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Carbon Partitioning in the Rhizosphere of an Annual and a Perennial Species of Bromegrass*

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Abstract

Two weeks' exposure to $^{14}CO_2$ of annual and perennial bromegrass grown on two soils of different fertility levels was repeated four times during the grown cycle from December to June. The ^{14}C content of soil respiration, shoot, roots, and soil was measured for each labelling, together with above and below ground biomass. There was a marked effect of the soil on plant growth as well as a distinct pattern of root development between annual and perennial species. Carbon partitioning in the rhizosphere indicated a higher rhizosphere effect (expressed as the sum of root derived carbon: CO_2 and soil carbon) for annuals than for perennials. This occurred mainly during the reproductive stages, with up to 65 and 80% of the translocated carbon in the poor and the rich soil respectively. The efficiency of root growth, expressed as the amount of root C per unit of translocated carbon, was higher in the poor soil than in the fertile one, regardless of the differences between species.

Keywords: *Bromus erectus*, *Bromus madritensis*, carbon partitioning, $^{14}CO_2$, rhizodeposition, rhizosphere effect.

Introduction

The overall effect of root growth in soil, often called "rhizosphere effect", has implications not only on the physical, chemical and biotic root environment but also on plant behaviour. Due to the release of carbon compounds by living roots, microbial populations are more numerous and often different in the rhizosphere than in non rhizospheric soil. These microorganisms can profoundly affect the growth of plants, either beneficially – by increasing nutrient availability, detrimentally – by competing for the same elements, or by pathogenic activity. Relying solely on root derived carbon for their energy, they are fully dependent on plant attributes (physiological

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traits, growth cycles etc.,). Two questions which arise often are: Is the rhizosphere effect a means for plants to colonize different environments? and To what extent does it contribute to soil changes, thereby preparing conditions for new colonizers?

The second question has often been investigated, and numerous studies have shown the effect of different crops on soil organic matter content through root derived carbon (Bartholomew and McDonald 1966, Martin and Kemp 1980, Helal and Sauerbeck 1984, Merckx et al., 1986). In these studies, the use of ^{14}C has proven very useful in assessing the amount of carbon released in the soil by roots and there is a general consensus that growing plants for long periods in $^{14}CO_2$ atmosphere gives the most reliable estimates. The specific plant effect in a given soil and the short term dynamic of rhizospheric processes, including the plant response, has seldom been studied, due to difficulties in separating root and microbial activities from complex soil-plant interactions. It is obvious that substantially higher amounts of carbon are released from roots than those measured after long periods of time, since part of it is quickly utilized by rhizospheric microflora. This part is precisely the one that is important for plant behaviour. Therefore, short term exposure of plants to $^{14}CO_2$, and careful analysis of the fate of carbon translocated below ground before the turnover of root ^{14}C, is most likely to give a dynamic picture of the rhizosphere effect.

In this paper, comparison is made between annual and perennial plants growing on soils with different fertility levels. Complete ^{14}C balances including root incorporated carbon, rhizospheric respiration and rhizodeposition are monitored throughout the growing season after repeated short term exposures of the plants to $^{14}CO_2$.

Material and Methods

An annual species of bromegrass, *Bromus madritensis* L. and a perennial species *Bromus erectus* Huds., were sown in pots (3 plants per pot) in autumn, and allowed to grow outside under the Mediterranean climate of southern France. The soils used were: (1) the A_1 horizon of a decarbonated brown soil whose characteristics were: pH = 6.8, total N = 0.35%, total C = 5.25%, and which was qualified as fertile soil (F); (2) the AB horizon of a silicious brown soil with pH = 6.7, total N = 0·09%, total C = 1.25%; this was classified as low fertility soil (P).

At different periods in the growth cycle, December, March, April and May, corresponding to early tillering, tillering, stem extension and late flowering, sets of plants were continuously exposed to $^{14}CO_2$ during two weeks. This was done indoors in a greenhouse, according to methods described previously (Warembourg et al. 1982). Soil and aerial atmospheres were tightly separated. Environmental parameters inside the chamber, CO_2 concentration, temperature and photoperiod were regulated according to ambient values at the time of experiment. The specific activity of CO_2 was maintained constant throughout the experiment using an ionization chamber.

The soil water content was measured with tensiometer and adjusted accordingly. Soil respired CO_2 was collected using an aeration train, and measurements of C and ^{14}C were carrier out every 4 hours.

Twenty four hours after the end of the labelling period (this delay has been proven long enough in order to get a stable distribution of the two weeks labelled assimilates into the plants), plants were harvested and separated into above and below ground components. Roots were carefully freed from soil by washing and the wash water collected. Root fragments remaining in the soil were removed by hand under a binocular. All material, plant and soil were dried and weighed. Carbon measurements were done using the dry combustion method and ^{14}C by scintillation counting. Soil solutions were only measured for ^{14}C content. Sets of non-labelled plants were harvested at the same intervals for biomass measurements.

All components of the plant-soil system – shoots, roots, soil solution, soil with and without root fragments-and respiration being measured, a balance of recovered ^{14}C was calculated for each labelling period. Respired $^{14}CO_2$ represented root respiration and microbial degradation of part of the exudated carbon. Rhizodeposition represented the amount of root-derived carbon left in the soil. The rhizosphere effect was estimated by comparisons between all below-ground compartments in the various treatments.

Statistical analysis of data on carbon allocation patterns – above and below-ground and in the below-ground compartments – between species, soils and phenological stages were assessed using three-ways analysis of variance (ANOVA) without replication and with logarithmic transformation of data (significant differences were established at $P < 0.05$ according to the Newman-Keuls test).

Results and Discussion

Plant growth and biomass distribution

As expected, plant growth was very limited for both species in the less fertile soil. Total plant biomass in June was less than one third or that measured in the fertile soil (Table 1). There were no significant difference in total biomass between annuals and perennials grown in the same soil. However, growth partitioning between shoots and roots showed very different patterns. Until April, root biomass exceeded shoot biomass in all plants. Thereafter it leveled off in the annual species, *B. madritensis*, with a shoot biomass increasing sharply until June. In the perennial species, *B. erectus*, the root biomass remained higher than the shoot biomass throughout the measurement period, with a marked difference in the poor soil. In June, the average root to shoot biomass ratios of the annual species were 0.5 and 0.7 in the fertile and non fertile soil, respectively. In the perennial species, the figures were 1.0 and 2.0. It is worth noting that seed production occurred normally in annual plants, with proportionally more

in the less fertile soil. The perennial species grown in the fertile soil showed relatively few reproductive tillers.

Table 1. Comparison between above and belowground plant biomass and carbon partitioning throughout one season in annual and perennial brome-grass grown in two different soils. Data are means ±S.D. Treatments with different lethers differ significantly at $P < 0.05$

	Carbon biomass (g. pl-3)						Carbon partitioning				
	total	SD	shoots	SD	roots	SD	above-ground mg.d−1	%	below-ground mg.d−1	%	
B. madritensis											
Fertile soil											
7–12	1.03	0.23	0.33	0.09	0.70	0.15	7	31	15	69	
10–03	1.64	0.49	0.62	0.06	1.02	0.44	12	40	18	60	a
26–04	2.10	0.12	0.85	0.14	1.25	0.12	29	69	12	30	
5–06	3.93	0.68	2.66	0.33	1.27	0.46	30	92	3	8	
											A
Poor soil											
7–12	0.14	0.07	0.04	0.04	0.09	0.03	3	25	9	75	
10–03	0.24	0.14	0.07	0.05	0.17	0.09	4	36	7	64	b
26–04	0.72	0.08	0.37	0.02	0.35	0.06	9	58	6	42	
5–06	1.47	0.32	0.83	0.13	0.63	0.22	21	88	3	12	
B. erectus											
Fertile soil											
7–12	0.47	0.12	0.20	0.08	0.27	0.04	6	29	13	70	
10–03	1.11	0.29	0.45	0.11	0.66	0.18	12	41	18	59	a
26–04	2.15	0.21	0.88	0.01	1.27	0.20	22	49	22	50	
5–06	4.47	0.38	2.25	0.07	2.22	0.45	38	62	23	38	
											B
Poor soil											
7–12	0.21	0.07	0.04	0.02	0.16	0.09	2	29	4	70	
10–03	0.20	0.11	0.05	0.03	0.15	0.08	2	21	8	79	b
26–04	0.57	0.03	0.19	0.01	0.37	0.02	6	34	12	66	
5–06	1.38	0.03	0.45	0.06	0.92	0.09	11	42	16	58	

Carbon partitioning above and below ground

The daily amounts of carbon remaining above and exported below ground were measured from the ^{14}C data gathered after each two weeks exposure to $^{14}CO_2$ (Table 1). Below ground partitioning included all carbon, incorporated into root structures, respired and deposited in the soil. In the annuals, significantly more carbon was translocated below ground than left above throughout the tillering stage. After March, a complete inversion occurred with a sharp increase of the proportions left above ground which reached 90% in June at the end of the flowering stage. This was associated with the development of reproductive structures. In the perennial species,

the rate of carbon translocated below ground increased throughout the season, as was that remaining above. The proportion of the later however, was more than 50% in June in the fertile soil, where the plants showed some reproductive structures.

Carbon partitioning in the rhizosphere

The relative proportions of carbon measured in the below-ground compartments throughout the season are illustrated in Fig. 1. Although it is difficult to analyze the pattern of each one individually, some significant trends can be observed as confirmed by the statistical analysis. The proportion of carbon incorporated into roots is significantly higher in the poor soil than in the rich one. It decreases throughout the season but significantly more sharply in the annuals than in the perennials. Consequently, the proportion of carbon lost either as CO_2 or in the soil as root-derived carbon increases accordingly. It is noteworthy that losses are more important than incorporated carbon in the annual species and that the maximum occurs in the more fertile soil. There is also a high correlation between this ratio and the phenological stage of the plants. The development of reproductive structures is correlated to more carbon losses in the rhizosphere. This shows even in the perennial species grown in the richer soil which presented some seeds. The major part of the losses are due to rhizospheric respiration which reached more than 40% of the carbon translocated in the annuals, 30% in the perennials with no significant effect of the soil type. Such high respiration rates have never been previously reported. They seem logical however, since an important part of it originates from the rhizosphere microflora, as discussed by Van Veen el al. (1989). Another part of the loss is due to rhizodeposition, which also showed a maximum during reproductive stages of plant growth.

An answer to the introductory question: Is the rhizosphere effect a strategy for the plants to colonize new environments? can now be attempted. In terms of "rhizosphere effect", the maximum of activity (root and microbial respiratory activity plus rhizodeposition) was recorded for the annuals during the reproductive stages of growth. It constituted 60 to 70% of the carbon translocated below ground. The minimum was measured for the perennial species grown on the poor soil which reached a peak of 40% in May. The maximum of the rhizosphere effect occurred when growth required the maximum of nutrients. This has already been shown for wheat plants (Billes et al. 1988) combined with a high mineralization rate of nitrogen in the soil during the same period. The drastic decrease of the root-incorporated carbon to respiration ratio measured in this study may indicate enhanced microbial activity. The simultaneous increase of rhizodeposition recorded corroborates this conclusion since part of root-derived carbon is integrated into microbial biomass. (Merckx et al. 1987). The fact that significantly more rhizodeposition in proportion of root translocated C was observed in the more fertile soil is remarkable, since nutrients

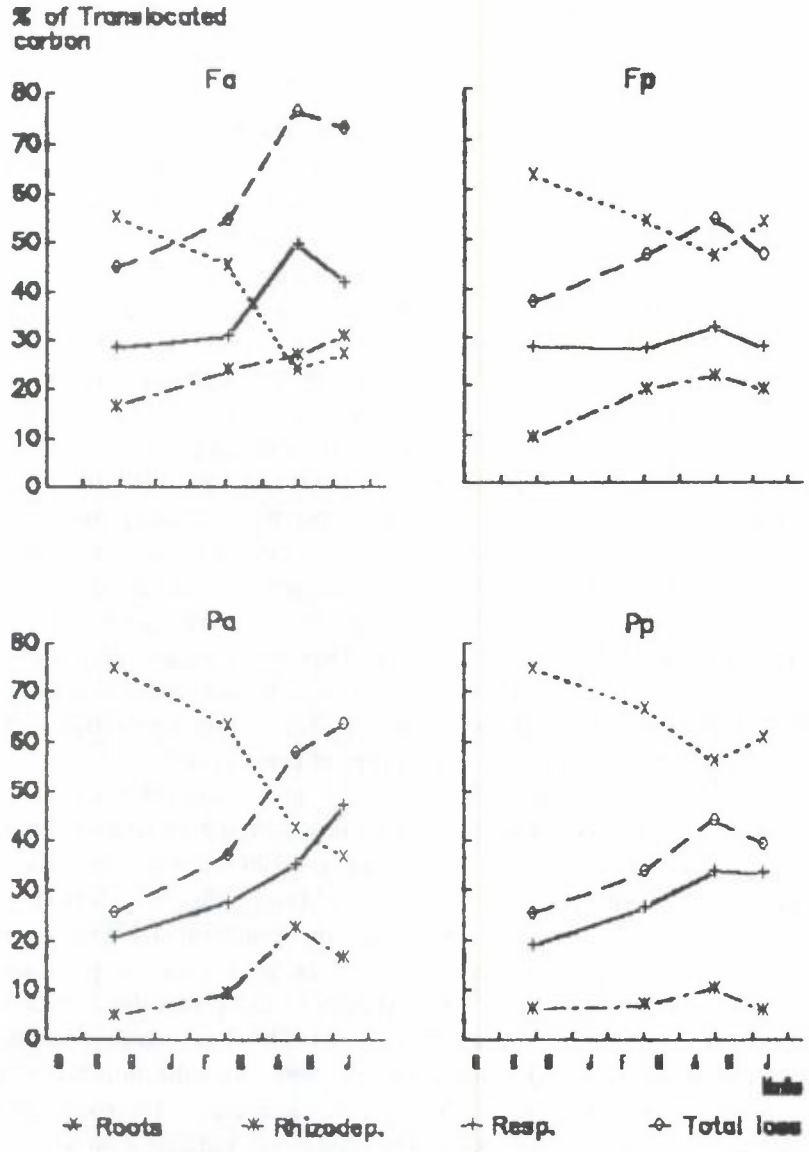

Figure 1. Seasonal carbon partitioning in the rhizosphere of an annual (*B. madritensis*) and a perennial (*B. erectus*) bromegrass grown in different soils (F: fertile soil, P: poor soil, a: annual, p: perennial). Statistical treatments are indicated in text.

should be more available under favourable edaphic conditions. However, as noticed by Merckx et al., (1987), at higher nutrient levels, no restriction exists for microorganisms to incorporate root-derived materials. This leads to increasing immobilization of nitrogen and other minerals as plants develop.

In terms of efficiency of root growth per unit of translocated carbon, the highest values were found in the low fertility soil, especially for the perennial species. The tendency of many species to increase root biomass at low nutrient levels is well-known (Brouwer 1966). However, the fact that this was not accompanied by substantial amounts of root-derived carbon was unexpected. This result may be connected with the small incorporation of root-derived carbon into microbial biomass. In this case, less immobilization of nutrients occured giving a better rate of root growth per unit of carbon invested.

Another interpretation for the high activity measured in the rhizosphere of annual plants is that as opposed to perennials, their roots stop growing after the stem extension stage. Concurrent with the onset of the reproductive stage, a portion of the annual's roots have begun to die contributing thereby to rhizodeposition and microbial respiration. It seems, however, that even though this process may have occured in our experiment, two weeks were not a long enough period to stimulate substantial turnover of the root ^{14}C.

The results obtained in this study indicate that even if the rhizosphere effect seems to be a constant characteristic of grasses – and perhaps of all terrestrial plants – partitioning and use of plant carbon in the rhizosphere showed distinct patterns among plants with different life cycles and with different environments. In order to accomplish their whole cycle during a short period of time, annuals seem to invest more carbon in the rhizosphere when root growth stops, while perennials continuously increase their root biomass. It will be of interest to examine the pattern of carbon partitioning in perennial grasses during the second year of growth, i.e. during their reproductive period. The exact role of the rhizosphere effect on actual plant development can not be demonstrated from this study. The few indications of a better nutrient availability through rhizospheric processes remain to be confirmed through a detailed analysis of the mineral status of both plant and soil during the whole season and for the different treatments.

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