic C into more resistant forms (Juma and Paul 1981).

Root respiration was not simulated in the model since it was negligible in the time period of the simulation (Chapter 5).

^{14}C flows between state variables

The flow of ^{14}C between different ^{14}C pools (kBq kg^{-1} soil d^{-1}) was calculated by multiplying the C flow rate (mg C kg^{-1} soil d^{-1}) with the specific activity (kBq mg^{-1} C) of the pools from which the ^{14}C was originating.

Parameters

All the parameters used in the model were obtained from literature [Hurst and Wagner 1969, Sauerbeck and Gonzalez (1977), Juma and Paul (1981), Hunt et al. (1984), Verbern et al. (1990) and Rutherford and Juma (1992)] and all the parameters are independent from the experiments for calibrating and validating the model. The complete list of the parameters used in the model are presented in Table VI.2.

More details of the model are shown in the appendix 1 and appendix 2.

Results

Model calibration with data of cultivar Abee

The model was calibrated with the data of the root decomposition *in situ* of barley cultivar Abee in a Black Chernozem (Typic Cryoboroll) as described in Chapter 5. It was possible to produce model outputs that fitted the observed data (Fig. VI.2). The predicted CO_2-C evolution and microbial C were closely fitted to the experimental data. The model simulated the water-soluble organic C well from Day 40 to Day 80, but under estimated it from Day 0 to Day 25. The CO_2-^{14}C recovery and the predicted microbial ^{14}C were within the standard error bars of the experimental data over the incubation period. Water-soluble organic ^{14}C was well simulated from Day 25 to Day 80 but over estimated from Day 0 to Day 25 by the model.

Model validation with data of cultivar Samson

The model was validated with the data of the root decomposition *in situ* of cultivar Samson in a Black Chernozem (Typic Cryoboroll) as described in Chapter 5. All the parameters in the model were not changed for the validation. The only changes made for validation were the initial pool sizes.

Table VI.2. Parameters used in the model

Symbol	Parameter description	Value	Unit	Reference
Krr-am	Uptake rate constant of labile root C by active microbial C	0.5	d^{-1}	Rutherford and Juma (1992)
Klr-am	Uptake rate constant of resistant root C by active microbial C	0.01	d^{-1}	Sauerbeck and Gonzalez (1977)
Kr-sol	Release rate constant of root C into soluble C	0.02	d^{-1}	Table IV. 1 in Chapter 4
Ksol-m	Uptake rate constant of soluble C by active and protected microbial C	0.5*	d^{-1}	Rutherford and Juma (1992)
Ka-pm	Uptake rate constant of active C by protected microbial C	0.003	d^{-1}	Rutherford and Juma (1992)
Kst-pm	Uptake rate constant of stable C by protected microbial C	0.00016	d^{-1}	Rutherford and Juma (1992)
Ka-st	Transfer rate constant of active C to stable C	0.0005	d^{-1}	Juma and Paul (1981)
Kamd	Death rate constant of active microbial C	0.5	d^{-1}	Verbern et al. (1990)
Kpmd	Death rate constant of protected microbial C	0.02	d^{-1}	Hurst and Wagner (1969)
Mm	Maintenance rate constant of microbial C	0.0025	d^{-1}	Rutherford and Juma (1992)
Yr	Maximum possible yield of root C	0.4	unitless	Hunt et al. (1984)
Ysol	Maximum possible yield of soluble C	0.4	unitless	Hunt et al. (1984)
Ya	Maximum possible yield of active C	0.4	unitless	Hunt et al. (1984)
Yst	Maximum possible yield of stable C	0.4	unitless	Hunt et al. (1984)
Mf	Microbial C to active C fraction coefficient	0.55	unitless	Hunt et al. (1984)

* If soluble C > 50 (mg kg^{-1} soil) then soluble C uptake rate = 0.5 * (soluble C - 50) else 0. Adsorbed soluble C is assumed to be 50 (mg kg^{-1} soil).

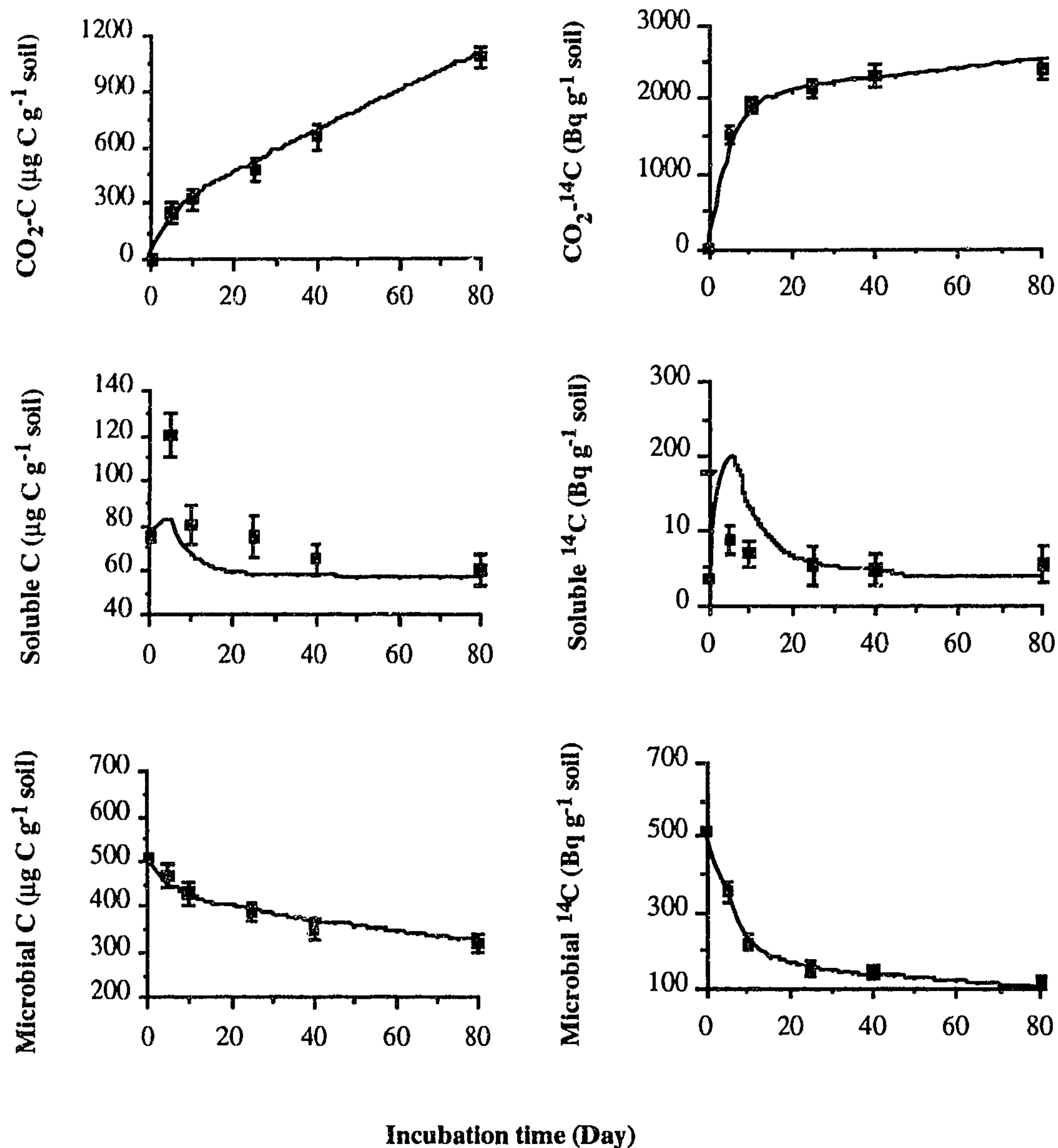

Fig. VI.2 Model outputs (lines) and experimental data (symbols and standard error bars) for CO_2-C, water-soluble organic C, microbial C, CO_2-^{14}C, water-soluble organic ^{14}C and microbial ^{14}C during the incubation period for Abee.

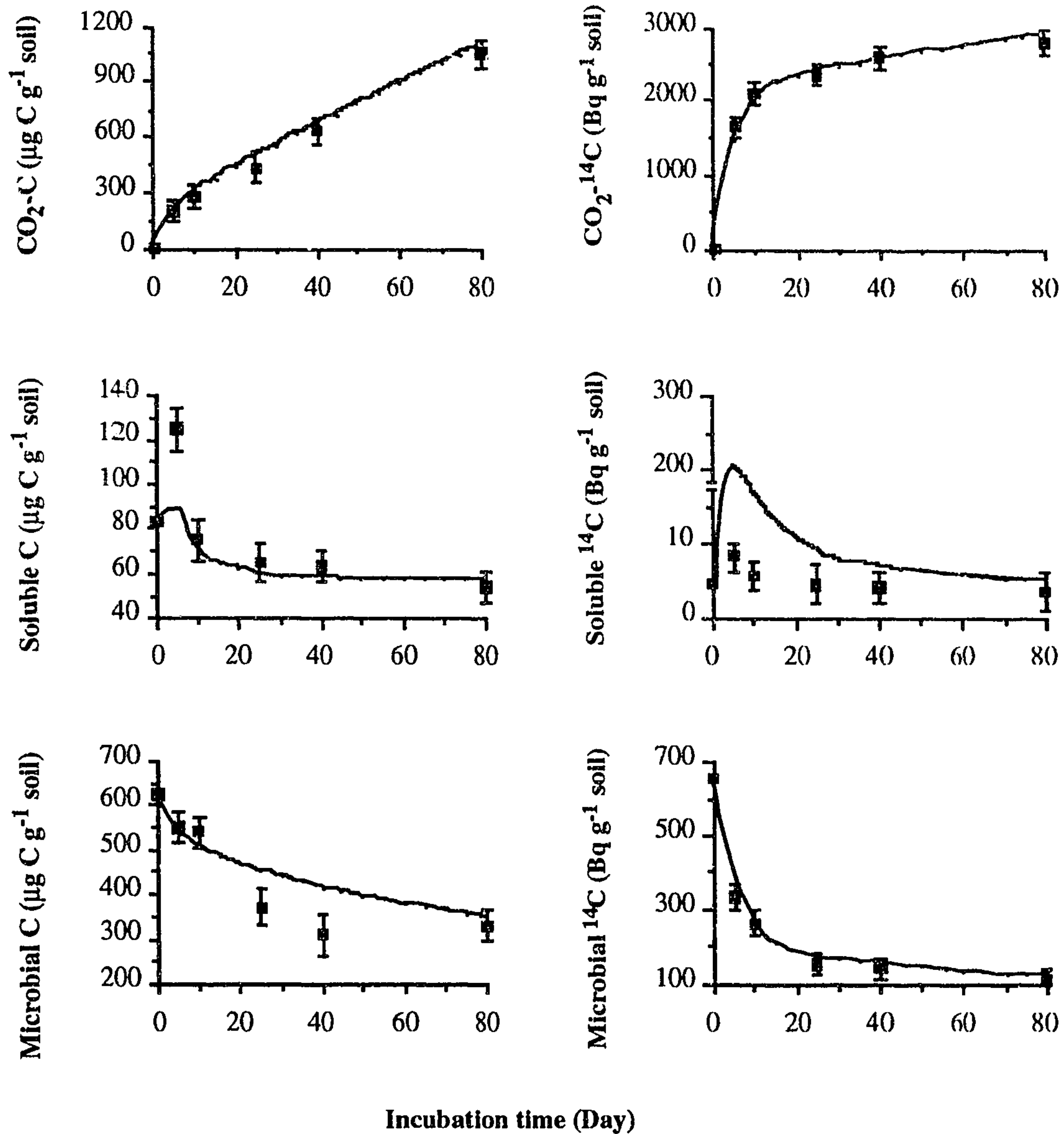

Fig. VI.3 Model outputs (lines) and experimental data (symbols and standard error bars) for CO_2-C, water-soluble organic C, microbial C, CO_2-^{14}C, water-soluble organic ^{14}C and microbial ^{14}C during the incubation period for Samson.

The model simulated water-soluble organic C well over the incubation period except on Day 5 when it was underestimated. The model closely simulated the microbial C on Day 0, Day 5, Day 15 and Day 80 but overestimated it on Day 25 and Day 40. The model accurately simulated the evolution of CO_2-^{14}C, but overestimated the water-soluble organic ^{14}C over the incubation period. The microbial ^{14}C was closely simulated over the incubation period

Dynamics of C under two barley cultivars

The incubation period was divided into two periods: a period of rapid changes (Day 0 - Day 15) and a period of slow changes (Day 15 - Day 80). The inputs and outputs and final pool sizes for the two time intervals of two barley cultivars were determined using the model (Table VI.3 and Table VI.4). The CO_2-C evolved from Day 0 to Day 15 accounted for about 32 and 31% of the total CO_2 evolved during the incubation period for Abee and Samson, respectively. During this interval, 51% of the CO_2 evolved was due to the decomposition of the root C for Abee and 39% for Samson. The rests were due to the decomposition of soil organic matter. Active microbial C was reduced by 95% during the first 15 d as almost all the labile root C was decomposed during this period. The protected microbial C was relatively stable and the decrease was less than 5% of its pool sizes for both cultivars during this period. The output of water-soluble organic C was greater than its input, therefore it decreased during the first 15 d for both barley cultivars. The input and output of water-soluble organic C were twice greater than its pool sizes for both barley cultivars, indicating that the turn over rate of the water-soluble organic C is more important than its pool size. Active C increased during the first 15 d as the input was greater than the output for both cultivars. Stable C decreased from Day 0 to Day 15 because the input is less than the output.

Table VI.3. Simulated inputs and outputs of C between Day 0 and Day 15 and between Day 15 and Day 80 for Abee.

variable	Day 15			Day 80		
	Input	Output	pool size	Input	Output	pool size
	Total C (mg C kg^{-1} soil)					
CO_2-C	345	0	345	719	0	1064
Labile root C	0	177	0	0	0	0
Resistant root C	0	27	165	0	79	86
Soluble C	150	165	60	249	252	57
Active microbial C	284	371	4	205	207	2
Protected microbial C	289	300	407	984	1066	325
Active C	179	161	3046	305	654	2697
Stable C	23	69	28731	93	297	28527
	^{14}C (kBq kg^{-1} soil)					
CO_2-^{14}C	1877	0	1877	473	0	2390
Labile root ^{14}C	0	1637	1	0	1	0
Resistant root ^{14}C	0	167	1028	0	492	536
Soluble ^{14}C	767	755	16	176	188	4
Active microbial ^{14}C	2719	3214	17	586	599	4
Protected microbial ^{14}C	406	272	134	265	306	93
Active ^{14}C	885	34	851	216	198	869
Stable ^{14}C	5	0	5	28	0	33

The CO_2-C evolved from Day 15 to Day 80 accounted for about 68 to 69% of the total CO_2 evolved during the incubation period for Abee and Samson, respectively. The main source of the CO_2 evolved during this period was soil organic matter instead of the root C. Forty four percent of the root C was decomposed between Day 15 and

Day 80 for Abee and 41% for Samson. The input of water-soluble organic C was less than its output, therefore it continued to decrease during this period for two cultivars. The two microbial C pools followed the same trend as water-soluble organic C and the outputs from these pools were still greater than the inputs. The input and output of the active microbial C were over 80 times greater than its pool size as estimated on Day 15 and the input and output of protected microbial C was over three times its pool size of Day 15 for the two barley cultivars. In contrast to the first 15 d, active C decreased during Day 15 and Day 80 as the output was greater than the input for both cultivars. Stable C continued to decrease during Day 15 and Day 80 for two barley cultivars.

Dynamics of ^{14}C under two barley cultivars

Seventy eight percent of the total CO_2-^{14}C evolved during the incubation period (80 d) was produced within the first 15 d for Abee and 73% for Samson. The inputs were less than the outputs for active microbial ^{14}C, therefore, active microbial ^{14}C decreased during the first 15 d for both barley cultivars. In contrast, the protected microbial ^{14}C increased during the same period since the input was greater than the output. Water-soluble organic ^{14}C, active ^{14}C and stable ^{14}C all increased during the first 15 d. The two barley cultivars had the similar trends.

The CO_2-^{14}C evolved between Day 15 and Day 80 accounted for about 22% of the total CO_2-^{14}C evolved during the incubation period for Abee and 27% for Samson. Water-soluble organic ^{14}C, active microbial ^{14}C and protected microbial ^{14}C decreased from Day 15 to Day 80 as the inputs were less than the outputs. Active ^{14}C and stable ^{14}C continued to increase form Day 15 to Day 80 as the inputs was greater than the outputs. The two barley cultivars had the similar trends in ^{14}C during Day 15 and Day 80.

Table VI.4. Simulated inputs and outputs of ^{14}C between Day 0 and Day 15 and between Day 15 and Day 80 for Samson.

variable	Day 15 Input	Day 15 Output	Day 15 pool size	Day 80 Input	Day 80 Output	Day 80 pool size
	Total C (mg C kg^{-1} soil)					
CO_2-C	330	0	330	746	0	1076
Labile root C	0	129	0	0	0	0
Resistant root C	0	29	174	0	83	91
Soluble C	162	184	61	279	283	57
Active microbial C	248	357	4	225	227	2
Protected microbial C	299	332	481	1006	1137	350
Active C	197	161	3064	340	661	2743
Stable C	23	69	28731	93	297	28527
	^{14}C (kBq kg^{-1} soil)					
CO_2-^{14}C	2040	0	2040	739	0	2779
Labile root ^{14}C	0	1624	1	0	1	0
Resistant root ^{14}C	0	262	1613	0	771	842
Soluble ^{14}C	847	833	19	245	258	6
Active microbial ^{14}C	2948	3575	23	901	916	8
Protected microbial ^{14}C	449	300	149	329	367	111
Active ^{14}C	1010	39	971	298	232	1037
Stable ^{14}C	6	0	6	33	0	39

Discussion

The simulation model supplies more information on root decomposition, especially on the intermediate processes which can not be measured experimentally. By Day 15, about 48% of the total ^{14}C fixed in roots was respired for Abee and 42% for Samson.

This indicated that the turnover rate of root ^{14}C of Abee was higher than that of Samson in the first 15 d. The percentage of water-soluble organic ^{14}C, active microbial ^{14}C and stable ^{14}C over the total fixed ^{14}C were relatively less and were not different between two barley cultivars. Active ^{14}C accounted for about 23% of the total fixed ^{14}C on Day 15 for Abee and 21% for Samson. On Day 80, the distribution of ^{14}C in different pools was CO_2-^{14}C (61%) > active ^{14}C (22%) > root ^{14}C (14%) > microbial ^{14}C (3%) > stable ^{14}C (0.8%) > water-soluble organic ^{14}C (0.1%) for Abee. The trend for Samson was the same: CO_2-^{14}C (58%) > active ^{14}C (22%) > root ^{14}C (18%) > microbial ^{14}C (3%) > stable ^{14}C (0.8%) > water-soluble organic ^{14}C (0.1%) (Table VI.5). From the analysis of the model for two barley cultivars, the total ^{14}C transformed into different soil pools (excluding CO_2-C and root C pools) for the two barley cultivars was similar (26% for Abee and 25% for Samson). The difference of ^{14}C remaining in soil between the two barley cultivars was mainly because of the difference of ^{14}C remaining in roots which have not been yet decomposed.

Table VI.5. Model simulation of ^{14}C distribution on Day 15 and Day 80 for two barley cultivars (%).

Variable	Abee		Samson	
	Day 15	Day 80	Day 15	Day 80
CO_2-^{14}C	47.8	60.9	42.3	57.6
Labile root ^{14}C	0	0	0	0
Resistant root ^{14}C	26.2	13.6	33.5	17.5
Soluble ^{14}C	0.4	0.1	0.4	0.1
Active microbial ^{14}C	0.4	0.1	0.5	0.2
Protected microbial ^{14}C	3.4	2.4	3.1	2.3
Active ^{14}C	21.7	22.1	20.1	21.5
Stable ^{14}C	0.1	0.8	0.1	0.8

The model was calibrated with the data from one barley cultivar (Abee) and validated with the data of the second cultivar (Samson). Although the data of the two barley cultivars are independent from each other, they were obtained in the similar conditions. The model has to be tested with the data obtained from different conditions, however, this could not be done because the data for root decomposition *in situ* could not be found in the literature.

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Chapter 7. Synthesis

Knowledges of below-ground C input and the transformation of the added C in soils are needed to maintain soil organic C. Campbell et al. (1991) found no significant differences in soil organic C content in wheat-wheat-fallow rotation over a period of 30 years amongst treatments where the straw was left on the surface or baled off. They suggested that root C input may be more important than straw C input in maintaining organic C in soil. Van Veen et al. (1991) reviewed the information of various processes of C cycling in agroecosystems and concluded that root-released C accounts for 20-40% of the photosynthetically fixed C by plants, but the root exudation had the lowest degree of certainty compared to other root processes (Table VII.1).

Table VII.1. Distribution of root-translocated C over different root processes[z]

	Percentage	Degree of certainty (0-10)
Root growth	11-13	9
Root C respiration	12-19	8
Mycorrhizal symbiosis	7-10	5
N_2 fixation	5-23	5
Exudation	5	4

[z] A low degree of certainty indicates a paucity of data available from the literature or a large disagreement amongst the available figures.

The above mentioned studies encouraged me to study the below-ground dynamics of C added through plants. The overall objective of my project was to study the transformation and stabilization of C in two barley-soil ecosystems. The specific sub-topics include (1) Above- and below-ground primary production of four barley cultivars in west Canada; (2) Above- and below-ground transformation of photosynthetically fixed C by two barley cultivars; (3) Relations between shoot C, root C, root length and root-released C of two barley cultivars and kinetics of root-released C decomposition in soil; (4); Root decomposition *in situ* of two barley cultivars; (5)

Simulation of root decomposition *in situ* for two barley cultivars. A simplified C flow chart in my study is presented in the Fig. VII.1.

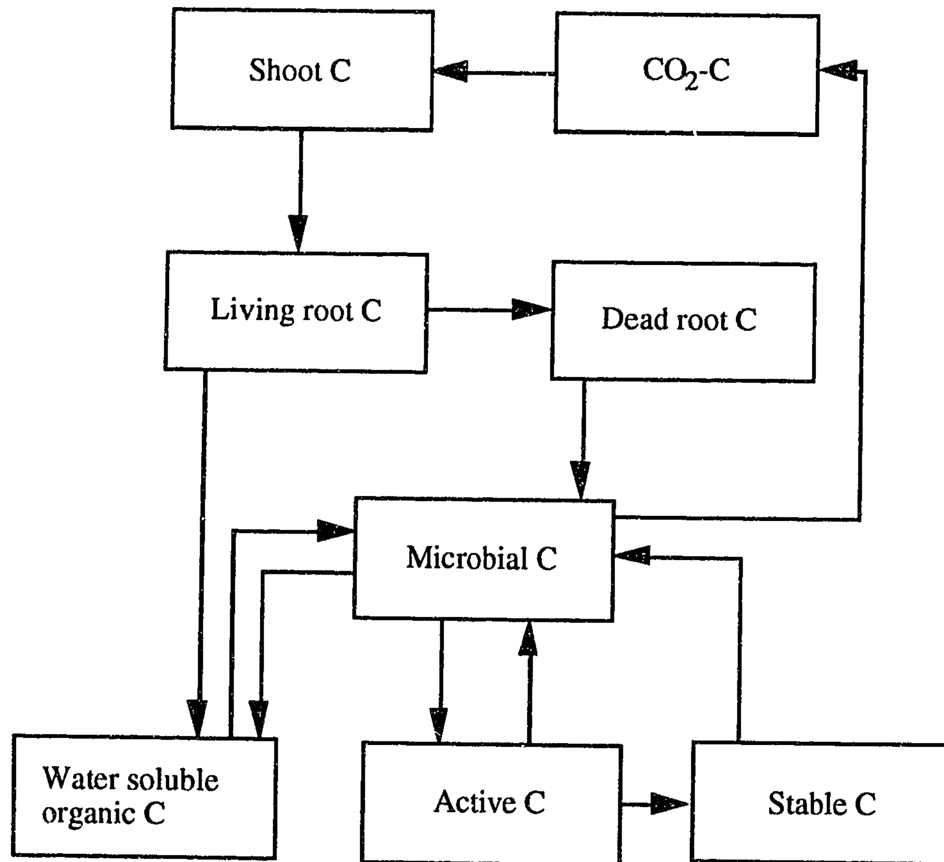

Fig. VII.1 The flow chart of C cycling in barley-soil ecosystem.

In this synthesis I will attempt to link the data obtained from the experiments at different scales (field experiment, greenhouse experiment and laboratory experiment and mathematical simulation). In the laboratory, using hydroponic method, I found that Samson released more C than Abee during the first 25 d growth. The ranking of the internal factors affecting the root-released C was root length > root C > shoot C. The experiment of ^{14}C-labelled root-released C added to soil showed that the average

half life (8.5 d) of the root-released C of Abee was shorter than that (10.9 d) of Samson.

In the greenhouse, the experiment of the root decomposition *in situ* showed that microbial ^{14}C, water-soluble organic ^{14}C and soil ^{14}C on Day 0 under Samson were greater than under Abee, which indicated that Samson released more C than Abee while the roots were alive during the growth period. Kinetics analysis of ^{14}C remaining in roots and soil showed that the proportion of the labile components (L) in roots of Abee (47.7%) was greater than that of Samson (38.8%), but the half lives of the labile and resistant components of the roots were not significantly different between the two barley cultivars.

In field conditions, the study using ^{14}C labelling technique showed that the total ^{14}C in roots under Samson was significantly higher than that of Abee. The ^{14}C remaining in soil, in microbial C and water-soluble organic C pools under Samson were also significantly higher than under Abee. Another field experiment showed that the slope of the decrease of root length after the heading stage was sharper under Abee than under Samson, which indicated that the fine roots under Abee decomposed faster than under Samson. This was consistent with the results obtained from laboratory and field conditions.

In order to obtain a further insight into the decomposition of roots and root-released C, a simulation model of Juma and Paul (1981) was expanded to include the decomposition of root C and root-released C. The mathematical simulation model showed that 36% of the CO_2-C evolved during the first 15 d for Abee and 34% for Samson. Seventy six percent of the root C and root-released C was decomposed during the first 15 d for Abee and 66% for Samson. Eighty two percent of the total CO_2-^{14}C evolved during the incubation period (80 d) was produced within the first 15 d for Abee and 73% for Samson. Seventy five percent of root ^{14}C disappeared during the first 15 d for Abee and 66% for Samson. The CO_2-^{14}C evolved between Day 15

and Day 80 accounted for about 18% of the total CO_2-^{14}C evolved during the incubation period for Abee and 27% for Samson. On Day 15, about 52% of the total ^{14}C fixed in roots was respired for Abee and 44% for Samson.

A general picture of the C flow and distribution in barley-soil ecosystem was obtained from the above research work and from the published literature. If 100 units of C are fixed by photosynthesis in shoot, about 37 units are transferred below-ground (Campbell et al. 1977; Nuttall et al. 1986; Zentner et al. 1987). In a growing season, around 85% of the C transferred below-ground were decomposed by microorganisms and evolved as CO_2 (Chapter 6). Therefore, about 5.5 units of the C fixed by photosynthesis can be stabilized in soil through root derived C each year.

My experiment at three scales showed that near twice more of soil ^{14}C was found 15 days after pulse labelling under Samson than under Abee at the stem extension and heading stages in the field conditions (Chapter 3). Twelve percent more C was released through roots by Samson than by Abee in the nutrient solutions (Chapter 4) and 3% more root ^{14}C was maintained in soil under Samson than under Abee (Chapter 5 and Chapter 6). This implies that the selection of appropriate cultivars of the same species can lead to an increase in soil organic matter.

Future work

A number of questions remain to be answered:

1, What is the effect of growth stage on the rate of root decomposition?

In the experiment, the study of root decomposition *in situ* was conducted with young plants. The growth stage influences the chemical composition of the roots (Martin and Kemp 1986), therefore, it can have a marked effect on the decomposition rate of roots in soil.

2, How do barley cultivars respond to different soil properties and different cropping practices?

The transformation and stabilization of C is also influenced by soil properties, such as soil texture and structure (Dinwoodie 1988; Rutherford and Juma 1992), therefore, it is important to study the effect of different soil texture and structure on barley growth.

There is a continual evolution of cropping practices ranging from conventional tillage to reduced tillage. These affect the soil physical, chemical and biological properties in the rooting zone. The interactions of barley cultivars and these management practices need to be studied.

3, What is the effect of barley cultivars on recently labelled organic matter?

In the present study, only the effect of barley cultivars on the quantity of C transformed and stabilized in soil was studied using ^{14}C pulse labelling technique. The amount of C in soil were calculated from the ^{14}C remaining in soil. Further research is needed to identify the chemical composition of these compounds.

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Appendix 1. Flow diagrams for simulation model

RRC_AMC_rate
LRC_AMC_rate
Active_Microb_C
SA_Active_Biomass
SolC_AMC_rate
AMC_CO2_C_rate_14
CO2_C_14
PMC_CO2_C_rate_14
Protected_Microb_C
SC_PMC_rate
AC_PMC_rate
SA_Soluble_C
SA_Active_C
SA_Stable_C
SolC_PMC_rate
SA_RRC
SA_Labile_RC
SA_Soluble_C
SA_Active_Biomass
AMC_SolC_rate
SA_Prot_Biomass_C
PMC_SolC_rate
Resistant_Root_C14
AMC_SolC_rate_14
PMC_SolC_rate_14
SA_Prot_Biomass_C
SA_RRC
RRC_AMC_rate
RRC_AMC_rate_14
SC_PMC_rate
AC_PMC_rate
SA_Stable_C
Labile_Root_C14
AMC_14
SolC_AMC_rate_14
Sol_PMC_rate_14
PMC_14
SA_Labile_RC
Soluble_C_14
PMC_AC_rate
SC_PMC_rate_14
RC_ABC_rate_14
AC_BC_rate_14
LRC_AMC_rate
SolC_AMC_rate
SA_Soluble_C
PMC_AC_rate_14
AC_SC_rate
Root_Leak_rate_14
SolC_PMC_rate
SA_Active_C
SA_Labile_RC
AMC_AC_rate_14
LRC_SolC_rate
Active_C_14
Stable_C_14
SA_Prot_Biomass_C
AC_SC_rate_14
ABC_AC_rate
SA_Active_Biomass

Total_Microb_C_14

AMC_14

PMC_14

SA_Active_Biomass

SA_TMC

SA_Prot_Biomass_C

Active_Microb_C

Total_Microb_C

Protected_Microb_C

CO2_C_14

SA_CO2

CO2_C

Labile_Root_C14

SA_Labile_RC

Labile_Root_C

Soluble_C_14

SA_Soluble_C

Soluble_C

Active_C_14

SA_Active_C

Active_C

Stable_C_14

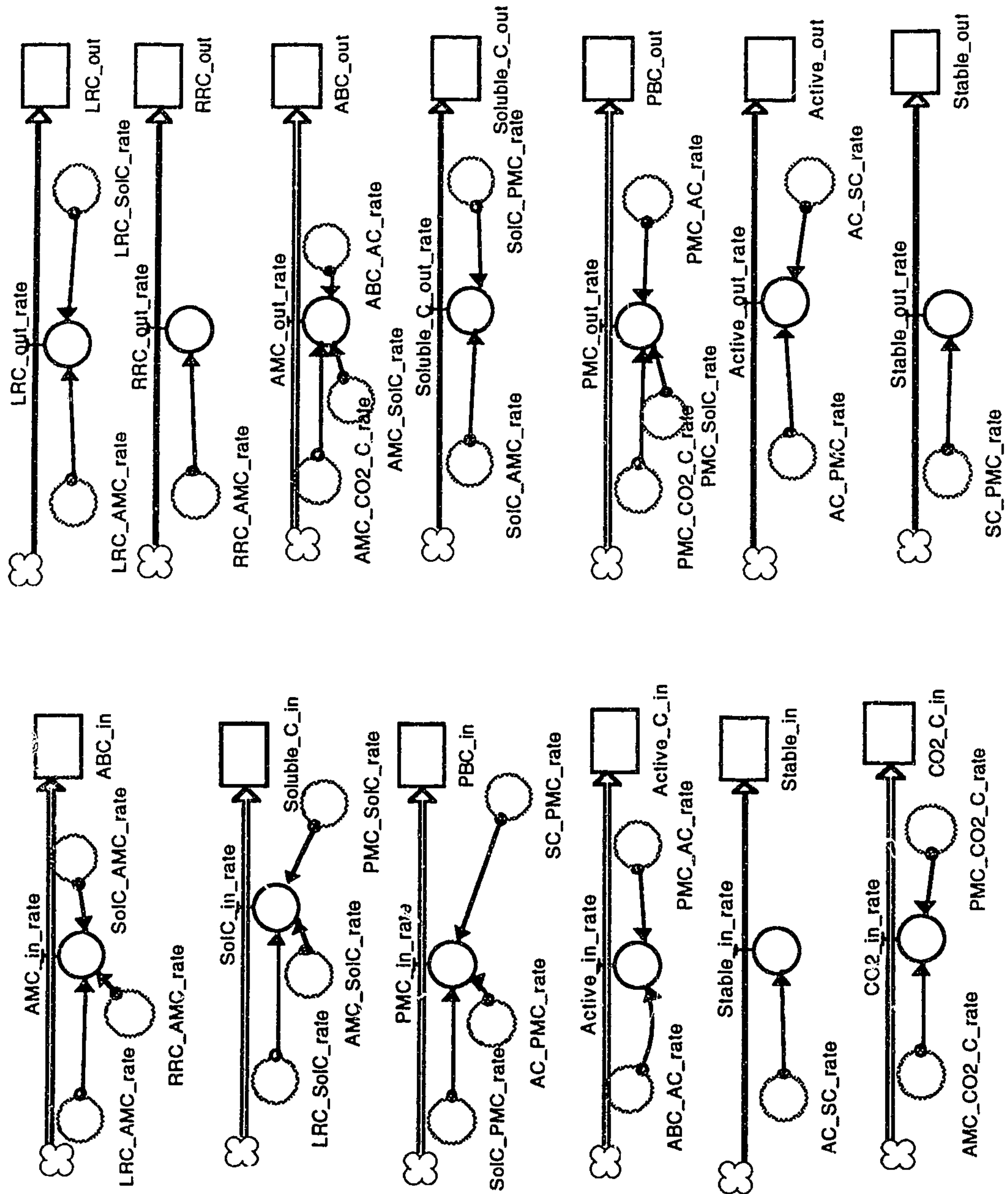
SA_Stable_C

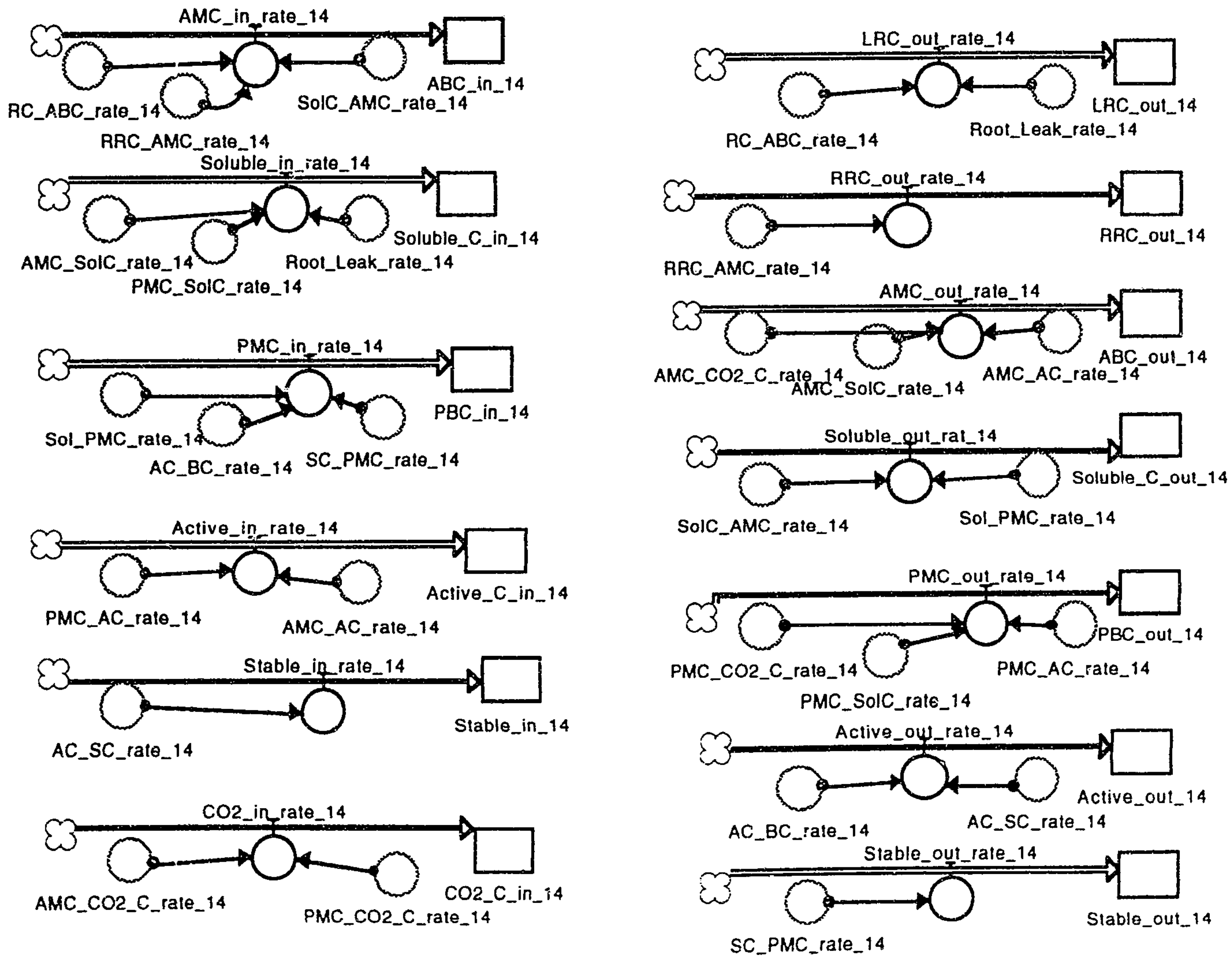
Stable_C

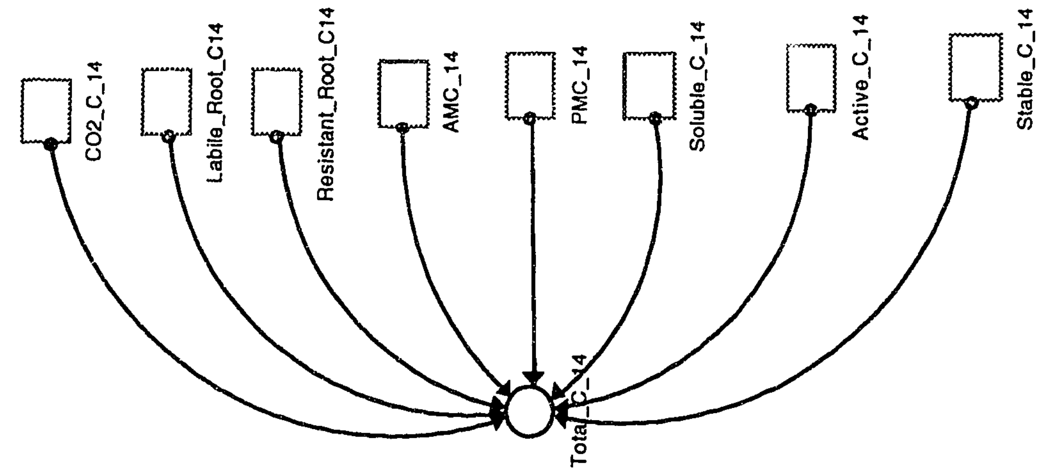
Resistant_Root_C14

SA_RRC

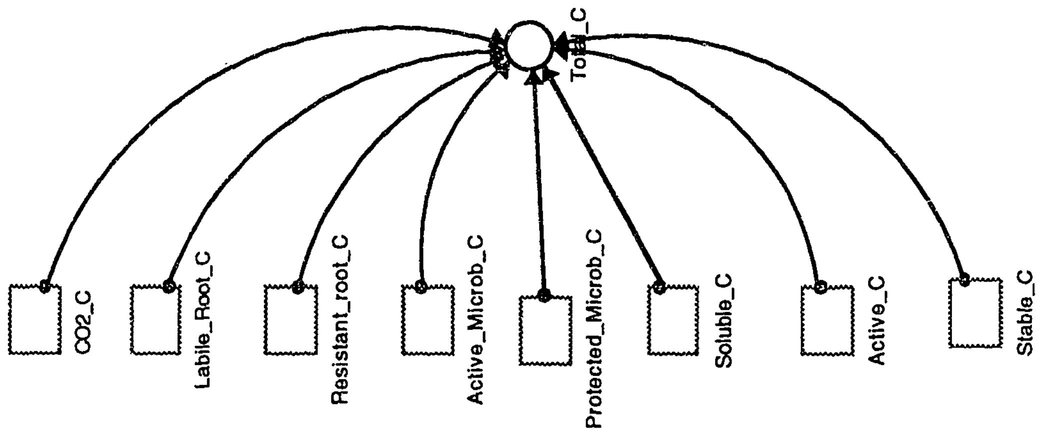
Resistant_root_C


LRC_out
LRC_out_rate
LRC_SolC_rate
LRC_AMC_rate
RRC_out
RRC_out_rate
RRC_AMC_rate
ABC_out
AMC_out_rate
ABC_AC_rate
AMC_SolC_rate
AMC_CO2_C_rate
Soluble_C_out
Soluble_C_out_rate
SolC_PMC_rate
SolC_AMC_rate
PBC_out
PMC_out_rate
PMC_AC_rate
PMC_SolC_rate
PMC_CO2_C_rate
Active_out
Active_out_rate
AC_SC_rate
AC_PMC_rate
Stable_out
Stable_out_rate
SC_PMC_rate
ABC_in
AMC_in_rate
SolC_AMC_rate
LRC_AMC_rate
RRC_AMC_rate
Soluble_C_in
SolC_in_rate
PMC_SolC_rate
LRC_SolC_rate
AMC_SolC_rate
PBC_in
PMC_in_rate
SC_PMC_rate
SolC_PMC_rate
AC_PMC_rate
Active_C_in
Active_in_rate
PMC_AC_rate
ABC_AC_rate
Stable_in
Stable_in_rate
AC_SC_rate
CO2_C_in
CO2_in_rate
PMC_CO2_C_rate
AMC_CO2_C_rate


AMC_in_rate_14
ABC_in_14
RC_ABC_rate_14
SolC_AMC_rate_14
RRC_AMC_rate_14
Soluble_in_rate_14
Soluble_C_in_14
AMC_SolC_rate_14
Root_Leak_rate_14
PMC_SolC_rate_14
PMC_in_rate_14
PBC_in_14
Sol_PMC_rate_14
AC_BC_rate_14
SC_PMC_rate_14
Active_in_rate_14
Active_C_in_14
PMC_AC_rate_14
AMC_AC_rate_14
Stable_in_rate_14
Stable_in_14
AC_SC_rate_14
CO2_in_rate_14
CO2_C_in_14
AMC_CO2_C_rate_14
PMC_CO2_C_rate_14
LRC_out_rate_14
LRC_out_14
RC_ABC_rate_14
Root_Leak_rate_14
RRC_out_rate_14
RRC_out_14
RRC_AMC_rate_14
AMC_out_rate_14
ABC_out_14
AMC_CO2_C_rate_14
AMC_SolC_rate_14
AMC_AC_rate_14
Soluble_out_rat_14
Soluble_C_out_14
SolC_AMC_rate_14
Sol_PMC_rate_14
PMC_out_rate_14
PBC_out_14
PMC_CO2_C_rate_14
PMC_AC_rate_14
PMC_SolC_rate_14
Active_out_rate_14
Active_out_14
AC_BC_rate_14
AC_SC_rate_14
Stable_out_rate_14
Stable_out_14
SC_PMC_rate_14



CO2_C_14
Labile_Root_C14
Resistant_Root_C14
AMC_14
PMC_14
Soluble_C_14
Active_C_14
Stable_C_14
Total_C_14



Total_C
CO2_C
Labile_Root_C
Resistant_root_C
Active_Microb_C
Protected_Microb_C
Soluble_C
Active_C
Stable_C

Appendix 2. Equations for simulation model

Equations for the C submodel

Active_C = Active_C + dt * (-AC_PMC_rate - AC_SC_rate + PMC_AC_rate + ABC_AC_rate)

INIT(Active_C) = 3028 {mg C/kg soil}

Active_Microb_C = Active_Microb_C + dt * (LRC_AMC_rate + SolC_AMC_rate - AMC_SolC_rate - AMC_CO2_C_rate - ABC_AC_rate + RRC_AMC_rate)

INIT(Active_Microb_C) =100 {mg C/kg soil}

CO2_C = CO2_C + dt * (PMC_CO2_C_rate + AMC_CO2_C_rate)

INIT(CO2_C) = 0.0001 {mg C/kg soil}

Labile_Root_C = Labile_Root_C + dt * (-LRC_AMC_rate - LRC_SolC_rate)

INIT(Labile_Root_C) = 369*0.48 {mg C/kg soil}

Protected_Microb_C = Protected_Microb_C + dt * (-PMC_CO2_C_rate + AC_PMC_rate + SC_PMC_rate - PMC_SolC_rate - PMC_AC_rate + SolC_PMC_rate)

INIT(Protected_Microb_C) =410 {mg C/kg soil}

Resistant_root_C = Resistant_root_C + dt * (-RRC_AMC_rate)

INIT(Resistant_root_C) = 369*0.52 {mg C/kg soil}

Soluble_C = Soluble_C + dt * (PMC_SolC_rate - SolC_AMC_rate + AMC_SolC_rate - SolC_PMC_rate + LRC_SolC_rate)

INIT(Soluble_C) = 75 {mg C/kg soil}

Stable_C = Stable_C + dt * (AC_SC_rate - SC_PMC_rate)

INIT(Stable_C) = 28777 {mg C/kg soil}

ABC_AC_rate = 0.5*Active_Microb_C*Fr

AC_PMC_rate =0.003*Active_C

AC_SC_rate = 0.0005*Active_C

{active C to stable C stablization rate}

AMC_CO2_C_rate = LRC_AMC_rate*(1-0.40)+RRC_AMC_rate*(1-0.40)+SolC_AMC_rate*(1-0.40)+Active_Microb_C*0.00025

AMC_SolC_rate = (ABC_AC_rate/Fr)*(1-Fr)

Fr = 0.55

LRC_AMC_rate = IF (Labile_Root_C>0) THEN 0.5*

Labile_Root_C ELSE 0

LRC_SolC_rate = IF (Labile_Root_C>0) THEN 0.02*

Labile_Root_C ELSE 0

PMC_AC_rate = 0.02*Protected_Microb_C*Fr

PMC_CO2_C_rate = ((AC_PMC_rate*(1-0.40)) +(SC_PMC_rate*(1-0.40)) + Protected_Microb_C*0.00025) + SolC_PMC_rate*(1-0.40)

PMC_SolC_rate = (PMC_AC_rate/Fr)*(1-Fr)

RRC_AMC_rate = IF (Resistant_root_C>0) THEN 0.01*

Resistant_root_C ELSE 0

SC_PMC_rate = 0.00008*Stable_C*2

SolC_AMC_rate = IF (Soluble_C>50) THEN 0.25*

(Soluble_C -50) ELSE 0

SolC_PMC_rate = IF (Soluble_C>50) THEN 0.25*

(Soluble_C -50) ELSE 0

Equations for the ^{14}C submodel

Active_C_14 = Active_C_14 + dt * (-AC_BC_rate_14 - AC_SC_rate_14 + PMC_AC_rate_14 + AMC_AC_rate_14)

INIT(Active_C_14) = 0.0001 {kBq/kg soil}

AMC_14 = AMC_14 + dt * (-AMC_CO2_C_rate_14 + SolC_AMC_rate_14 - AMC_SolC_rate_14 - AMC_AC_rate_14 + RC_ABC_rate_14 + RRC_AMC_rate_14)

INIT(AMC_14) = 512 {kBq/kg soil}

CO2_C_14 = CO2_C_14 + dt * (PMC_CO2_C_rate_14 + AMC_CO2_C_rate_14)

INIT(CO2_C_14) = 0 {kBq/kg soil}

Labile_Root_C14 = Labile_Root_C14 + dt * (-RC_ABC_rate_14 - Root_Leak_rate_14)

INIT(Labile_Root_C14) = 2219 {kBq/kg soil}

PMC_14 = PMC_14 + dt * (-PMC_CO2_C_rate_14 + AC_BC_rate_14 + SC_PMC_rate_14 - PMC_SolC_rate_14 - PMC_AC_rate_14 + Sol_PMC_rate_14)

INIT(PMC_14) = 0 {kBq/kg soil}

Resistant_Root_C14 = Resistant_Root_C14 + dt * (-RRC_AMC_rate_14)

INIT(Resistant_Root_C14) = 1195 {kBq/kg soil}

Soluble_C_14 = Soluble_C_14 + dt * (PMC_SolC_rate_14 - SolC_AMC_rate_14 + AMC_SolC_rate_14 - Sol_PMC_rate_14 + Root_Leak_rate_14)

INIT(Soluble_C_14) = 3.5 {kBq/kg soil}

Stable_C_14 = Stable_C_14 + dt * (AC_SC_rate_14 - SC_PMC_rate_14)

INIT(Stable_C_14) = 0.0001 {kBq/kg soil}

AC_BC_rate_14 = AC_PMC_rate*SA_Active_C

AC_SC_rate_14 = AC_SC_rate*SA_Active_C

AMC_AC_rate_14 = ABC_AC_rate*SA_Active_Biomass

AMC_CO2_C_rate_14 = LRC_AMC_rate*(1-0.40)*SA_Labile_RC+ SolC_AMC_rate*(1-0.40)*SA_Soluble_C + RRC_AMC_rate*(1-0.4)*SA_RRC+Active_Microb_C*0.00025*SA_Active_Biomass

AMC_SolC_rate_14 = SA_Active_Biomass*AMC_SolC_rate

PMC_AC_rate_14 = PMC_AC_rate*SA_Prot_Biomass_C

PMC_CO2_C_rate_14 = AC_PMC_rate*(1-0.40)*SA_Active_C + SolC_PMC_rate*(1-0.40)*SA_Soluble_C + SC_PMC_rate*(1-0.40)*SA_Stable_C + Protected_Microb_C*0.00025*SA_Prot_Biomass_C

PMC_SolC_rate_14 = PMC_SolC_rate*SA_Prot_Biomass_C

RC_ABC_rate_14 = SA_Labile_RC*LRC_AMC_rate

Root_Leak_rate_14 = LRC_SolC_rate*SA_Labile_RC

RRC_AMC_rate_14 = SA_RRC*RRC_AMC_rate

SC_PMC_rate_14 = SC_PMC_rate*SA_Stable_C

SolC_AMC_rate_14 = SA_Soluble_C*SolC_AMC_rate

Sol_PMC_rate_14 = SA_Soluble_C*SolC_PMC_rate

Equations for calculating ^{14}C specific activities

SA_Active_Biomass = AMC_14/Active_Microb_C

SA_Active_C = Active_C_14/Active_C

SA_CO2 = CO2_C_14/CO2_C

SA_Labile_RC = Labile_Root_C14/Labile_Root_C

SA_Prot_Biomass_C = PMC_14/Protected_Microb_C

SA_RRC = Resistant_Root_C14/Resistant_root_C

SA_Soluble_C = Soluble_C_14/(Soluble_C - 50)

SA_Stable_C = Stable_C_14/Stable_C

SA_TMC = Total_Microb_C_14/Total_Microb_C

Total_Microb_C = Active_Microb_C+Protected_Microb_C

Total_Microb_C_14 = AMC_14+PMC_14

Equations for calculating inflows and outflows of C pools

ABC_in = ABC_in + dt * (AMC_in_rate)

INIT(ABC_in) = 0

ABC_out = ABC_out + dt * (AMC_out_rate)

INIT(ABC_out) = 0

Active_C_in = Active_C_in + dt * (Active_in_rate)

INIT(Active_C_in) = 0

Active_out = Active_out + dt * (Active_out_rate)

INIT(Active_out) = 0

CO2_C_in = CO2_C_in + dt * (CO2_in_rate)

INIT(CO2_C_in) = 0

LRC_out = LRC_out + dt * (LRC_out_rate)

INIT(LRC_out) = 0

PBC_in = PBC_in + dt * (PMC_in_rate)

INIT(PBC_in) = 0

PBC_out = PBC_out + dt * (PMC_out_rate)

INIT(PBC_out) = 0

RRC_out = RRC_out + dt * (RRC_out_rate)

INIT(RRC_out) = 0

Soluble_C_in = Soluble_C_in + dt * (SolC_in_rate)

INIT(Soluble_C_in) = 0

Soluble_C_out = Soluble_C_out + dt * (Soluble_C_out_rate)

INIT(Soluble_C_out) = 0

Stable_in = Stable_in + dt * (Stable_in_rate)

INIT(Stable_in) = 0

Stable_out = Stable_out + dt * (Stable_out_rate)

INIT(Stable_out) = 0

Active_in_rate = ABC_AC_rate+PMC_AC_rate

Active_out_rate = AC_PMC_rate+AC_SC_rate

AMC_in_rate = LRC_AMC_rate+SolC_AMC_rate+RRC_AMC_rate

AMC_out_rate = AMC_CO2_C_rate+AMC_SolC_rate+ABC_AC_rate

CO2_in_rate = AMC_CO2_C_rate+PMC_CO2_C_rate

LRC_out_rate = LRC_AMC_rate+LRC_SolC_rate

PMC_in_rate = SolC_PMC_rate+AC_PMC_rate+SC_PMC_rate

PMC_out_rate = PMC_CO2_C_rate+PMC_SolC_rate+PMC_AC_rate

RRC_out_rate = RRC_AMC_rate

SolC_in_rate = LRC_SolC_rate+AMC_SolC_rate+PMC_SolC_rate

Soluble_C_out_rate = SolC_AMC_rate+SolC_PMC_rate

Stable_in_rate = AC_SC_rate

Stable_out_rate = SC_PMC_rate

Equations for calculating inflows and outflows of ^{14}C pools

ABC_in_14 = ABC_in_14 + dt * (AMC_in_rate_14)

INIT(ABC_in_14) = 0

ABC_out_14 = ABC_out_14 + dt * (AMC_out_rate_14)

INIT(ABC_out_14) = 0

Active_C_in_14 = Active_C_in_14 + dt * (Active_in_rate_14)

INIT(Active_C_in_14) = 0

Active_out_14 = Active_out_14 + dt * (Active_out_rate_14)

INIT(Active_out_14) = 0

CO2_C_in_14 = CO2_C_in_14 + dt * (CO2_in_rate_14)

INIT(CO2_C_in_14) = 0

LRC_out_14 = LRC_out_14 + dt * (LRC_out_rate_14)

INIT(LRC_out_14) = 0

PBC_in_14 = PBC_in_14 + dt * (PMC_in_rate_14)

INIT(PBC_in_14) = 0

PBC_out_14 = PBC_out_14 + dt * (PMC_out_rate_14)

INIT(PBC_out_14) = 0

RRC_out_14 = RRC_out_14 + dt * (RRC_out_rate_14)

INIT(RRC_out_14) = 0

Soluble_C_in_14 = Soluble_C_in_14 + dt * (Soluble_in_rate_14)

INIT(Soluble_C_in_14) = 0

Soluble_C_out_14 = Soluble_C_out_14 + dt * (Soluble_out_rat_14)

INIT(Soluble_C_out_14) = 0

Stable_in_14 = Stable_in_14 + dt * (Stable_in_rate_14)

INIT(Stable_in_14) = 0

Stable_out_14 = Stable_out_14 + dt * (Stable_out_rate_14)

INIT(Stable_out_14) = 0

Active_in_rate_14 = PMC_AC_rate_14+AMC_AC_rate_14

Active_out_rate_14 = AC_BC_rate_14+AC_SC_rate_14

AMC_in_rate_14 = RC_ABC_rate_14+SolC_AMC_rate_14+RRC_AMC_rate_14

AMC_out_rate_14 = AMC_CO2_C_rate_14+AMC_SolC_rate_14+AMC_AC_rate_14

CO2_in_rate_14 = AMC_CO2_C_rate_14+PMC_CO2_C_rate_14

LRC_out_rate_14 = RC_ABC_rate_14+Root_Leak_rate_14

PMC_in_rate_14 = Sol_PMC_rate_14+AC_BC_rate_14+SC_PMC_rate_14

PMC_out_rate_14 = PMC_CO2_C_rate_14+PMC_SolC_rate_14+PMC_AC_rate_14

RRC_out_rate_14 = RRC_AMC_rate_14

Soluble_in_rate_14 = AMC_SolC_rate_14+PMC_SolC_rate_14+Root_Leak_rate_14

Soluble_out_rat_14 = SolC_AMC_rate_14+Sol_PMC_rate_14

Stable_in_rate_14 = AC_SC_rate_14

Stable_out_rate_14 = SC_PMC_rate_14

Equations for calculating the total C and total ^{14}C in the model

Total_C =
Protected_Microb_C+Active_Microb_C+Labile_Root_C+Resistant_root_C+CO2_C+Soluble_C+Active_C+Stable_C

Total_C_14 =
PMC_14+AMC_14+Labile_Root_C14+Resistant_Root_C14+CO2_C_14+Soluble_C_14+Active_C_14+Stable_C_14