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The rhizosphere as part of the plant-soil system

1. INTRODUCTION

The organic materials formed by higher plants during the process of photosynthesis are decomposed mainly by microorganisms. These breakdown processes take place primarily in the soil. The constituents of the aerial parts of the plant become available to the microflora by volatilization from the leaves, leaching by rain, mist, or dew, and by the falling of leaves or branches. The subterranean parts provide the microorganisms with root excretions, sloughed-off cells, and dead roots.

The present discussion is mainly concerned with the processes occurring under the influence of the carbon provided by the living root system. It should be kept in mind, however, that compounds originating from intact aerial parts, i.e., leached and volatilized products, may considerably alter the surface layers of the soil around the plant. Many of these compounds are toxic to other plant species or inhibit the germination of their seeds. The important ecological effects of these allelochemicals supplied by the aerial parts will not be discussed here; the reader is referred to reviews by TURKEY (1969), WHITTAKER (1970, 1971), WENT (1970), and RICE (1974).

The present paper deals with the problem of whether the microbial processes going on in the environment of the root, i.e., the rhizosphere, are influenced by the plant in a specific way and thus contribute to niche differentiation. Special attention will also be given to the effects of the rhizosphere microflora on the availability of plant nutrients such as nitrogen and phosphorus. For a discussion of other aspects of rhizosphere research, the reviews given by ROVIRA (1974) and MANGENOT (1975) should be consulted.

For an understanding of microbial processes in the soil, a few points should be kept in mind. Due to the small dimensions of the microorganisms their environmental conditions differ widely from place to place and fluctuate strongly in time. In the surface layers appreciable differences in temperature occur, the availability of moisture and oxygen in the interior and on the surface of soil aggregates may be completely different, and the supply of energy and nutrients is highly variable in space and time. Consequently, microorganisms may easily loose their niche because of changes in environmental conditions and thus become subject to mineralization. Due to

these variations in conditions on a millimeter scale, many microbial processes may proceed simultaneously at different places in the rhizosphere: for instance, mineralization of nitrogen may be accompanied by its immobilization, fixation of atmospheric nitrogen into organic compounds may coincide with the decomposition of nitrate into gaseous products.

Much of our insight into the processes going on in the rhizosphere is based on experiments done in arable and horticultural plant species, most of which are rapidly growing annuals. As far as perennial plants are concerned the data available derive almost exclusively from species of permanent grasslands. Our knowledge of these processes as they occur in natural vegetations is still very incomplete, and much work will have to be done before a more satisfactory picture can be obtained.

In such natural vegetations the primary production is often limited by a lack of nutrients or water, and a surplus of energy is available in the form of carbonaceous materials. For their nitrogen and phosphorus supply, these plants depend almost completely on the mineralization of organic compounds by microorganisms, whereas arable and horticultural crops, which are usually given fertilizers at the beginning of the growth season, have a surplus of nitrogen available during a great part of the year and energy is the factor limiting microbial activities. Therefore, it is hardly surprising that experiments with such crops have yielded different results from those performed in natural, unfertilized vegetation.

2. DESCRIPTION OF THE RHIZOSPHERE

The rhizosphere is composed of three zones. The rhizosphere in the strict sense which consists of the soil around the roots in which soluble and volatile compounds excreted by the roots diffuse. The rhizoplane, which comprises the root surface and the mucigel covering part of the roots behind the root cap. The endorhizosphere, which consists of epidermis and cortex cells invaded by saprophytic microorganisms. It should be noted that no microorganisms have been observed in the cells of the central cylinder.

The number of microorganisms in the rhizosphere (R) is much higher than in the soil further away from the root (S). R/S ratios of about 6 are usually found, but in poor soils the rhizosphere effect is much more pronounced, as can be seen from Table 1, which shows data obtained from arable crops by ROUATT & KATZNELSON (1961) and from species of poor dune soils by WEBLEY *et al.* (1951). High R/S values are found particularly in the rhizosphere of leguminous plants.

The rhizosphere effect can often be observed at considerable distances from the root. This is illustrated by data of PAPAVIZAS & DAVEY (1961) obtained with Blue Lupine (Table 2).

TABLE 1. *Colony counts of bacteria in root-free soil and in the rhizosphere of crop plants and wild species*

Species	Colony counts (10^6/g soil)		
	Rhizosphere	Root-free soil	R/S ratio
*Trifolium pratense**	3,260	134	24
*Avena sativa**	1,090	184	6
*Linum usitatissimum**	1,015	184	5
*Zea mays**	614	184	3
*Atriplex babingtonii***	23.3	0.016	1455
*Ammophila arenaria***	3.58	0.016	223
*Agropyron junceum***	3.56	0.016	222

* Data from ROUATT & KATZNELSON (1961)

** Data from WEBLEY *et al.* (1951)

TABLE 2. *Extent of the rhizosphere of Blue Lupine* (PAPAVIZAS & DAVEY 1961)

Distance from root (mm)	Microorganisms (10^3/g oven-dry soil)		
	Bacteria	Streptomycetes	Fungi
0	159,000	46,700	355
0- 3	49,000	15,500	176
3- 6	38,000	11,400	170
9-12	37,400	11,800	130
15-18	34,170	10,100	117
>80	27,300	9,100	91

TABLE 3. *Composition of the microflora of the rhizosphere of a 2-year-old sand culture of perennial ryegrass, of permanent grassland on sand and of sandy arable soil, respectively* (WOLDENDORP 1963)

	Rhizosphere	Grassland	Arable soil
% of total number			
Bacteria	75	70	90
Streptomycetes	25	30	9
Fungi	0	0	1
% of bacteria			
G(-) rods	60	58	11
Bacilli	3	10	14
Coryneforms	37	32	75

Fungi and streptomycetes were stimulated mainly in the rhizoplane, the effects on bacterical numbers occurred over greater distances. From these findings it can be concluded that under a permanent cover of plants the microbial processes in the upper layer of the soil are under the influence of the roots. Consequently, the composition of the microflora of grassland has much more in common with that of the rhizosphere soil (Table 3).

In the rhizosphere the microorganisms are not evenly distributed over the root surface. The region of the newly formed root-cap cells is generally free of bacteria and fungal hyphae, but the mucilaginous sheath around the roots soon becomes colonized by bacteria, some of which are able to lyse the mucigel (BREISCH *et al.* 1975). The older root parts are often densely colonized by many layers of bacterial cells, but the bacteria occur commonly in colonies with only a limited number of cells. These colonies are particularly common at the junction of cell walls and at places where lateral roots emerge. This uneven distribution of the microorganisms over the root surface was also shown by NEWMAN & DOWEN (1974), who used the techniques developed by GREIG-SMITH (1964) to study patterns in vegetation. Although some parts of the root are densely colonized, most of the root surface is devoid of microorganisms. At most 15 per cent of the root surface is covered by microorganisms, but ROVIRA *et al.* (1974) found lower values for a number of grassland species (Table 4).

TABLE 4. *Percentage of root surface covered by bacteria in grassland species* (ROVIRA *et al.* 1974)

Species	% cover	Species	% cover
Hypochaeris radicata	9.3	*Cynosurus cristatus*	6.4
Holcus lanatus	8.6	*Rumex acetosa*	6.3
Lolium perenne	8.4	*Trifolium repens*	6.2
Anthoxanthum odoratum	8.1	*Plantago lanceolata*	4.7

Our knowledge of the distribution of microorganisms on the root surface has been greatly increased by studies done with transmission and stereoscan electron microscopy (JENNY & GROSSENBACHER 1963; DART & MERCER 1964; GREAVES & DARBYSHIRE 1972; ROVIRA *et al.* 1974; BREISCH *et al.* 1975; OLD & NICHOLSON 1975). For such investigations use should be made of soil-grown roots, because it has been found that the rhizoplane populations of these roots are many times smaller than those of roots grown on agar or water culture.

From the foregoing it is clear that microorganisms must be taken into consideration in studies on plant physiology, because of their presence in appreciable areas of the root surface.

3. ROOT EXCRETIONS AND THEIR EFFECTS ON THE RHIZOSPHERE

3.1. QUANTITATIVE ASPECTS

Initially, the quantitative aspects of root excretions were investigated in sterile (axenic) plants grown in water culture. As a rule, only the compounds with a low molecular weight were analysed. Under such conditions, small quantities were found to be excreted.

Later it was found, however, that considerably higher quantities were supplied to the rhizosphere by plants grown in soil. This difference from water cultures has been ascribed to the greater damage undergone by the roots in soil (for a review of this subject, see HALE *et al.* 1971). The quantities of excreted products were also found to be higher for non-sterile plants (see e.g. BILES & CORTEZ 1975). To explain this difference it has been suggested that the rhizosphere microflora may affect root exudation by altering the metabolism and permeability of the root. Finally, the soluble compounds constitute only a small fraction of the total amounts supplied by the living plant to the soil. Gaseous products and non-soluble compounds of high molecular weight are quantitatively of much greater importance. The ratio between water soluble compounds, water isoluble compounds, and volatile compounds, has been estimated to be 1 : 3-5 : 8-10 (ROVIRA & DAVEY 1974). Seventy to eighty per cent of the volatile compounds consists of carbon dioxide originating from respiration by the root and microorganisms (ROVIRA 1972).

When these effects are taken into account, it is not surprising that much higher quantities of compounds deriving from the living root system were recently found in experiments with soil-grown, non sterile plants (Table 5). The data in Table 5 are to be regarded as minimum values, since some of the labelled carbon dioxide originating from respiration may have escaped.

TABLE 5. *Reported quantities of carbon supplied to the soil by living root systems*

Reference	Conditions	Quantities of carbon
VANCURA (1964)	Water stress, 10 days	7-10% of biomass
SHAMOOT *et al.* (1968)	14 CO_2, whole growth period	9-42 g/100 g of roots
MARTIN (1973)	14 CO_2, whole growth period	10-38 g/100 g of roots 6% of photosynthesis
BREISCH (1974)	14 CO_2, 1 day	10-20% of photosynthesis
WAREMBOURG (1975)	14 CO_2, 3 days	12-16% of photosynthesis
BILLES *et al.* (1975)	Leached sugars, 35 days	4.5-8% of biomass
BALANDREAU & HAMED-FARES (1975)	Calculated from N_2 fixation	10-20% of biomass

A large share of this carbon is contributed by sloughed-off rootcap cells. According to CLOWES (1971), these cells have a lifespan of only one day. For maize, the amount of sloughed-off rootcap cells has been estimated at 10 tons of dry matter per hectare (SAMTSEVITCH 1971).

The carbon dioxide evolved in the rhizosphere is only partially derived from root respiration. A roughly equal part originates from microorganisms in the rhizosphere (Table 6).

TABLE 6. *Contribution of the microflora to CO_2 production in the rhizosphere. The data were obtained by comparing sterile and non-sterile plants*

LUNDEGÅRDH (1927)	33%	REUSZER (1949)	60%
WAKSMAN & STARKEY (1931)	45%	NILOVSKAYA (1970)	35%
STILLE (1938)	>90%	TROLLDENIER (1972)	50%
BARKER & BROYER (1942)	50%		

More or less similar results were obtained by WOLDENDORP (1963), who compared the oxygen uptake of sterile and non-sterile root systems of pea plants and found that about 40 per cent of the total respiration could be ascribed to the microflora. However, these results should be considered with some caution, because it is well known that microorganisms influence the morphology and the metabolism of the root system considerably, which complicates comparison between sterile and non-sterile plants. Nevertheless, it is evident that the rhizosphere is the scene of considerable metabolic activity giving rise to locally high concentrations of carbon dioxide and low concentrations of oxygen. That the rhizosphere in permanent grasslands is the main site of respiratory activities in the soil is also indicated by data of WOLDENDORP (1963), who found that in grassland about 90 per cent of the total soil respiration was due to the living root system.

3.2. QUALITATIVE ASPECTS

In the study of the composition of root excretions, it is essential to avoid not only modification of these compounds by microorganisms but also their contamination by either leached or volatilized products from the aerial parts or root-decomposition products. Consequently, most investigations have been carried out in axenic plants grown in water or in sand. In such studies many different water-soluble compounds were found to be excreted. As an example, compounds reported in the literature on axenic wheat roots are cited in Table 7. Many of these compounds are involved in the normal metabolism of the plant, but many of the secondary metabolic products could also be detected in

small amounts in the medium in which axenic roots were grown. Among these products are phenols and terpenes, which are toxic to bacteria, as well as compounds which inhibit or stimulate the growth of fungi and compounds which are inhibitors or attractants of nematodes. Furthermore, compounds supplied to the leaves, such as herbicides (see HALE *et al.* 1971), were found to be excreted in the root medium. For instance, an inhibitor of nematodes isolated from the rhizosphere of *Asparagus* was found to inhibit nematodes in the rhizosphere of tomato plants (ROHDE & JENKINS 1958) when applied to their leaves.

TABLE 7. *Compounds excreted by axenic wheat roots*

Volatile compounds	Low-molecular compounds	High-molecular compounds
CO_2	Sugars (10)	Polysaccharides
Ethanol	Amino acids (27)	Enzymes
Isobutanol	Vitamines (10)	
Isoamylalcohol	Organic acids (11)	
Acetoin	Nucleotides (4)	
Isobutyric acid		

The polysaccharides (Table 7) isolated from the rhizosphere are thought to originate from the mucigel formed by the Golgi apparatus of the plant cells. The composition of the mucigel resembles that of the sugars and uronic acids of the cell wall (BURKE *et al.* 1974). In this respect there are considerable differences between monocotyles, dicotyles, and gymnosperms. Among the enzymes found in the rhizosphere, the plant origin of peroxidase, nuclease, and invertase has been established (COLLET 1975). Other enzymes, e.g. urease, ATPase, and phosphohydrolases, are not excreted but are localized close to the root surface.

From the published work done in sterile root systems it is difficult to establish essential differences between plant species. This is due to the divergence between the conditions of cultivation, the age of the plants and the methods of analysis used by the various investigators. As SCHROTH & HILDEBRANDT (1964) showed, four investigators who studied the excretion of amino acids by oats obtained completely different results.

Only in a limited number of cases have specific differences in the nature and quantities of the excreted compounds been definitely established. A number of investigators have shown that legumes in general excrete higher amounts and relatively more nitrogenous compounds than other plant species (VANCURA & HANZLIKOVA 1972), and a comparative study on varieties of rice which were

either resistant or susceptible to root disease showed quantitative and qualitative differences in excreted products (MACRAE & CASTRO 1967).

Under non-sterile conditions it is even more difficult to establish the specific nature of the excreted products. Not only are the quantities altered by microorganisms but their composition is modified as well. In non-sterile plants MARTIN (1971) found that 45 per cent of the water-soluble compounds had a molecular weight higher than 10,000 and 75 per cent higher than 1,000, whereas the compounds excreted by axenic roots were of low molecular weight. Moreover, the extent and the composition of the mucigel is influenced by microorganisms.

Some evidence that different plant species have a specific rhizosphere has been obtained by analysis of their microflora. It was found by NEAL *et al.* (1970, 1973) that about 20 per cent of the bacteria in the rhizosphere of the resistant wheat variety *Apex* were antagonistic to the root-rot fungus *Cochliobolus sativus* (Table 8).

TABLE 8. *Microorganisms in the rhizosphere of one susceptible and two root-rot resistant varieties of wheat* (NEAL *et al.* 1970)

Variety	Bacteria ($x10^6$)	Fungi ($x10^3$)	Root-rot antagonists (%)
Apex, resistant	251.5	352.9	20
S-616, susceptible	576.8	123.7	0
S-A5B*, resistant	266.5	81.5	19
Non-rhizosphere soil	44.9	119.5	7

* susceptile variety S-615 on which resistance was conferred by substitution of *Apex* chromosome 5B

In the rhizosphere of the susceptible variety S 615 such antagonistic bacteria were absent. However, when resistance was conferred on the susceptible variety by substitution of the *Apex* resistance chromosome, 20 per cent of the bacteria in the rhizosphere became antagonistic to the plant disease. The composition of the microflora of the susceptible variety differed from that of the resistant ones in other respects too (see Table 8).

Another example of such specific rhizosphere effects was given by COLEY-SMITH & KING (1970), who studied the fungus *Sclerotium cepivorum*. This fungus, which can persist for many years in the soil as sclerotia, is pathogenic only to *Allium* species. Under natural soil conditions, the sclerotia will germinate only in the rhizosphere of *Allium*. Germination was also obtained with root extracts of *Allium* species, whereas extracts of other plant species had no effect. The *Allium* extracts proved to contain antibiotic substances (alkylthiosulphinates). Moreover, it was found that other organic

compounds in sterilized soils also induced germination of the sclerotia. The results were explained by assuming that components of the microflora normally suppress germination in the soil. The *Allium* species excrete antibiotic substances which inhibit these components of the microflora, thus releasing the fungistatic action. But the concentration of the antibiotic compounds responsible for the germination is so low that no effect on the bacteria could be expected. But since no suppression of the bacterial flora in the rhizosphere of *Allium* species has been found either, the excretion of specific antibiotic compounds by the roots of *Allium* species still cannot be considered to have been established beyond doubt. Other examples from the realms of phytopathology point similarly to the plant-specific nature of the rhizosphere, but in no case has it been demonstrated that such differences resulted from specific root excretions rather than from different proportions of the same substances (LOUVET 1975).

It is not clear whether the allelochemicals accumulating in arid regions under vegetations like the chapparal in California or the *Rosmarino-Ericion* in the Mediterranean are excreted by the roots or originate from leaching and volatilization from the aerial parts or from the decomposition of dead plant materials. For instance, the latter have been seen as the source of the cyanide that accumulates in soils under a monoculture of peaches. The compound is thought to be formed by the decomposition of the roots, which can accumulate amygdaline in concentrations up to 6 per cent of their dry weight (JUSTE 1975). The cyanide accumulation prevented replanting of peaches. Many other plant species also contain cyanogenic glucosides that give rise to cyanide, but in soils with a normal moisture level the compound is decomposed, which results in an accumulation of cyanide-resistant or decomposing micro-organisms. For instance, from the rhizosphere of flax a strain of *Bacillus pumilus* was isolated which was extremely resistant to cyanide (STROWZONSKI & STROBEL 1969) and from that of tapioca strains of *Streptomyces* sp. and *Aspergillus* sp. which used HCN as a nitrogen source (SADASIVAM 1974).

The accumulation of cumarine-decomposing microorganisms in the rhizosphere of *Anthoxanthum odoratum* can be similarly explained. Cumarine decomposition in soil must be rather complete, because a suppressing effect of *A. odoratum* on other plant species has not been found.

Other examples of soil fatigue and also the suppression of wheat by poppies or of annual weeds by buckwheat, are in all likelihood to be ascribed likewise to the decomposition of root remains rather than to the excretion of toxic compounds by the living root system. The same explanation may also hold for the effects of legumes on the nitrogen supply of other plant species.

Even though their origin is not definitely established, there is ample chemical evidence that in arid regions compounds toxic to other plant species may accumulate in the soil around plants. In the temperate regions the existence of specific rhizosphere effects is suggested by the composition of

the microflora, but these effects can often be explained in terms of detoxification instead of accumulation of toxic compounds. Much more research is required before it can be concluded that plants influence each other by means of their root excretions and thus contribute to niche differentiation.

3.3. FACTORS AFFECTING EXCRETION

3.3.1. General remarks

The effects of environmental factors on excretions and the rhizosphere microflora have been the subject of many studies recently reviewed by HALE *et al.* (1971), ROVIRA & DAVEY (1974), LESPINAT & BERLIER (1975), and TROLLDENIER (1975). A few comments will suffice here.

It should be noted that the effects of these factors on the composition of the excretions have been studied in experiments with sterile plants in which only the water-soluble compounds were analysed. As has been discussed above (see 3.1.), such studies give an incomplete picture of the real level of excretion. The effects of the environmental factors on the composition of the microflora and on respiration in the rhizosphere by the microflora were investigated with non-sterile plants. But to obtain a correct picture of these effects, studies must be done with both sterile and non-sterile plants.

3.3.2. Plant age and stage of development

In studies on the effect of plant age it has been found (e.g. HAMLEN *et al.* 1972) that the excretions per gram of roots were highest in the first weeks after germination. These studies were all performed with annual crops and the decreasing excretion may be due to the tendency of maturing annuals to transport the assimilates from the leaves to their seeds rather than to the roots. In perennials a different picture is to be expected. In experiments with perennial ryegrass, WOLDENDORP (1963) observed that toward the end of the growing season considerable quantities of nitrogen were transported back to the root system and also to the soil.

With respect to the composition of the microflora, appreciable changes were found to occur during the plant development. Initially, Gram-negative rods predominate but these are gradually replaced by Coryneform bacteria, as shown for instance by the author (Table 9). In experiments with a mixture of pure cultures of an *Arthrobacter* and a *Pseudomonas* strain added to axenic flax plants, a similar replacement was found (WOLDENDORP 1975). This replacement was not necessarily caused by a change in the composition of the excretion products.

A similar replacement was found when the mixture of the two bacteria was cultivated in a dialysis culture continuously supplied with low quantities of mineral salts and glucose. When glutamic acid was used as carbon source, the replacement occurred much more slowly. The results could be explained by

TABLE 9. *The influence of plant age on the proportions of G(-)rods and Coryneforms in the rhizosphere of flax* (WOLDENDORP 1975)

Plant age (weeks)	G(-)rods (%)	Coryneforms (%)	Other microorganisms (%)
1	90	4	6
4	81	14	5
8	60	32	8
12	49	48	3

assuming that initially the roots are colonized by rapidly growing Gram-negative rods. When further increases in the number of microorganisms are impossible because of a shortage of nutrients, the more efficient Coryneforms take over. This hypothesis was confirmed by experiments in which the growth rate and the maintenance requirement of a *Pseudomonas* and a *Arthrobacter* strain were determined (Table 10).

TABLE 10. *The influence of glucose and glutamic acid on the generation time and maintenance requirement of* Pseudomonas *str 64 and* Arthrobacter *str 356*

Strain	Substrate	Generation time (min)	Maintenance requirement (mg/g dr.m./h)
P 64	Glucose	30	12
A 356	Glucose	56	4
P 64	Glutamic acid	21	9
A 356	Glutamic acid	78	7

These results also indicate that the stimulation of Gram-negative rods by amino acids is caused by an increased growth rate and is not due to a specific requirement for these compounds, as suggested by many investigators.

3.3.3. Mineral nutrition

It has been shown that the quantities of excreted products are increased by nutrient deficiencies. COLLINS & RAILLY (1968) found that higher amounts of amino acids and organic acids were excreted when sulphate was replaced by chloride in the culture solution. Similar increases were found by SHAY & HALE (1973) and by EL-KHAB-BASHA & BEKHASI (1973) under calcium deficiency conditions. TROLLDENIER (1971a) observed an increased excretion of amino acids by potassium deficient wheat plants (Table 11).

TABLE 11. *Amino acids and amides (10^{-9} Mole/g root dr. m.) in the rhizosphere of wheat as a function of the K supply* (TROLLDENIER 1971a)

Amino acid	K supply	
	7 meq	28 meq
Alanine	149.3	19.1
Glutamic acid	72.7	5.4
Arginine	56.8	62.8
Proline	53.9	60.8
Glucine	65.2	26.6
Aspartic acid	40.6	18.8
Threonine	31.0	0.0
Asparagine	28.6	0.0
γ-aminobutyric acid	25.2	7.7
Serine	11.4	12.7
Lysine	7.1	4.4
Total	541.8	218.1

Working with non-sterile plants, this author found higher numbers of microorganisms under a potassium shortage, and the contribution of the microorganisms to root respiration increased from 57 per cent in the presence of sufficient potassium to 66 per cent under a deficiency of this element (TROLLDENIER 1971b).

However, the reverse effect has been observed for nitrogen, i.e., the amounts of excreted products increased with increasing levels of this element (see e.g. MACURA 1961). The number of the bacteria and the proportion of Gram-negative rods were also higher the higher the nitrogen level (WOLDENDORP 1963).

3.3.4. Defoliation

According to a number of authors, defoliation stimulates excretion by the root system (VANCURA 1969; MARTIN 1971; HAMLEN *et al.* 1972), but in experiments with perennial ryegrass given labelled nitrogen, WOLDENDORP (1963) and HUNTJENS (1972) found that after defoliation nitrogen was transported to regrown tops and more soil nitrogen was taken up than before. These results point to a decreased excretion of carbonaceous compounds, as will be discussed below (see section 5). The discrepancy might be explained by assuming that in the former experiments part of the root system was killed by the defoliation and then decomposed. Since defoliation by mowing and grazing are important measures in nature management, more insight is needed into the effects on the accumulation of soil organic matter and recycling of nutrients.

3.3.5. Moisture stress

Under conditions of moisture stress, increased excretion has been observed. This occurred particularly in wilting plants (VANCURA 1964; VANCURA & GARCIA 1969; REID 1974). In such dry soils a partial sterilization takes place, which kills off part of the microflora. Remoistening of the soil leads to a rapid regrowth of usually a restricted number of microbial species, which use the accumulated excretion products of the plants and the killed microorganisms as a source of food. This gives rise to a flush in the mineralization of nutrients to which specialized plant species, such as winter annuals, are adapted.

3.3.6. Other factors

The light intensity and the temperature at which plants grow affect the amount and composition of the excreted products. At high light intensities a positive effect was observed, and no decrease occurred during the night (LESPINAT & BERLIER 1974). However, it has been claimed that the production of respiratory carbon dioxide is related to the photoperiod (OSMAN 1971). Under anaerobic conditions, particularly at high CO_2 concentrations in the atmosphere of the rhizosphere, there is also a quantitative and qualitative shift in the excreted compounds (RITTENHOUSE & HALE 1971). When the carbon dioxide level in the atmosphere reached 30 per cent, the roots showed an ethanol content of 300 mg per gram of dry matter (SMUCKER 1971).

3.3.7. Conclusions

From the data presented above it is evident that the quantities and the nature of the root excretions are considerably influenced by environmental factors. These effects do not run parallel with dry matter production. Some of them, for instance wilting, anaerobic conditions, and Ca and K deficiencies, which affect dry-matter production adversely, have a stimulating effect on the excretions, and the same holds for other factors such as a high light intensity or an ample supply of nitrogen, which influence general productivity favourably.

As far as the excretion of primary metabolic products is concerned, our insight into the combined effects of these factors on processes going on in the rhizosphere of non-sterile plants is very incomplete, and nearly nothing is known about plant-specific effects.

4. EFFECTS OF RHIZOSPHERE MICROORGANISMS ON PLANTS

In the foregoing, ways in which living plant roots influence their environment have been discussed. Conversely, the enhanced microbial activity induced by the root excretions affects the growth of the plant in various ways. Due to the inhomogeneity of the rhizosphere, particularly in the rhizoplane, some of these effects occur very locally.

The growth and morphology of the root system are considerably changed by microorganisms. Generally, the root length was found to be decreased by the microflora, the roots being stunted, yellowish-brown, and limp. Sometimes they were more branched and the root hairs better developed (BOWEN & ROVIRA 1961; BLONDEAU 1970; DARBYSHIRE & GREAVES 1970). Other investigators, however, observed increased root growth under non-sterile conditions (MILLER & CHAN 1970).

When pure cultures of microorganisms or extracts of such cultures were added to sterile plants, conflicting results were also obtained. SOBIEZCZANSKI (1966) divided his collection of rhizosphere bacteria into three groups: strains without an effect on root growth, strains which stimulated root growth, and strains which inhibited root growth.

Although it is not yet possible to reconcile these conflicting results, two aspects may play a role here. Firstly, stimulation under non-sterile conditions was found mainly when the plants were cultivated in sterilized soil which had been inoculated with a soil suspension. In such experiments the sterilization procedure may have led to increased mineralization of nutrients. Secondly, inhibition or stimulation by the same compounds is often a question of concentration, which was not known in these experiments. Furthermore, stimulatory and inhibitory substances may cancel each other's effects. In any case, it is clear that the rhizosphere microflora has a marked influence on the growth and development of the root system and thus also on its respiration and nutrient uptake.

The effects of the microflora on the morphology of the root system are probably to be ascribed to phytohormones such as auxins, gibberellins, and cytokinins. Many species of microorganisms produce such compounds in pure culture (for a review, see BLONDEAU 1975), but the quantities formed under normal soil conditions are unknown. Therefore, this subject will not be discussed here.

Other effects of the rhizosphere microflora on plant growth, such as protection against pathogens, detoxification of secondary plant metabolites, and effects on the rhizosphere atmosphere, have already been referred to above (see 3.1. and 3.2.). The profound effects of the microorganisms on the availability of nutrients will be treated below in more detail.

5. EFFECTS OF THE RHIZOSPHERE MICROFLORA ON THE AVAILABILITY OF NITROGEN

5.1. GENERAL REMARKS

Apart from small inputs by rain and electrical discharge, the plants of natural vegetations are completely dependent on the activities of micro-organisms for their nitrogen supply. The microorganisms provide the plants with nitrogen by the fixation of atmospheric nitrogen and the mineralization of organic nitrogenous compounds. In the various steps of the nitrogen cycle (Fig. 1), bacteria in particular play a major role.

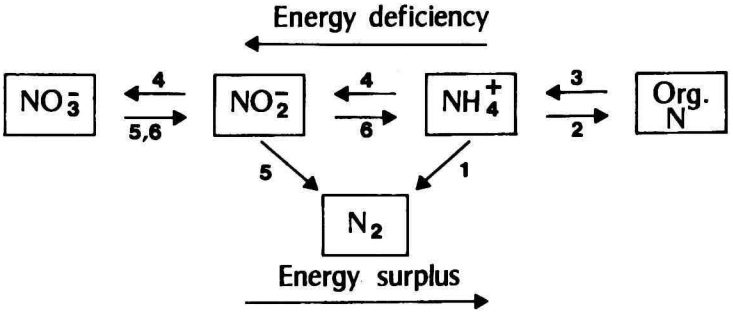

FIG. 1. *Schematic representation of the nitrogen cycle*

1. *Nitrogen fixation*
2. *Ammonium immobilization*
3. *Nitrogen mineralization*
4. *Nitrification*
5. *Denitrification*
6. *Nitrate assimilation*

This cyclic chain of nitrogen transformations is kept going by the continuous input of solar energy (MOROWITZ 1966, WOLDENDORP 1975). This means that the nitrogen cycle is closely related to the carbon cycle.

When sufficient energy is available in the form of organic compounds, the energy-demanding steps of the nitrogen cycle predominate (i.e., nitrogen fixation, nitrogen assimilation, denitrification); consequently, nitrogen is found in a reduced state, i.e. as organic nitrogen. In the absence of energy, nitrification is the predominant process, which leads to the most oxidized state of nitrogen, viz. nitrate.

Form the foregoing it is clear that the state in which nitrogen occurs in the soil is to a high degree determined by the presence or absence of organic carbon. Therefore, plants have a profound influence on the nitrogen transformations in the soil, because they provide carbonaceous matter. Under those natural conditions where nitrogen and not photosynthesis is the limiting factor in the productivity of plants, immobilization prevails and

nitrogen remains predominantly in the reduced state. The conditions for the fixation of atmospheric nitrogen are in principle likewise favourable, but nitrogen-fixing microorganisms have to compete with other microorganisms for the organic compounds. The process of denitrification will be stimulated when nitrate is present, but because the conditions for nitrification are generally not favourable in natural vegetations, this will usually not be the case. As a rule, plants have to compete with the nitrogen-immobilizing microorganisms for mineralized ammonium to satisfy their nitrogen demand. It should be kept in mind here that due to the inhomogeneity of the rhizosphere, locally nitrogen is not a limiting factor; at such spots, conditions may permit nitrification.

The various nitrogen transformations going on in the rhizosphere will be discussed below in more detail.

5.2. MINERALIZATION AND IMMOBILIZATION OF NITROGEN

It has been found that a constant mineralization of soil-organic nitrogen occurs in all soils. The energy liberated during this breakdown process is used by the microflora to re-immobilize part of the mineralized nitrogen; this continuous mineralization-immobilization cycle has been called nitrogen turnover (JANSSON 1958). A relative shortage of carbonaceous compounds leads to an increase of the total mineral nitrogen, a surplus to a decrease of the total inorganic nitrogen level (ammonium plus nitrate). The existence of nitrogen turnover in the soil can be easily demonstrated by the addition of ^{15}N-labelled ammonium: under all conditions the label will be incorporated into the organic matter in the soil, as shown in Table 12. In this example 6 mg labelled ammonium was incorporated into soil organic matter after 27 days and, in addition, 3 mg was chemically fixed into clay minerals.

TABLE 12. *Nitrogen turnover after the addition of 30 mg $^{15}NO_3^-$ and 28 mg $^{15}NH_4^+$-N to grassland soil* (WOLDENDORP 1963)

Treatment	Days	NO_3^--N		NH_4^+-N		Organic
		14 + 15 N	15 N	14 + 15 N	15 N	15 N
Control	0	0	0	3	0	0
"	27	63	0	9	0	0
NH_4^+-N	0	0	0	30	27	3
"	27	73	10	18	9	9
NO_3^--N	0	30	30	3	0	0
"	27	92	29	9	0.5	0.5

However, hardly any of the added nitrate was immobilized. This is due to the preference of microorganisms for ammonium over nitrate in the immobilization process. Therefore, nitrate immobilization will occur only when sufficient ammonium nitrogen is not available. It is also clear that the process of nitrification (which requires the presence of ammonium) will not occur simultaneously with nitrate immobilization.

Studies with labelled nitrogen have shown that only part of the organic nitrogen (about 5-10 per cent) is involved in nitrogen turnover (JANSSON 1958), the rest forming a passive pool (Fig. 2).

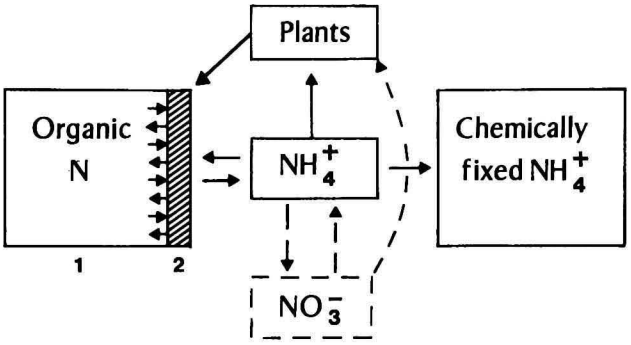

FIG. 2. *Nitrogen turnover in soil and competition for ammonium between immobilization, nitrification, and plants. 1= Passive organic nitrogen pool, 2= Active organic nitrogen pool*

The small active nitrogen pool proved to consist of the soil microflora and their direct decomposition products. The equilibrium in the microflora is easily disturbed, which results in the death of some species and their replacement by others. Such disturbances as mixing of a grassland soil by ploughing or activity of animals (e.g. moles), cutting of trees, changes in pH (lime), drying and remoistening, and changes from anaerobic to aerobic conditions, result in considerable flushes of nitrogen. These flushes are ecologically very important, and plant species such as biennials and winter annuals are specially adapted to them.

Plants have to compete with heterotrophic microorganisms for the mineralized ammonium (Fig. 2). From the above considerations it can be concluded that the extent of the turnover cycle rather than its net result governs nitrogen uptake by plants.

In most vegetations where plant growth is not limited by a lack of moisture, there is a surplus of carbonaceous matter. RICHARDSON (1938), who studied the availability of nitrogen in grassland soils, invariably found low levels of mineral nitrogen. According to WOLDENDORP (1963), even these low levels are artefacts resulting from analytical errors. HUNTJENS (1972), who made an extensive study of the availability of mineral nitrogen in grassland soils,

has shown that a gradual accumulation of organic nitrogen takes place under the influence of the living root system. It was indeed the living root system that suppressed mineralization, because killing of the grass resulted in a rapid nitrogen mineralization.

Under a permanent cover of plants, therefore, ammonium will be the principal source of nitrogen to plants. It is only on partially bare soils, after a spell of dry weather or some other disturbance of the equilibrium in the microflora, that mineralization may exceed the demands of the microflora and plants, and nitrification can take place. In this respect the present author agrees with Jansson (1958), who considered the nitrate fraction in soil as a storage pool formed by the surplus nitrogen not used in immobilization, uptake by plants, or chemical fixation.

5.3. NITRIFICATION

In the foregoing it has been shown that in vegetations where productivity is limited by the nitrogen supply, nitrification is of minor importance. Since the 1938 publication of RICHARDSON, who found no nitrate in unfertilized grassland, nitrification in the vicinity of plant roots has been the subject of many studies. A number of investigators also came to the conclusion that the absence of nitrification in grassland and forest soils is due to the unavailability of ammonium for the process, because of the predominance of ammonium immobilization and plant uptake (see e.g. GORING & CLARK 1948; PURCHASE 1974).

However, in 1951 THERON advanced another theory. This author ascribed the suppression of nitrification in the vicinity of roots to a toxic effect of root excretions. This hypothesis, which has been investigated by a number of authors (MUNRO 1966a, b; NEAL 1969; RICE 1974; MOORE & WAID 1971), is consistent with the susceptibility of the chemolithotrophic nitrifiers to organic compounds. Plant species of climax ecosystems were thought to inhibit the nitrification more than those of pioneer vegetations. According to RICE (1974), the suppression of nitrification should have a selective advantage for the plant, because nitrogen losses by the leaching of nitrate are avoided and no energy is necessary for the reduction of nitrate to ammonia in the plant. Therefore, by using ammonium instead of nitrate, species of climax ecosystems can reach a higher efficiency of nitrogen utilization than pioneer plants. It has been shown that plant roots indeed contain compounds -such as phenols, terpenes, and alkaloids- which are toxic to nitrifying bacteria.

Although the hypothesis that plants of climax vegetations suppress nitrification by means of toxic compounds is attractive, the evidence put forward to support it is not completely convincing. There is no proof that under natural conditions the toxic compounds in the rhizosphere reach levels at which nitrification is suppressed. The results of experiments in which the

process was inhibited by root extracts or leachates which were obtained under non-sterile conditions and whose composition was insufficiently characterized, cannot be considered conclusive evidence. Furthermore, certain facts are not in accordance with the theory. For instance, NAKOS (1975) found that nitrification could not be restored by leaching of the soil and the addition of nitrifying bacteria. However, nitrification started immediately after the removal of grasses or trees (WOLDENDORP 1963; BRAR & GIDDENS 1968; HUNTJENS 1972). In some grassland soils which normally showed no nitrification, the process was found to occur when rain followed a prolonged dry period.

Most of the advocates of the suppression of nitrification by toxic compounds do not mention the fact that THERON, who formulated the theory, withdrew it in 1963 in favour of the immobilization explanation. In the present state of our knowledge, the low rates of nitrification in the vicinity of plant roots must still be ascribed at least partially to the absence of ammonium.

A good qualitative impression of the process of nitrification can be obtained by counting nitrifying bacteria, since these organisms are dependent on the oxidation of inorganic nitrogen. Rhizosphere counts have given conflicting results. For the rhizosphere of wheat, for example, lower (KATZNELSON *et al.* 1956), similar (MOLINA & ROVIRA 1963), and higher RIVIÈRE 1960) numbers of nitrifying organisms as compared with those in non-rhizosphere soil have been reported. Plants of different ages had different effects on nitrifiers (ROVIRA 1965). In the presence of mature plants, low numbers of nitrifying organisms were generally found. This was also the case for permanent grassland soils (ROBINSON 1963; MEIKLEJOHN 1968).

It should be kept in mind that the absence of nitrate in the rhizosphere is not necessarily an indication of the absence of nitrification. Nitrate has been found in grasstops even though the compound could not be detected in the soil (VAN BURG 1962).

In conclusion it can be stated that several different approaches are required for the study of nitrate supply to plants in natural vegetations. Such investigations should include simultaneous determination of the number of nitrifying bacteria, the rate of formation of nitrate after the removal of the living plants, the accumulation of nitrate inside the plants, and the level of nitrate reductase in various parts of the plants.

5.4. DENITRIFICATION

The denitrification process is performed by bacteria that use nitrate instead of oxygen as a terminal electron acceptor. In this process, which can only occur under anaerobic conditions, nitrate is reduced to gaseous nitrogen and nitrous oxide. For the occurrence of denitrification in the soil, which has been discussed in detail by WOLDENDORP (1968, 1975), two conditions must be

met, viz. a low level of oxygen in the soil solution and the presence of hydrogen donors, in the form of organic compounds, to reduce the nitrate. In soils without a cover of plants, denitrification occurs only under more or less waterlogged conditions. But in the rhizosphere these two prerequisites are at least partially fulfilled under soil conditions which are considered to be well aerated.

When labelled nitrate was applied to sods of permanent grassland, 10 to 20 per cent was lost by denitrification (Table 13).

TABLE 13. *Denitrification losses after the addition of labelled nitrate to grassland sods* (WOLDENDORP 1963)

Soil type	Herbage	Roots	Soil	Loss
Sandy soil	65%	10%	10%	15%
Clay	57%	11%	7%	25%
Peat	57%	2%	22%	19%

Sods with killed root systems showed much lower losses, thus demonstrating the influence of the living root system on the process (WOLDENDORP 1963). These results were fully confirmed by Australian investigators (STEVENSON 1972, 1973).

The utilization of root excretions in the denitrification process was shown in experiments in which nitrate was supplied to perennial ryegrass and peas planted in soil devoid of organic matter (WOLDENDORP 1963). The rate of the process was influenced by the age and species of the plants. Root excretions from pea plants led to a higher denitrification rate than those from grass plants. This difference was traced to the excretion of relatively more amino acids by the legume.

In the above-mentioned experiments external nitrate was added to the soil. As mentioned under 5.3., in many natural vegetations little if any nitrate is formed. This raises the question of whether denitrification is an important process in such vegetations. To the best of the author's knowledge, there are no publications that deal with this question adequately, but the experiments performed by NOMMIK (1961) may offer an indirect answer. This author grew oats in soils containing different amounts of straw and labelled nitrate. When straw was added, a rapid immobilization of nitrate occurred. Subsequently, the nitrogen was partly remineralized and taken up by the oats. Treatments without added organic material led to a deficit in the nitrogen balance amounting to between 10 and 20 per cent. This result can be explained by assuming that nitrogen mineralized from soil organic matter is not lost by volatilization in the rhizosphere. This nitrogen was probably taken up by the plant in the ammonium form.

In the present author's opinion, the tentative conclusion to be drawn is that due to a low nitrification rate and nitrogen uptake by the plant in the form of ammonium, losses by denitrification are of minor importance in natural vegetations. On the other hand, there is no reason to suppose that any nitrate formed in the soil would behave differently than added nitrate. Therefore, denitrification losses could occur.

5.5. NITROGEN FIXATION

Under natural vegetations considerable stores of organic nitrogen often occur. It has been claimed that these stores derive partially from the fixation of atmospheric nitrogen by microorganisms. Such fixation processes are said to occur particularly in the tropics. Similar gains in organic soil nitrogen were also observed in vegetations which were virtually devoid of leguminous plants. MOORE (1966), who discussed the older literature on the subject, concluded that short-term field trials are too inaccurate to permit any conclusions concerning gains due to nitrogen fixation. Since lysimeters permit much more accurate nitrogen balances be made, WOLDENDORP (1968) analysed the published data obtained in lysimeter experiments, and found that in planted lysimeters receiving no nitrogen or only small amounts, small nitrogen gains occurred, whereas lysimeters given higher additions of nitrogen showed losses. In more recent experiments the nitrogen-fixing capacity of soils was investigated with the $^{15}N_2$ and acetylene reduction techniques. The results show that only gains amounting at most to 10-20 kg N per hectare per year occurred unless an additional carbon source was supplied (CLARK & PAUL 1970). BALANDREAU (1975) too found similar gains under field conditions (Table 14).

TABLE 14. *Nitrogen fixation under field conditions* (BALANDREAU 1975)

Plant cover	N gains (kg/ha/year)
Savanna (Africa)	10
Rice, wet (Africa)	30
Maize (France)	1-3.5
Lolium perenne	6.3
Dactylis glomerata	5.6
Festuca elatior	5.0

Only in rice on waterlogged soils were higher values found. Low values (1-3 kg) were found for nitrogen fixation in the temperate regions also by KAPUSTKA & RICE (1976). In dune vegetations nitrogen fixation contributed only a few kilograms to the nutrition of *Ammophila arenaria* (ABDEL WAHAB 1969).

Nitrogen gains have been ascribed to fixation by free-living, nitrogen--fixing bacteria in the rhizosphere, which use plant excretion products as a source of reduction power. In the rhizosphere of a number of grasses, especially C_4-species, nitrogenase activity was found (DOMMERGUES *et al.*1973; DÖBEREINER *et al.* 1972; DAY *et al.* 1975; DAY & DÖBEREINER 1976; DE-POLLI *et al.* 1977). Particularly the rhizosphere of Bahia grass (*Paspalum notatum*) showed high values, which were ascribed to the presence of the free-living nitrogen fixer *Azotobacter paspali*, which so far has only been isolated from the rhizosphere of Bahia grass. *Spirillum lipoforum* was isolated from the rhizospheres of *Digitaria decumbens* and maize.

The high value of 90 kg per hectare initially recorded by DÖBEREINER *et al.* (1972) could not be substantiated in subsequent work and is possibly to be ascribed to the long preincubation of their samples. At two recent symposia (Salamanca 1976, Uppsala 1976) the problem of nitrogen fixation in the rhizosphere was discussed in detail. It seems possible that nitrogen fixation may only be of quantitative importance for plants grown in waterlogged soil, for instance rice, *Juncus balticus*, and *Agrostis tenuis* (BALANDREAU 1975; TJEPKEMA & EVANS 1976).

5.6. CONCLUSIONS

As shown in the foregoing, under a cover of vegetation the carbonaceous compounds provided by the plants have a conservational effect on the nitrogen contained in the system. Mineralized ammonium is either re-immobilized or taken up by the plants. Nitrification is often limited, and is usually induced by a disturbance of the soil ecosystem. Small increases in the total nitrogen content of the plant-soil system may result from fixation of atmospheric nitrogen.

6. EFFECTS OF THE RHIZOSPHERE MICROFLORA ON THE AVAILABILITY OF PHOSPHORUS

In natural vegetations phosphorus is often a limiting factor in plant growth. There is a great deal of similarity between the phosphorous and nitrogen transformations in the rhizosphere section. As shown above under the influence of the living root system there is a surplus of carbonaceous compounds in the rhizosphere. The rhizosphere microflora using these compounds immobilizes soluble phosphates in microbial tissue. During phosphate turnover, plants roots have to compete with the microorganisms for the soluble phosphates. Due to the immobilization process, there is a gradual accumulation of organic phosphate in the soil. In established soil profiles more than half of the total phosphorous content is often in the organic form (Table 15), the main components being phytine (myo-inositol-hexaphosphate), glycerophosphates, nucleotides, and nucleic acids.

TABLE 15. *Phosphorus in components of a native grassland ecosystem (g P/m^2)* (HALM *et al.* 1972)

Green plant material	0.21
Standing dead plant material	0.21
Consumers	< 0.1
Litter	0.07
Roots + rhizomes	1.07
Soil fauna + microorganisms	1.98
Water soluble P	10^{-7}
Organic P	137.5
Inorganic P	153.8

When mineralization occurs, the phosphate may be re-immobilized in new microbial tissue, sorbed by plant roots, or revert to Al-, Fe-, or Ca-bound inorganic phosphates of varying solubility.

In grassland soils the organic-phosphorus fraction plays a vital role in the phosphorus supply of the plants (HALM *et al.* 1972). The organic compounds are hydrolysed by phosphatehydrolases originating from the rhizosphere bacteria, the mycorrhizas, and the plant roots. The role of each of these in the decomposition of organic phosphorus has yet not been established (see also the paper by Mosse in this volume). In this respect it has been claimed that organic phosphates such as phytine and lecithins are taken up directly by the root system (ROGERS *et al.* 1940; MARTIN 1973). It is the opinion of the present author that much work will have to be done on transformation of organic phosphorus in the rhizosphere before a more complete picture can be obtained.

Since GERRETSEN (1948) found that non-sterile plants take up more phosphate from insoluble rock phosphates than do sterile plants, the influence of rhizosphere organisms other than mycorrhiza on the solubilization process has been the subject of many investigations. Although GERRETSEN's original findings could not be confirmed, a number of investigators found an increase in the rhizosphere or organisms which dissolved insoluble phosphates in laboratory studies (KATZNELSON 1962). This result may have been due to the production of 2-ketogluconic acid by the bacteria. This compound, which is a chelating agent of Fe^{3+} and Ca^{2+} ions, is accumulated by Gram-negative rods, e.g. *Pseudomonas* species, during the breakdown of glucose via the Entner-Doudoroff pathway. Other compounds produced by fungi such as citric acid, are also chelating agents of Ca, Fe and Al, and thus may contribute to the solubilization of the phosphate salts of these ions. However, there is no indication that these compounds are produced by the organisms in question under rhizosphere conditions. The claims that H_2S and CO_2 affect the

solubilization of rock phosphates in the rhizosphere could not be substantiated either.

The role played by the rhizosphere microflora in the uptake of soluble phosphate has been controversial too. BARBER and co-workers (see e.g. BARBER 1974) demonstrated trapping of phosphate by rhizosphere microorganisms. At low external phosphate concentrations in water culture the effect was of practical significance, because less phosphate was available to the plants. Since significant trapping occurred at concentrations of up to 3×10^{-5} M phosphate, the trapping process was considered to be of ecological significance. However, EPSTEIN (1972) found that Barber's conclusions had to be rejected. It should be noted that Barber's results are fully explained by the phosphorus turnover cycle in the soil, which leads to its immobilization. On the other hand, it seems likely that the phosphorous incorporated into the microorganisms is relatively more available to the plant than Ca, Fe, and Al phosphate or rock phosphate.

Therefore, in the present author's opinion, many aspects of the role of the rhizosphere microflora in the phosphorous supply of the plant are still obscure and no definite conclusions can be drawn.

7. GENERAL CONCLUSIONS

It is clear from the foregoing that plant species rarely change the surroundings of their root system to such an extent that the growth of other plant species is influenced. There is no direct proof that different species excrete different compounds under field conditions. Nevertheless, it has been shown that the rhizosphere microflora may react in a specific way, particularly as regards the occurrence of phytopathogens. This specific microflora often seems to be involved in the decomposition of specific secondary plant metabolites. Only when the rate of this decomposition process is too low, which can occur in arid regions or after abrupt killing of plants (e.g. by ploughing), may toxic compounds affect the germination or growth of other species. Future research will undoubtedly provide more examples of specific processes going on in the rhizosphere. Nevertheless, it seems unlikely that these processes will be found to contribute to the process of niche differentiation.

The rhizosphere microflora has a profound influence on the availability of nutrients. At low nutrient levels, considerable amounts are immobilized into soil organic matter by the microflora for which root excretions serve as a carbon source. In natural vegetations, plants are dependent on the activities of microorganisms for their nitrogen en phosphorous supply. Consequently, these activities must be included in investigations on the availability of nutrients to plants.

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9. DISCUSSION

WENT (Nevada): You mentioned that often in grassland soils hardly any nitrification occurs. Is it also suppressed in forest soils?

WOLDENDORP: According to the literature, nitrification is often suppressed in forest soils, too. Chemolitholiophic nitrifying bacteria, which are an indication for the occurrence of the process, are usually found in low numbers. But in my opinion, root distribution, which is related to the suppression of nitrification, is much more inhomogeneous in forest soils than in grassland soils. Therefore, in forest soils the conditions for microbial activity may vary from point to point more than they do in grassland soils. Also, when animals such as beetles die in the soil there is a flush of ammonia during the decomposition of the proteinaceous compounds. This temporary presence of ammonia may give rise to a local flush in nitrification.

MINDERMAN (Arnhem): I have always found some nitrate formation in oak-forest soils, but I expect it to be absent in the acid pine forest soils of The Netherlands.

LOSSAINT (Montpellier): What is your opinion on the inhibition of nitrification in climax vegetations?

WOLDENDORP: The evidence put forward to prove the inhibition of nitrification in climax vegetations is in my opinion not very convincing. Most investigators have worked with extracts or leachates of plants of climax vegetations and found inhibition of nitrification. It is well known that the nitrifying bacteria are inhibited by many kinds of organic compounds, for instance by amino acids. Since such compounds were probably present in the leachates, the inhibition is not surprising. But under normal field conditions in the temperate regions, these compounds will be released slowly and are probably decomposed as soon as they are released by the plant. I will not go as far to say that inhibition does not occur, but there is no proof. The absence of nitrification in climax vegetations, which without any doubt has often been found, can equally well be ascribed to the absence of ammonia, because all mineralized ammonia will be re-immobilized immediately when there is a surplus of carbon. The latter is often the case in climax vegetations.

MULDER (Wageningen): Is anything known about the quantities excreted under tropical conditions? Are they higher than in temperate regions? In our laboratory BESSEMS found the quantities excreted in the phyllosphere to be higher in the tropics.

WOLDENDORP: I know of no clearcut evidence which demonstrates that the quantities of the root excretions in the tropics are higher too. For that purpose the same plant species should be compared, and that has not been done under field conditions as far as I know. However, there is some indirect evidence. In laboratory experiments the quantities of root excretions, particularly carbohydrates, were found to be higher at high light intensities. Also, the quantities of atmospheric nitrogen fixed in the rhizosphere, for which excreted carbonaceous compounds are needed, are generally higher in the tropics, as has been shown by BALANDREAU (1975). These findings suggest that in the tropics root excretions are quantitatively more important than in regions with lower light intensities.

MULDER: I agree that the same species should be compared.That is why BESSEMS studied the phyllosphere of maize in Surinam as well as in The Netherlands.

WENT: Are root excretions the sole source of carbohydrates in the soil? In my opinion the fungi may contribute to it too.

WOLDENDORP: Because the fungi are heterotrophic organisms, they are dependent on the plant for their carbon supply. They can only contribute to the carbohydrate level in the soil by the transformation of other compounds, which are derived from the plant. As could be seen in my Table 2, the numbers of fungi are also higher in the rhizosphere than in the non-rhizosphere soil.

ANONYMOUS: Are any unambiguous cases of allelopathy known under temperate conditions?

WOLDENDORP: Such cases are not known to me as far as excretions by viable plant roots are concerned. Under the moist soil conditions of temperate

regions, toxic organic compounds which are gradually released by the plant, are decomposed by the microflora. Only in dry soils can they accumulate to sufficiently high levels. There are some cases of allelopathy in the upper soil levels that are due to leaching from the leaves, e.g. those of walnut trees. And of course the decomposition of dead plant materials can inhibit germination and growth of other plant species. For instance, when grass is resown in ploughed meadows, germination is sometimes very bad because of the accumulation of organic acids (e.g. butyric acid) formed during the decomposition of the plant residues.