The 'rhizosphere effect': a plant strategy for plants to exploit and colonize nutrient-limited habitats

Fernand R. Warembourg

Abstract

Warembourg, F. R.: The 'rhizosphere effect': a plant strategy for plants to exploit and colonize nutrient-limited habitats. — Bocconea 7: 187-194. 1997. — ISSN 1120-4060.

Under natural conditions, plant growth and species composition of the vegetation are often limited by the availability of soil nutrients rather than by light or water. This paper tries to answer the question: Are there differences in the interactive effects of plant individuals, physico-chemical factors and the community of soil microorganisms that indicate the development of different plant strategies for survival in nutrient-poor habitats? After a definition of the effect plant roots may have on the surrounding soil (the rhizosphere effect), the paper reviews the evidence for its role on soil organic matter mineralisation and therefore, of nutrient availability on different species and on soils of different fertility. Comparison between annual and perennial species of *Bromus*, indicates a better efficiency of the former to thrive in nutrient-poor habitats, both in relative quantities and in terms of the cost of mining soil nutrients.

Introduction

In order to grow and eventually reproduce, plants as other organisms require energy, water and nutrients. In terrestrial ecosystems, the stock of nutrients is located in the soil. Beside being often limited, this stock is never directly available since it is integrated into soil organic matter, either plant material from previous years, animal or microbial bodies or humified compounds. Availability of nutrients, or soil fertility, is something that hummans had to cope with since the beginning of agriculture. Indeed, among other, mineral stress is one of the more obvious in natural situations. It has a strong influence on plant distribution and always limits plant production and therefore reproduction. Nutrient availability relies on the activity of decomposers whose role is to mineralise the soil organic matter. This process depends upon a succession of steps involving a succession of organisms and is governed by a subtle balance between the energy and the nutrient contents of the matter to be mineralised. Furthermore, when mineralisation occurs, there is competition between plants and other organisms for the same nutrients. In this series of processes, the plants can play an important role by the effect their roots have in changing the soil conditions in the rhizosphere.

This 'rhizosphere effect' has been recognised since the beginning of the century as an integration of processes having a strong influence on plant development (Hiltner 1904).Nevertheless it is still often neglected as a potential key factor in mineral nutrition. Part of the reason for this comes from the fact that the root environment is very complex and includes a tremendous diversity of organisms whose interactions among each other and with the soil's abiotic components are unlimited. This may lead to results that are difficult to interpret when dealing with the rhizosphere as a whole. This is partly due to methodological difficulties of investigatiing the rhizospehere. However, the role of the so called 'rhizosphere effect' on nutrient availability is obvious under most environmental conditions. In fact, apart from fertilizers and small input by rain, plants are dependent on microbial activity to obtain their nutrient supply and the rhizosphere is known to host an important microflora. This paper will review recent work on the rhizosphere effect; it compares the importance of the rhizosphere for different species and under various conditions of soil fertility. Before that, attention will be given to the concept of the rhizosphere, and to what we know about the determinants of microbial activity that can be from root origin and what are those that may particularly affect the mineralization of soil organic matter. Emphasis will also be given to the actual methodology for measuring the 'rhizosphere effect' and determining its role in enabling plants to compete in nutrient limited habitats.

The 'rhizosphere effect'

Since the pioneer work of Hiltner in 1904, studies on the rhizosphere were based on two facts: 1) Around the roots, microbial populations are more numerous and often differ in species composition from those in the outer soil, 2) Living roots release a great variety of compounds at different times during the life cycle of plants. The link between these two facts is that the plant provides microbial substrates together with hormones and vitamins, as well as toxins and other antagonistic compounds which may exert a selective effect on microorganisms. In turn, microorganisms exert influences on plants which range from beneficial, neutral or detrimental effects, so that the relationships between plants andmicrobes may be commensals, mutualists, or parasites. As regards mineral nutrition, specific organisms involved in the acquisition of nitrogen (free living or symbiotic nitrogen fixers) and phosphorus (mycorrhizae) are well known and their effects on plant development iswell documented. However, the role of the rhizosphere microflora as a whole is not always clear.

Substrates in the rhizosphere

According to a classical terminology (Rovira & al. 1978), the carbon compounds released by living roots have been classified into four groups according to the mode of production: 1) passive exudates and 2) metabolically mediated secretions, from intact cells, consisting of low molecular weight compounds including sugars, amino acids, organic acids, hormones, enzymes and vitamins; 3) mucilages of the root tip and epidermal cells; 4) lysates from senescing tissues and roots. Because most studies have concentrated on the apical tip of the roots of seedlings and young plants grown in nutrient solutions, much emphasis has been given to the first three categories. In considering the whole period of plant development under natural conditions, the balance of these compounds, changing with plant age and phenology, may well be influenced by the fourth category which includes the senescing parts of the whole root system. Today the term 'rhizodeposition' (Whipps & Lynch 1985) is now used to include all four categories of material and to express the total amount of carbon liberated by the roots.

The contribution of these carbon compounds to the organic matter in the soil and their role in influencing the soil's physical properties are well recognised. However, the benefit to the plant of such expenditure is not well defined. Since these compounds provide substrates for microbial growth, and since the activities of soil organisms result in soil organic matter mineralisation and therefore nutrient cycling, the release of these compounds should provide at least indirect benefit to the plants. One may ask if the carbon deposited in the soil by plant roots enables plants to exert some control on nutrient availability. Furthermore, do different plants have different abilities to mine (through rhizosphere processes) nutrients according to the richness of their habitats? Answering this question presupposes that there are means of measuring rhizosphere activities, both plant activity (rhizodeposition) and microbial activity (use of root derived energy for metabolism that results in nutrient cycling).

There is now a general consensus that the use of $^{14}CO_2$, in pulses or long term exposures, is the more acceptable method for investigating rhizosphere activities and because it is able to separate current carbon from older carbon, i.e. plant carbon from soil organic matter carbon. Current studies are attempting to estimate carbon budgets of the rhizosphere by analysing, over increasing periods of time after $^{14}CO_2$ feeding of the plants, and the ^{14}C content of the different rhizosphere components: roots, root and soil respiration, soil organic matter. Estimations of microbial biomass associated with root development in soil have also been attermptede, but quantification is difficult since the methods are rather imprecise.

Applications of these techniques to determine carbon transfers in the rhizosphere have been numerous, but few of them were aimed at ascertaining the role of the rhizosphere in plant nutrition under different soil conditions and for different plant species. In any case they were always indirect estimates based on comparison either between soil organic matter behaviour in bare and cropped soils or 'performances' of different species in soils of different fertility. Experiments involving multifactor analysis were very seldom performed.

'Rhizosphere effect' and soil organic matter mineralisation

Most of the early studies (Fuhr & Sauerbeck 1968, Shields & Paul 1973, Jenkinson 1977) were carried out in the field, where soil amended with ^{14}C labelled material was left unplanted, cultivated, or kept with natural grassland vegetation. They all demonstrated that the presence of plants significantly decreased the decomposition of the added material if compared to soils without plants. Experiments undertaken in the laboratory under controlled temperature and soil moisture, where labelled material was incorporated into the soil (Reid & Goss 1982, 1983, Sparling & al. 1982, Billes & Bottner 1981, Billes & al.

1986), showed the same depressive effect. However, Helal & Sauerbeck (1982-1984), using another technique (which consisted of growing maize plants in a $^{14}CO_2$ atmosphere on non-amended soil), reported an increased soil organic carbon mineralisation compared to the soil in the control. This increase was even higher than the amount of carbon deposited by the roots during the cropping period. In a long term experiment (2 years) involving successive cultures of wheat on soil amended with labelled material, Sallih and Bottner (1988), made a careful analysis of $^{14}CO_2$ mineralisation rate. This study indicated that during the early stages of decomposition, when the decomposer activity is high, mineralisation is not induced by the presence of roots. Later on, when the available nutrients are exhausted both by plants and microflora, the roots stimulated soil carbon mineralisation. In a further study (Bottner & al. 1988), it was suggested that the availability of nutrients in the soil greatly affected the mineralisation of soil organic matter through its effects on the size of the microbial biomass, which regulates nutrient transfers between the soil and the plant roots. In fact it was demonstrated that the presence of roots and therefore the rhizosphere effect significantly affected the rate of decomposition, compared to bare soil, only after the labile compounds were exhausted from the soil organic matter pool.

'Rhizosphere effect' and soil fertility

As indicated previously, soil freshly amended with plant material failed to show a significant effect of roots on the mineralisation rate and therefore nutrient turnover. In fact, the incorporated material acts as fertilizer for the microflora without improving mineralisation. Therefore, it does not readily benefit to the plant (Bottner & al. 1988). In a series of rhizosphere investigations performed on soils of different fertility, Merckx & al. (1987) showed that nutrient concentration in the soil changes the interactions between roots, soil, and microorganisms. Though these experiments provided data on the influence of soil nutrient status on the production and use of root-derived material, and not directly of their effect on nutrient turnover, it is possible to provide valuable information also for the deduction of the mechanisms involved. It is well known that a decrease of nutrient availability changes the dry matter distribution between shoot and roots in favour of the roots, increasing undoubtedly the absolute amount of root derived carbon deposited in the soil. As noted by Merckx & al. (1987), this does not explain the higher proportion of the total amount of fixed carbon that is present in soils rich in nutrient status. It is known (Merckx & al., Warembourg & al. 1990) that increasing amounts of carbon are released into the rhizosphere in nutrient rich soil. In that case, there are no restrictions on the microorganisms incorporating this root-derived material of high C/N ratio into their biomass which indirectly implies increasing nutrient immobilisation as the plant develops. In soils poor innutrients, less carbon is lost by the roots, either because of less plant production or because of physiological differences in root exudation. Less carbon is therefore available for the microbial biomass and due to low nutrient supply in the soil, this biomass is not restricted by the decrease of energy input. There is even an accumulation of carbon compounds which could have been available for biological transformation (Merckx & al. 1987). These rather unexpected results obtained in low nutrient soils, indicate that microbial growth may not be restricted by carbon supply but by mineral nutrients. They show that the decomposition processes, even at a low rate of activity, will continue to degrade low C/N ratio stable compounds, thus increasing mineralisation rates as compared to nutrient rich soils.

'Rhizosphere effect' and plant species

Rhizosphere effects may be expected to vary among plant species differing in life history, habitats or other features. For obvious technical reasons, including the difficulties of maintaining plants in an artificial atmosphere containing $^{14}CO_2$ for long periods of time, most rhizosphere studies have been performed on annual plants, mainly crop plants with relatively short life cycles.. Even among annual plants, however, studies have shown differences (Martin 1975, Johnen & Sauerbeck 1977, Merckx & al. 1986). Most of them have been attributed either to differences in the shoot to root production ratios, or in the relative growth rates of roots (Merckx & al. 1986). It has been reported that the influence of the phenological stage on the rhizosphere activity may be greater than that of plant species, with a decreasing root respiration and exudation and an increasing microbial activity with increasing plant age (Whipps & Lynch 1985). This is in direct relation to the switching from vegetative to reproductive stages, i.e. the complete change over of the shoot to root production ratio and to the increasing proportion of rhizosphere carbon originating from senescing roots relative to that coming from exudation by growing roots (Warembourg & al. 1990). The magnitude and the nature of the 'rhizosphere effect' through both root and microbial activities is therefore highly dependent on the plant's phenological stage, as is the nutrient uptake requirement of the plants. Mineralisation studies (Billes & Bottner 1981) have indicated the effects of these phenological differences: a depressing effect during high root activity (vegetative stage) and a positive effect at maturation (reproductive stage).

The life cycle of plants has seldom been investigated as regards to rhizosphere activity. In one of the few studies performed with perennial species and using similar tracer techniques to those currently used for annuals, Dormaar & Sauerbeck (1983) have indicated that over 70 % of net photosynthesis was transferred to the roots of grasses in grassland, compared to average of 30 to 50 % in annual plants. The fact that the root system is maintained throughout the year, with alternate phases of root growth, induces an overall higher carbon investment in rhizosphere activity in perennials than in annual species on a year-round basis. It should also be emphasized that because of the long lifespan of perennial plants, their vegetative periods are longer than in annuals, with all the resulting differences noted above concerning the nature of the rhizosphere effect.

Significance of the rhizosphere activity under different nutrient availabilities

In view of the difficulties in measuring the direct effect of rhizosphere activity on plant growth and performance under different conditions, the comparison was made during the complete growth cycle of annual and perennial species grown in soils of different fertility (Warembourg & al. 1990).

Two brome grass species, the annual *Bromus madritensis* L. and the perennial *Bromus erectus* Huds., were sown in 2 types of soils containing respectively 5.25 and 1.25 % of C and 0.35 % and 0.09 % of N, with a pH around 6.8 for both. Two weeks exposure to $^{14}CO_2$ were repeatedly performed on different sets of plants during the two-year period of the experiment in order to estimate periodic carbon partitioning among shoots, roots, root respiration and rhizodeposition. At each harvest, which occurred approximately one week after labelling, the carbon and nitrogen content of the plants were determined, as well as the proportion of respiration that originated from root carbon and soil organic carbon. Control soils without plants were tested in order to estimate soil respiration, and for comparison with cropped soils.

The presence of plants significantly affected the yearly rate of mineralisation of soil organic matter and therefore nutrient availability (Table 1). However there were differences between the two *Bromus* species, the perennial inducing twice as much mineralisation compared to the annual one in both soils. This may be related to the length of the growing period (the annual matured in June whereas the perennial continue to grow throughout the year). The difference between the two soils was also very important, with a maximum on the less fertile soil. Here the perennial induced a threefold mineralisation rate compared to the control, while the annual only a twofold rate.

Table 1. Comparison of the rhizosphere effect of an annual and a perennial brome grass species (*B. madritensis* and *B. erectus*) grown on two different soils; including carbon investment per unit of extracted N and mineralization of soil organic matter.

	Fertile soil		Poor soil	
	Annual	Perennial	Annual	Perennial
Biomass C				
(mg.pl^{-1})	1320	1710	490	1260
SD	200	171	110	190
Exported N				
(mg.pl^{-1}.y^{-1})	19.6	55.5	12.0	34.9
SD	3.0	6.0	3.0	4.0
Below-gr. C				
(mg.pl^{-1}.y^{-1})	1140	1439	397	898
SD	90	120	50	60
C Investment				
(mg.C/mg.N)	58.2	25.9	33.1	25.7
Mineralization				
(% soil C. y^{-1})				
- control	10.9 (a)	10.9 (a)	6.7 (d)	6.7 (d)
- with plants	13.1 (b)	16.5 (c)	12.7 (e)	18.7 (f)
Plant effect	2.2	5.6	6.0	12.0

When the rhizosphere activity was compared in terms of carbon investment in the root system, including respiration and rhizodeposition per unit of nutrient mineralised (expressed in N exported from the soil to the plant), important differences were also observed (Table 1). The annual grass invested more carbon: 58 and 33 units of C per unit of N in fertile and poor soils respectively, compared to 26 in the perennial in both soils. This indicates that in terms of cost, the perennial species is much more efficient in mining nutrients in the soil, whatever their availability, and that an extra loss of carbon is associated with annual plants grown on fertile soils. This can be related to 1) the presence of a rich microflora, which may capture a relatively higher proportion of root carbon, thus inducing more release ; or to 2) an ample supply of carbon from photosynthesis, which is wasted through rhizodeposition and respiration.

Considering plant performance in term of growth, the perennials are less affected than the annuals by the low soil fertility, since the biomass after one year is only reduced by 25 %, against 63 % for the annuals near the end of the growth cycle (Table 1). As indicated by the above results, this may be linked to a better ability of the perennials to mine nutrients and to a lesser cost for the plants compared with the annuals. However, a correlation between rhizosphere activity and plant growth does not necessarily imply a direct relationship. Too many unknowns still remain, mainly regarding the role of the rhizosphere microflora and on the control effect the plant may have on its activity.

Conclusion

In conclusion, rhizosphere studies tend to build up information on the active and specific impact of plants on the soil environment by a significant carbon investment that varies according to the type of soil and nutrient availability. It will be however premature to deduce an adaptive process. In fact, the exact effects of plant derived carbon on the microflora involved in the soil organic matter mineralisation requires further investigation. A more exhaustive estimation of the importance of the rhizosphere effect in the ability of plants to colonise and survive in different soil environments requires experiments where exudation and rhizodeposition processes are fully controlled. In the current state of knowledge, conceptual and methodological improvement have still to be achieved in order to estimate *in situ* the interactive effects of plants and the community of soil organisms. Conservation and proper management of wild plants require this kind of knowledge.

References

Billes, G. & Bottner, P. 1981: Effet des racines vivantes sur la décomposition d'une litière racinaire marquée au ^{14}C. — Plant Soil **62:** 193-208.

—, Gandais Riollet, N. & Bottner, P. 1986: Effet d'une culture de graminées sur la décomposition d'une litière végétale marquée au ^{14}C et ^{15}N dans le sol en conditions contrôlées. — Oecol. Plant **7:** 273-286.

Bottner, P., Sallih, Z. & Billes, G. 1988: Root activity and carbon metabolism in soils. — Biol. Fertil. Soils **7:** 71-78.

Dormaar, J. F. & Sauerbeck, D. R. 1983: Seasonal effects of photoassimilated carbon-14 in the root system of blue gramma and associated soil organic matter. — Soil Biol. Biochem. **15:** 475-479.

Fuhr, F. & Sauerbeck, D. R. 1968: Decomposition of wheat straw in the field as influenced by cropping and rotation: Isotopes and radiation in soil organic matter studies. — IAEA Vienna, 241-250.

Helal, H. M. & Sauerbeck, D. R. 1984: Influence of plant roots on C and P metabolism in soil. — Plant Soil **76:** 175-182.

Hiltner, L. 1904: Uber neuere Erfahrungen und Probleme auf dem Gebiet der Bodenbaksteriologie und unter besonderer Berücksichtigung der Gründüngung und Brache. — Arb. Dtsch. Landwirt. Ges. **98:** 59-78.

Jenkinson, D. S. 1977: Studies on decomposition of plant material in soil: IV The effect of the rate of addition. — J. Soil Sci. **28:** 423-471.

Johnen, B. G. & Sauerbeck, D. R. 1977: A tracer technique for measuring growth, mass and microbial breakdown of plant roots during vegetation. — Pp. 366-373 in: Lohm, V. & Persson, T. (ed.), Soil organisms as components of ecosystems. — Ecol. Bull Stockolm. **25.**

Martin, J. K. 1975: ^{14}C labelled material leached from the rhizosphere of plants supplied continously with $^{14}CO_2$. — Soil Biol. Biochem. **7:** 395-399.

Merckx, R., Dijkstra, A., den Hartog, A. & Van Veen, J. A. 1987: Production of root derived material and associated microbial growth in soil at different nutrient levels. — Biol. Fertil. Soils. **5:** 126-132.

—, van Ginkel, J. H., Sinnaeve, J. & Gremers, A. 1986: Plant induced changes in the rhizosphere of maize and wheat. I Production and turnover of root derived material in the rhizosphere of maize and wheat. — Plant Soil. **96:** 85-93.

Reid, J. B. & Goss, M. J. 1982: Suppression of decomposition of ^{14}C labelled plant roots in the presence of living roots of maize and perennial ryegrass. — J. Soil Sci. **33:** 387-395.

— & — 1983: Growing crops and transformations of ^{14}C labelled soil organic matter. — Soil Biol. Biochem. **15:** 687-691.

Rovira, A. A., Foster, R. C. & Martin, J. K. 1978: Origin nature and nomenclature of the organic materials in the rhizosphere. — In: Harley, J. L. & Scott Russel, R. (ed), The soil root interface **1-4**. — Academic Press, London.

Sallih, Z. & Bottner, P. 1988: Effect of wheat (*Triticum aestivum*) roots on mineralisation rates of soil organic matter. — Biol. Fertil. Soils **7:** 67-70.

Shields, J. A. & Paul, E. A. 1973: Decomposition of ^{14}C labelled plant material under field conditions. — Can. J. Soil Sci. **53:** 297-306.

Sparling, G. S., Chechire, M. V. & Mundie, C. M. 1982: Effect of barley plants on the decomposition of ^{14}C labelled soil organic matter. — J. Soil Sci. **33:** 89-100.

Warembourg, F. R., Estelrich, D. H. & Lafont, F. 1990: Carbon partitioning in the rhizosphere of an annual and a perennial species of bromegrass. — Symbiosis **9:** 29-36.

Whipps, J. M. & Lynch, J. M. 1985: Energy losses by the plant in rhizodeposition. — Ann. Proc. Phytochem. Soc. Eur. **26:** 59-71.

Address of the author:
Dr. F. R. Warembourg, Centre d'Ecologie Fonctionnelle et Evolutive, CNRS, BP 5051, F-34033 Montpellier Cédex 1, France.