

Chemical soil factors determining plant growth*

1. INTRODUCTION

Much has been written about the plant-soil relationship in the context of ion uptake and the transport and utilization of chemicals by plants. These papers emphasize the diversity of soils and the diversity of plants. There are also many other problems, such as the mineral nutrient supply in space and time and the competition, both between and within species, for the elements in the soil. In contrast to other abiotic factors such as light or temperature the chemical situation in soils is complex, if only because of the presence of more than hundred chemical basic elements. This situation is made essentially more complicated by combination of these chemicals and by the organic compounds formed, for instance the humic acids of soils.

If we restrict the problem to the basic elements, we can arrange these chemical elements according to their frequency and their function in plant metabolism (Table 1). The current classification of these elements according to their function into (a) major or macronutrients, (b) minor or micronutrients, and (c) oligo-(trace) elements, reflects a large and small requirement, and no physiological need for these elements by plants, respectively. Whereas all of the classical macronutrients (C, H, O, N, P, S, K, Ca, Mg) are universally required by plants, not all of the micronutrients (Fe, Mn, Cu, Zn, Mo, B, Cl, Na, Si, Co), and especially silica and cobalt, have been shown to be necessary for all plants. For the functioning of ecosystems, the plant also has to supply animals with certain elements which are -at least at times- not required for plant metabolism such as J, F, Se, V, and perhaps Cr (LEE 1975). Another point here is that oligo-elements such as aluminium are sometimes present in the soil in larger amounts than micro- or macronutrients and may influence plant growth and thus plant distribution. The individual plant has only a very small possibility to escape from an environment, in which it has been established by a propagule which means that it must have evolved special adaptations enabling it to endure the quantity and quality of these elements both in space and in time.

With respect to soils, little is known concerning the geochemistry of the elements and the soil factors governing their distribution. In terms of nutrient

* Dedicated to Prof. W. Baumeister

TABLE 1. Frequency of occurrence of the chemical elements in the rock material of the earth's crust (mM), with indication of the macro- (*) and micronutrients (**) for plants and the additional micronutrients (***) for animals

10^3		10^2		10^1		10^0		10^{-1}		10^{-2}	
O	29.5*	K	7.2*	Ti	9.8	S	9.7*	Zn	9.2**	Pb	7.2
Si	10.9**	Ca	7.1*	F	3.8***	Cl	9.3**	B	8.3**	Sm	5.7
Al	2.9	H	6.9*	C	2.7*	Li	4.3	Ni	7.5	Gd	5.6
Na	1.1**	Fe	6.3**	P	2.6*	Ba	4.3	Cu	5.4**	Pr	5.4
		Mg	5.7*	Mn	1.3**	Sr	3.3	Y	3.8	Th	4.7
						V	1.9***	La	3.2	Dy	3.8
						Zr	1.8	Sc	3.1	Br	3.6
						N	1.4*	Ga	2.5	As	2.3
						Rb	1.4	Nb	2.2	Sn	2.5
						Cr	1.3	Be	2.2	Er	2.0
								Nd	2.1	Cs	2.0
								Co	2.0**	Yb	2.0
										Ta	1.9
										Ge	1.8
										Hf	1.7
										U	1.5
										Ho	1.1
										Mo	1.0**
										J	0.4***
										Se	0.1***

reactions, clay forms the most important part of the soil, but its components are so small that only the recent development of X-ray diffraction techniques may make it possible to resolve many of the current problems on nutrient availability (GIESEKING 1975). With respect to the plant-soil relationship, the concept of the availability of nutrients has been prominent in the attempts to measure the amount of available chemical elements in soils by chemical extraction procedures. In the present state of our knowledge concerning the plant-soil relationship, we should deliberately realize that despite all of the possibilities offered by chemical extractions, the availability of nutrients ultimately depends on the properties of the plant. Besides, plants vary greatly in their absorption and excretion activities. Next to the available quantity, the chemical quality of the elements has to be considered. However, our knowledge of some compounds, such as humic substances, is restricted to series of chemical similarity, in this case fulvic acids, humic acids, or hyatomelanic acids (FLAIG *et al.* 1975) and nearly nothing is known about the basic substance

itself. This is hardly surprising because the chemical constitution of these compounds depends on the interaction between various biological pathways and on environmental factors.

Furthermore, there are the allelopathic substances interfering in mineral nutrition. These compounds, which are excreted by plants and are accumulated in the soil, are effective inhibitors of the growth of other plants (WHITTAKER 1970; RICE 1974; QUINN 1974).

These few remarks will suffice to show the impossibility of covering the broad field of the chemical aspects of the plant-soil relationship here. I shall therefore confine the discussion to some of these aspects.

2. HALOPHYTES AND MARITIME SALINE SOILS

The first example of the effect of mineral nutrients on plant growth refers to an environment where the relevant ions are more or less completely available to the plants in large quantities. These ions are chloride and, to a certain degree, sodium and potassium. Many ecological and physiological experiments have been carried out with plants of saline environments (for reviews see: WAISEL 1972; RANWELL 1972; CHAPMAN 1974; REIMOLD & QUEEN 1974; FLOWERS 1975; POLJAKOFF-MAYBER & GALE 1975). But are the interactions of the halophyte with its saline habitat understood? A synthesis of the research done on different biological levels may supply the answer to this question.

I shall focus on one of the halophytes, *Suaeda maritima*, which occurs on salt marshes in Europe. In the field, optimal growth is observed in those places where there is a strong daily fluctuation of the tidal submergence, but the seasonal variations in sodium and chloride content are low (ESSING 1972). In this environment *Suaeda maritima* grows in monoculture, sometimes mingled with *Salicornia europaea*, *Spartina townsendii* and *Puccinellia maritima*. On the middle salt marsh with the plant community *Puccinellietum maritimae* characterized by a great seasonal variation of the salt level, the annual biomass production of *Suaeda maritima* is low, sometimes amounting to no more than 0.01 g dry matter m⁻² (KETNER 1972). The germination capacity to *Suaeda maritima* is the same in both saline and non-saline environments (BINET 1968; BOUCAUD & UNGAR 1976). In physiological experiments, the growth of *Suaeda maritima* is promoted by sodium levels well in excess of amounts needed by non-halophytes (PIGOTT 1969). Comparison of the biomass production of *Suaeda maritima* in the natural habitats with that in sand culture experiments (FLOWERS 1972; YEO 1974) shows a discrepancy between the physiological and the ecological optimum (ELLENBERG 1958). Optimal growth in physiological experiments proves to be confined to lower salt concentrations (Fig. 1). The results of sophisticated experiments such as in-vitro culture of isolated tissues (HEDENSTRÖM & BRECKLE 1974) also indicate a lower tolerance for sodium chloride than is found in the total plant. Last, but not least, at the subcellular level, cytoplasmic enzymes such as nitrate

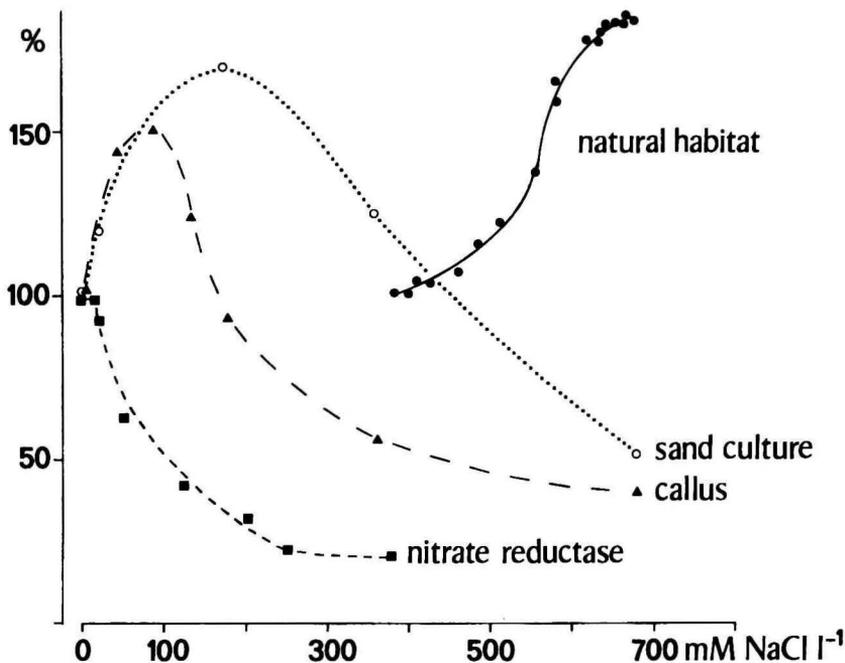


FIG. 1. *Suaeda maritima*. Effect of increasing concentrations of NaCl on the growth of plants in the field (ERNST unpublished) and in sand culture (YEO 1974), on the growth of callus (HEDENSTRÖM & BRECKLE 1974), and on the in-vitro activity of nitrate reductase in leaves (ERNST unpublished). Control values at 0 mM NaCl l⁻¹ are defined as 100%

reductase, which is a key enzyme in nitrogen metabolism, are the least able to tolerate sodium chloride, which is in agreement with the in-vitro behaviour of the enzymes of other halophytes (AUSTENFELD 1974; FLOWERS 1975). The implication of these findings is the assumption that metabolic regulation is necessary for the maintenance of a low level of salt in the cytoplasm; otherwise, salts could disrupt the structure and/or function of enzymes or other macromolecules and thus damage cellular organelles and hamper metabolism. One of the pre-conditions for this regulation is a compartmentation of ions within the cell and possibility for the storage of ions. A form of compartmentation is the selective accumulation of salts in the vacuoles of halophytes. This requires a special mechanism for the arrangement of an osmotic equilibrium between cytoplasm and the vacuoles. The osmotic pressure of the cytoplasm in the cell is found to be generated by an accumulation of proline (STEWART & LEE 1974), glycerol (BEN-AMOTZ & AVRON 1973), or betaine (STOREY & WYN JONES 1975; WYN JONES *et al.* 1977); some of these compounds also play an effective role under various stress conditions such as drought (proline: BARNETT & NAYLOR 1966) or flooding (glycerol: VESTER 1972). What distinguishes halophytes from plants of

non-saline habitats is not the ability to withstand physiological drought, but their ability to regulate selectively ion concentrations. Halophytes, in particular, have to cope with an excess of sodium chloride in their environment that impedes the acquisition of other essential nutrients, for instance potassium.

For this reason, we shall focus here on two of the alkali metals in this environment, i.e. sodium, which seems to govern growth in halophytes (e.g. *Salicornia europaea*, BAUMEISTER & SCHMIDT 1962; and *Aster tripolium*, WEISSENBOCK 1969) and is abundantly available in the salt marsh; and potassium, of which large amounts are required for optimal plant development, but which occurs in small amounts in saline environments. Despite this imbalance, the mechanisms of ion absorption in roots are sufficiently specific to permit the absorption of an ion (potassium) occurring in a low concentration in the presence of an ion (sodium) occurring in a high concentration. This means that in *Suaeda maritima* there is an enrichment of potassium relative to the concentration in the soil solution. In the root of this halophyte the Na/K-ratio is 3.7 as against 22.5 in the soil solution, which suggests a competitive advantage of the potassium uptake mechanism (Table 2). Even in the leaves with sodium

TABLE 2. Concentration of sodium and potassium in the soil solution of a lower salt marsh site (Wadden Sea) in relation to the levels in the cell sap of leaves and in plant organs of *Suaeda maritima*

Factor	Soil solution (mM l ⁻¹)	Cell sap	Enrichment factor	Leaves (mM kg ⁻¹)	Shoots (dry weight)	Roots
Na	607.8	564.0	0.93	4350	1925	2001
K	27.0	58.1	2.15	450	393	537
Na/K-ratio	22.5	9.71		9.67	4.90	3.72

storage in the vacuoles, the Na/K-ratio is lower than in the soil solution, as has been confirmed by results obtained in various European salt marshes (CAPPELLETTI PAGANELLI 1967; ESSING 1972; ALBERT & KINZEL 1973; ALBERT & POPP 1977). Within the plant, the Na/K-ratio is generally higher in the leaves than in the roots indicating a more effective translocation of sodium than of potassium (cf. HALL *et al.* 1974 for *rubidium*). The rate of the potassium uptake (v_{\max} 50.1 \pm 7.9 $\mu\text{M K h}^{-1} \text{g}^{-1}$ fresh weight from a solution with 8-20 mM K l⁻¹) is higher than the rate of sodium uptake (v_{\max} 28.3 \pm 4.7 $\mu\text{M Na h}^{-1} \text{g}^{-1}$ fresh weight from a solution with 100-500 mM Na l⁻¹), but the rate of sodium uptake in halophytes (see FLOWERS 1975) is of the same order as that of glycophytic barley roots (RAINS & EPSTEIN 1967).

To understand halophytes, the function of sodium chloride in their metabolism must be known. Despite the extensive research on these plants, uncertainty prevails. A supply of chloride ions, however not of sodium ions may change the balance between the C_3 and C_4 carbon fixation pathways by regulation of the activity of phosphoenolpyruvate carboxylase, thus stimulating CO_2 -fixation (BEER et al. 1975; TIKU 1976) and reducing transpiration. (Na-K)-activated ATPases may also play a role, but they do not explain a special physiological function of sodium in the metabolism (KYLIN & QUATRANO 1975). This problem can only be solved by applying the ecotype concept developed by TURESSON (1922), according to which the smallest overall difference in basic metabolism is ensured; it cannot be approached comparing peas or beans with halophytes (FLOWERS 1972; AUSTENFELD 1976).

Another unsolved ecological problem is the difference between optimal biomass production of *Suaeda maritima* in the field and in the greenhouse. Extrapolation from fertilization experiments (STEWART et al. 1973) suggests that *Suaeda maritima* demands high amounts of nitrogen which do not occur in the upper zone of salt marshes. The *in vivo* nitrate reductase activity in *Suaeda maritima* was found to be as much as 50 times higher in plants from the lower salt marsh ($5.55 \mu M NO_2 h^{-1} g^{-1}$ fresh weight) than in plants from the upper marsh (STEWART et al. 1972). The sparseness of this species in environments with lower salinity is due to low nitrogen levels, not to the low salinity. Nevertheless, despite strong growth of *Suaeda maritima* at low salinity in the laboratory, the equivalent biomass of the production in the field is not reached. This is due to the omission from the physiological experiment of one of the main environmental factors, i.e. temporary submersion. As shown for *Salicornia europaea* (LANGLOIS 1971), the temporary submersion of shoots induces changes in protein and carbohydrate metabolism and causes perhaps also leaching of salts from the plants. Therefore, physiological and ecological optima may not be compared unless the experimental design is adequate, in this special case also with respect to the supply of boron (BRECKLE 1976), bromine (PEDERSEN et al. 1974), and iodine (FOWDEN 1959). Until more is known, every shift of the ecological optimum above the physiological optimum must be taken to indicate insufficient knowledge of the ecology of the plant and its environment even when it seems to offer a quite simple example of an "extreme" environment (see also the section on the qualitative aspects of mineral elements).

3. OXIDATION STATUS AND THE AVAILABILITY OF NUTRIENTS

For most of the mineral elements under consideration, there is a difference between the total amount in the soil and the amount available to plants. This is the most important complication encountered in the study of the mineral nutrition of plants in the field. One of the factors determining availability

is the oxygen supply in the soil, which is unfavourably affected by an excess of water. Flooding -dependent on its frequency, seasonality, or permanency- displaces air in the soil and permits the development of a reducing system rather than oxidizing conditions. The sequence of events after flooding of a mineral soil is shown in Fig. 2. The first consequence of waterlogging is the

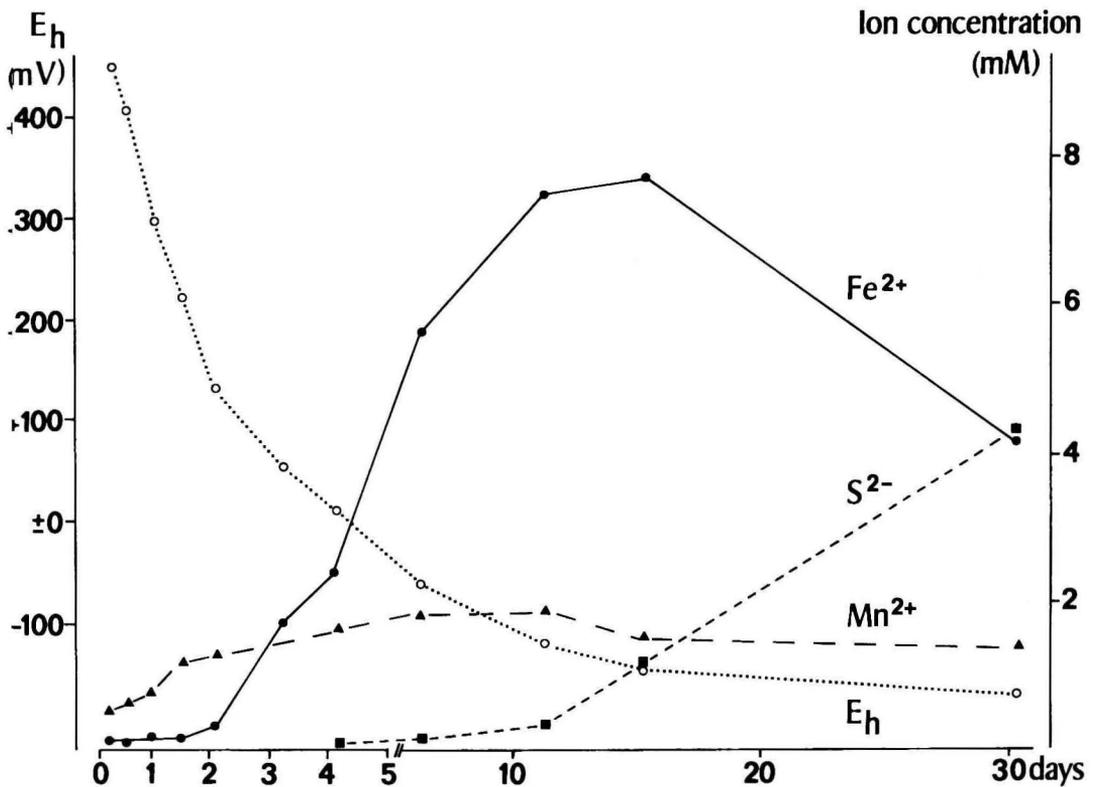


FIG. 2. Redox potential and contents of sulphide and of water soluble and exchangeable ions of Mn^{2+} and Fe^{2+} of a soil, in relation to the saturation time with seawater. (Reproduced in a modified form, with permission, from BRÜMMER 1974)

limited supply of oxygen, which leads certain soil microorganisms to make use of alternative electron acceptors for their respiratory oxidation. Nitrate is the first nutrient to be used as an oxygen source by anaerobic microorganisms (PATRICK & MAHAPATRA 1968). Further lowering of the redox potential causes a reduction of manganese-(IV, III)-oxides to the water-soluble and plant-available manganese-(II)-ions, which occur already within two days of waterlogging. Therefore, frequent fluctuations in the oxygen status of the soil increase the availability of this heavy metal. When the redox potential of the soil decreases to about 150 mV, apart from amorphous iron, iron-(III)-oxides are

reduced to the water-soluble Fe-(II)-ions, which usually does not start until the third of the fifth day of flooding. Persistence of waterlogging conditions causes the reduction of sulphate to soluble sulphides such as S^{2-} , HS^- , or H_2S . These sulphides not only react with the plant-available iron and thus create an iron deficiency, but are considered to be highly toxic to plants and may be responsible for the vegetation differentiation in wet grassland communities (YERLY 1970).

Iron in the ferrous form gives waterlogged soils their black, grey or blueish-green colour, whereas the ferric state is characterized by a brown, red or yellow colour. This colour difference makes it possible for the ecologist to estimate the efficiency of oxygen transport from the shoot via the aerenchyma to the root. If the oxygen loss by diffusion from the roots is sufficiently rapid and the demand for oxygen by the microorganisms in the vicinity of the roots is lower than the diffusion rate, an oxygenated zone will build up around the roots. Waterlogged soils offer an example of how microorganisms create a stress environment and the way in which higher plants can restore the situation, in this case via an efficient aerenchyma. But not all plant species are capable of evolving an efficient oxygen transport system. For an analysis of the impact of waterlogging on plant growth, we will consider a gradient from a dry to a wet environment and limit ourselves to the effects of mineral nutrition. (For the effects of oxygen deficiency, see the paper by BROUWER in this volume).

The effect of waterlogging on plants in a mineral soil over a period of 90 days was investigated by comparing plants with a different tolerance for flooding. Inundation has a tremendous effect on the biomass production of the common weed *Stellaria media* (Table 3); it decreases the growth of *Holcus lanatus* slightly

TABLE 3. Effect of waterlogging on biomass production (mg d.w.) and the iron and manganese content ($\mu M \text{ g}^{-1}$ dry weight) of *Stellaria media* (non-tolerant), *Holcus lanatus* (moderately tolerant), and *Juncus articulatus* (very tolerant)

		<i>Stellaria</i>		<i>Holcus</i>		<i>Juncus</i>	
Biomass	dry*	3,508 ± 448		2,271 ± 105		2,143 ± 251	
	wet	136 ± 59		1,573 ± 97		2,575 ± 526	
		<u>root</u>	<u>shoot</u>	<u>root</u>	<u>shoot</u>	<u>root</u>	<u>shoot</u>
Fe content	dry	12.39	1.46	18.44	1.97	9.67	2.54
	wet	19.46	1.43	27.57	2.86	17.01	2.65
Mn content	dry	1.47	0.86	1.49	0.75	0.38	1.07
	wet	1.49	1.13	1.89	0.69	2.17	3.49

* During the 90 days of the experiment the wet soil conditions were maintained by keeping the water-table at the soil surface and the dry soil was kept at 70% of its field capacity

and stimulates the growth of *Juncus articulatus*. Waterlogged plants of all three species take up more iron from the soil than do plants of the same species in drier conditions. The increase was particularly marked in the roots, as had already been found for other graminoids and herbs (JONES & ETHERINGTON 1970; JONES 1972; ROZEMA & BLOM 1977). The degree to which internal concentrations of these heavy metals affect the metabolism of the plant seems to be dependent on the internal compartmentation, as reported for *Ericaceae* (HENRICHFREISE 1973; BAUMEISTER & ERNST 1978), and remains to be determined for all other species. In our experiment the same total amount of iron and manganese caused toxicity in *Stellaria media* and promoted growth in *Juncus articulatus*.

The liberation of soluble divalent manganese and iron not only determines vegetation differentiation on dunes and dune slacks (JONES 1972) and wetlands, but also regulates the distribution of woodland plants of well-drained microhabitats, for instance *Mercurialis perennis* (iron-sensitive), and those of less well-drained situations, for instance *Primula elatior* (iron-tolerant), as demonstrated by MARTIN (1968).

4. SOIL REACTION AND THE AVAILABILITY OF ALUMINIUM

The emphasis put on pH values in ecological studies is due more to the ease of determination than to the complex correlation of pH values with many interacting mineral elements. Hydrated ions of aluminium, the third most common element in the earth's crust, play an important role in the buffering of soils against excess acidity. In all primary and secondary clay minerals, aluminium is essential for the chemical structure and the exchange capacity of the soil more or less saturated with H^+ , Al^{3+} or hydroxy-aluminium polymers.

As demonstrated by the analysis of twenty-five woodland soils in Germany, exchangeable aluminium tends to increase with increasing hydrogen ion concentrations, i.e. pH values lower than 5, which is in good agreement with the results of experimental studies on this problem (SCHEFFER & SCHACHTSCHABEL 1976). The exchangeable amounts increase from 0.4 mM at pH 6.0 to more than 90 mM $Al\ kg^{-1}$ dry weight at pH 3.0, independent of the total amount of $437 \pm 100\ mM\ kg^{-1}$ (Fig. 3). The same tendency is found for the water soluble fraction. Despite these known chemical aspects of acid soils, few attempts have been made to analyse the effect of aluminium ions on plant growth. Most plants are very susceptible to aluminium, especially those growing on soils with a pH of 5.0 and higher (CLYMO 1962; HACKETT 1965; CLARKSON 1966, 1969; HENRICHFREISE 1976). The growth of roots particularly is affected, since aluminium interferes with DNA synthesis (SAMPSON *et al.* 1965). These results have been confirmed by the comparison of two populations of *Agrostis tenuis*, one collected from an acid (pH 3.2) and the other from an alkaline site (pH 7.2). Plant growth was strongly reduced by aluminium in the alkaline population, but was only weakly decreased in the acid population. These results suggest that in soils with lower pH

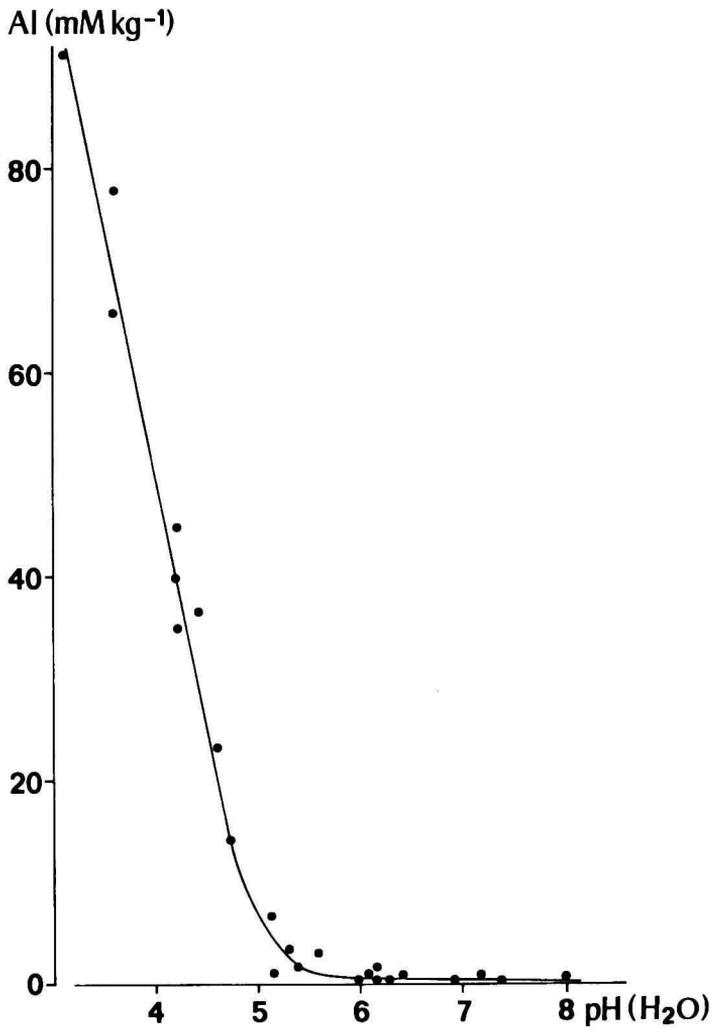


FIG. 3. Relationship between pH (H₂O) and the (NH₄-oxalic acid)-extractable amount of aluminium ions of woodland soils in northern Germany. The total amount of aluminium is $437 \pm 100 \text{ mM kg}^{-1}$ dry weight

values aluminium will form a barrier to the colonization by plants originating from neutral or alkaline habitats. But even within species of acid sites there seems to be a dramatic differentiation in the sensitivity to aluminium (HENRICHFREISE 1976; GRIME & HODGSON 1969).

The ecological importance of pH values is often exaggerated. Other basic soil factors are of greater importance than the hydrogen ions. This may be illustrated by data on *Deschampsia flexuosa*. According to ELLENBERG (1958) this plant has its ecological optimum in the vicinity of its physiological minimum. However, GIGON & RORISON (1972) found good indications that a physiological optimum of

pH 7.2 can only be achieved by supplying nitrogen as ammonia, not as nitrate. Under natural conditions, ammonium ions are not present at this pH (DIERSCHKE 1974), which means that the growth optimum of this species depends not on pH values but on the oxidation status of nitrogen. Furthermore, *Deschampsia flexuosa* has a high demand for iron, but at high pH values there is a decrease in availability of this metal (HENRICHFREISE 1976).

5. COMPLEXATION OF METALS AND PLANT GROWTH

Susceptibility of plants to high concentrations of heavy metals in the soil is a question not only of quantity, but also of quality. The availability of heavy metal cations is influenced in characteristic ways by the soil environment. Under acid conditions these cations have the highest solubility and are most available to plants. If they are tightly bound or fixed to silicate clays they are unavailable. On soils containing organic matter, organic ligands may form stable complexes (chelates) with metal ions. Plants growing on heavy metal rich soils are more or less specifically tolerant to the particular heavy metal predominating in the habitat of the plant to which they belong (for reviews see ANTONOVICS *et al.* 1971; ERNST 1974, 1976; and PROCTOR & WOODSELL 1975). But as in halophytes, there seems to be a discrepancy between the ecological and the physiological growth optima with respect to the metal concentration (Fig. 4). *Silene cucubalus*, one of the prominent species in such habitats, appears to tolerate up to 21.1 mM water-soluble zinc in its habitat, whereas in water culture the plant can only tolerate up to 2 mM ZnSO₄ with a growth optimum at 0.8 mM Zn (BAUMEISTER 1954; ERNST 1974). In contrast, cell tissues of shoots and leaves are zinc resistant up to 200 mM Zn (GRIES 1966), whereas the enzyme nitrate reductase only tolerates 0.0015 mM Zn *in-vitro* (ERNST *et al.* 1974; MATHYS 1975), which indicates a strong compartmentation within the cells. This situation is complicated by the different responses of ecotypes from normal and zinc-enriched environments; the non-tolerant populations have optimum growth at concentrations, where the zinc-tolerant populations grow under suboptimal conditions. The low zinc efficiency of zinc-tolerant plants is not associated with a lower uptake of this element -as is the case for differences in iron efficiency (BROWN *et al.* 1971)- but it is related to internal competition between zinc complexation (followed by transport to the vacuole system) and the zinc-stimulated enzymes (ERNST 1976). Non-tolerant plants lacking this tolerance mechanism have a higher zinc efficiency and show better growth at low zinc concentrations, but have a lower zinc resistance than tolerant plants.

Let us restrict the problem to the occurrence of tolerant populations of *Silene cucubalus* in the field and their growth in the laboratory. A careful analysis of the water-soluble zinc in the soil revealed the impact of complexation. Dependent on the organic status of the soil from 27.6 up to 100 per cent of the zinc was organically complexed (ERNST 1974). In the water culture experiments

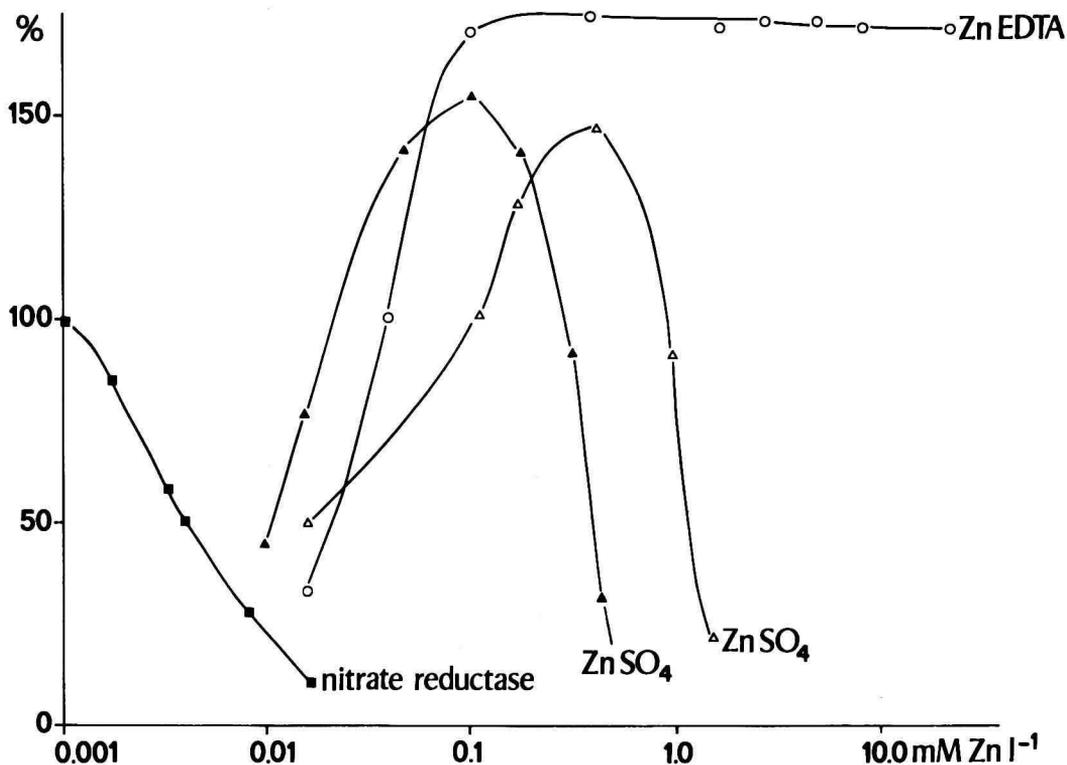


FIG. 4. *Silene cucubalus*: effect of increasing concentrations of zinc on the in-vitro activity of nitrate reductase (ERNST et al. 1974) and on the growth of zinc-tolerant (open symbols) and non-tolerant (solid symbols) plants in the presence of ionic and complexed zinc (ERNST 1968, 1974, and unpublished). Control values of the optimum of activity and growth of a non-tolerant population at 0.03 mM Zn are defined as 100%

with zinc in the ionic and the complexed form as Zn-EDTA - EDTA is one of the best known chelating agents and has been applied to soils as an extractant of heavy metals (LINDSAY 1972) - no growth reduction was found up to 9.2 mM Zn in the presence of the metal bridge complex (ERNST 1968). This indicates that there is no difference between the physiological and ecological optima.

So far, most experiments with complexing agents have been carried out with artificial complexes such as EDTA (aluminum-EDTA: BARLETT & RIEGO 1972; iron-EDTA: BROWN & AMBLER 1974; manganese-EDTA: HENRICHFREISE 1976), all of which reduce the toxicity of the element. To approximate the natural situation we carried out some experiments with natural complexes, such as fulvic and humic acids for comparison with the artificial compounds (FRANCKE 1976; FIT 1977). The first results obtained with the natural compounds (Fig. 5) indicate that metal complexes with fulvic acid have the same or even more negative effects on plant growth than metals in the ionic state. However, the effect of humic

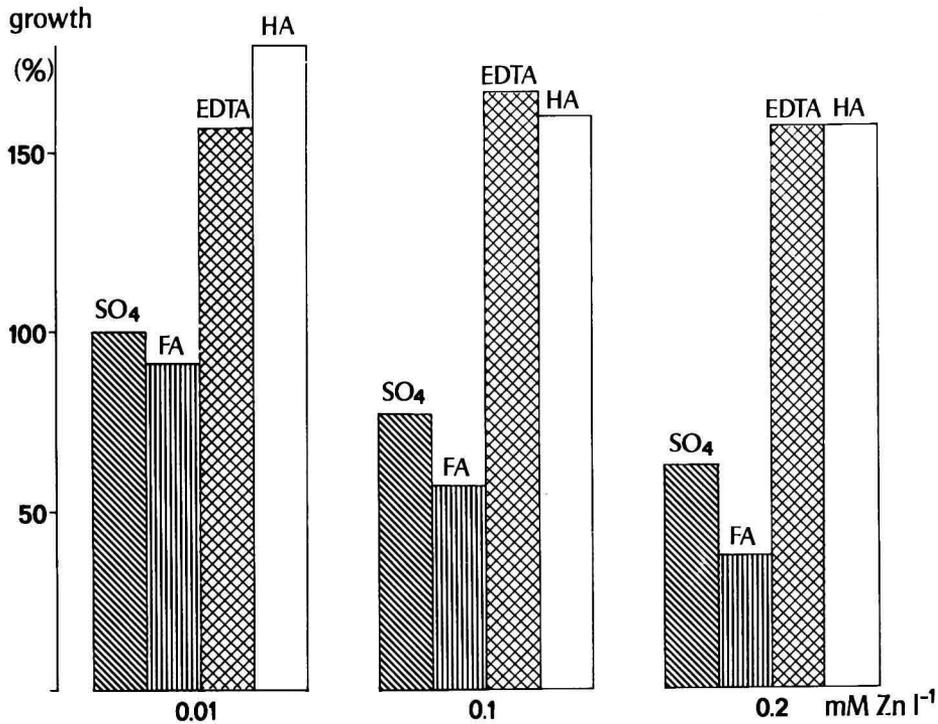


FIG. 5. Effect of ionic and complexed zinc on the growth of a non-zinc-tolerant population of *Agrostis stolonifera*. Growth in a culture solution with 0.01 mM ZnSO₄ was calculated to 100%. Complexing agents: EDTA = ethylene diaminetetraacetic acid, HA = humic acid, FA = fulvic acid (FRANCKE 1976)

acid is generally comparable with that of EDTA, both lowering the toxicity of high amounts of zinc (ERNST 1968) and copper (SCHILLER 1974) and stimulating plant growth.

Both, fulvic and humic acids are essential parts of the humic substances synthesized by the humification process in every soil (FLAIG *et al.* 1975). At present we have a rough idea on the ratio of humic acid to fulvic acid in soils. The fulvic acid content of soils is inversely related to the content of humic acid; the latter predominates in rendzina soils, whereas fulvic acids are characteristic for podzolic and brown soils. Humic and fulvic acids are occurring in most of the environments and are able to interact with all metals, so that they are certain to become important objects in the future plant ecology. The effect of these substances on the soil should be evident from a podzol profile. Beneath a 40-60 year old coniferous woodland on the sandy soil of the Veluwe region of The Netherlands fulvic acids and other organic compounds have caused loss of iron and manganese from the upper soil horizon and enrichment of these metals in the lower horizons (Plate 1). The difference in colour between horizons

rich and poor in iron and manganese makes this process visible, but it occurs in the same way for other transportable nutrients such as potassium, magnesium, phosphorus, nitrate, and sulphate which have no colour. Therefore, real progress in the analysis of ecosystems or small parts of them, especially the so called moderate environments, is only to be expected from investigations of the local differentiation of the soil profile.

6. NUTRIENT AVAILABILITY IN SPACE

6.1. SOIL PROFILES

Undisturbed soils are characterized by a profile which is the product of the interaction of the atmosphere and biosphere on the one hand, with the lithosphere and hydrosphere on the other hand. The soil profile may be quite simple or very complicated, as already shown for podzolic soils. Anyway, the profile determines the distribution of minerals in the soil, as can be demonstrated for an acid (podzolic) and a neutral (rendzina) soil (Fig. 6). Independent of the soil type, exchangeable calcium, magnesium, and potassium, phosphorus and available nitrogen in the form of nitrate are not equally distributed over the various soil horizons. The biological accumulation of these elements in the top layers is evident in these soils, as has repeatedly been demonstrated for macro- and micronutrients in forest soils (see e.g. WRIGHT *et al.* 1955; SHAROVA 1957; SCHMIDT 1970; DIERSCHKE 1974; HINNERI 1974). The soil habitat exhibits small-scale mosaics varying in nutrient availability which can interact with the rooting behaviour of plants.

If we consider the distribution of roots in a beech wood on calcareous rocky soil (rendzina type) we can distinguish between a group of plant species rooting only in the upper 5 cm of the A_{h1} horizon such as *Anemone nemorosa* and *Galium odoratum*, a group rooting in the A_{h1}/A_{h2} horizon to a depth of 10-15 cm, for instance *Mercurialis perennis*, *Milium effusum*, *Carex sylvatica*, and *Sanicula europaea*, and those plants whose roots penetrate to a depth of 30 cm, but not beyond the lower limit of the C_v horizon (*Allium ursinum*, *Arum maculatum*, shrubs, and trees). This distribution of the roots in the soils has the advantage of decreasing the competition for space, but it creates different nutritional situations for the species in question. The heterogeneously distributed nitrate may be suitable for a further analysis of this aspect, because these woodlands are rich in nitrate, permitting luxury consumption. In fact, analysis of the cell sap of leaves as a storage pool for nitrate (SCHNURBEIN 1967) showed that nitrate was more abundant in the leaves of the flat-rooted species *Anemone nemorosa* and *Galium odoratum* than in the deep rooted *Allium ursinum* and *Arum maculatum*, independent of the calcareous woodland sites sampled (NIESKE 1973; SUTTNER 1974; PLADEK-STILLE 1974). The nitrate concentrations were in *Anemone nemorosa* 29.9 μM , *Galium odoratum* 26.5 μM , *Mercurialis perennis* 11.0 μM , *Sanicula europaea* 15.7 μM , *Allium ursinum* 12.7 μM , and *Arum maculatum* 15.4 μM .

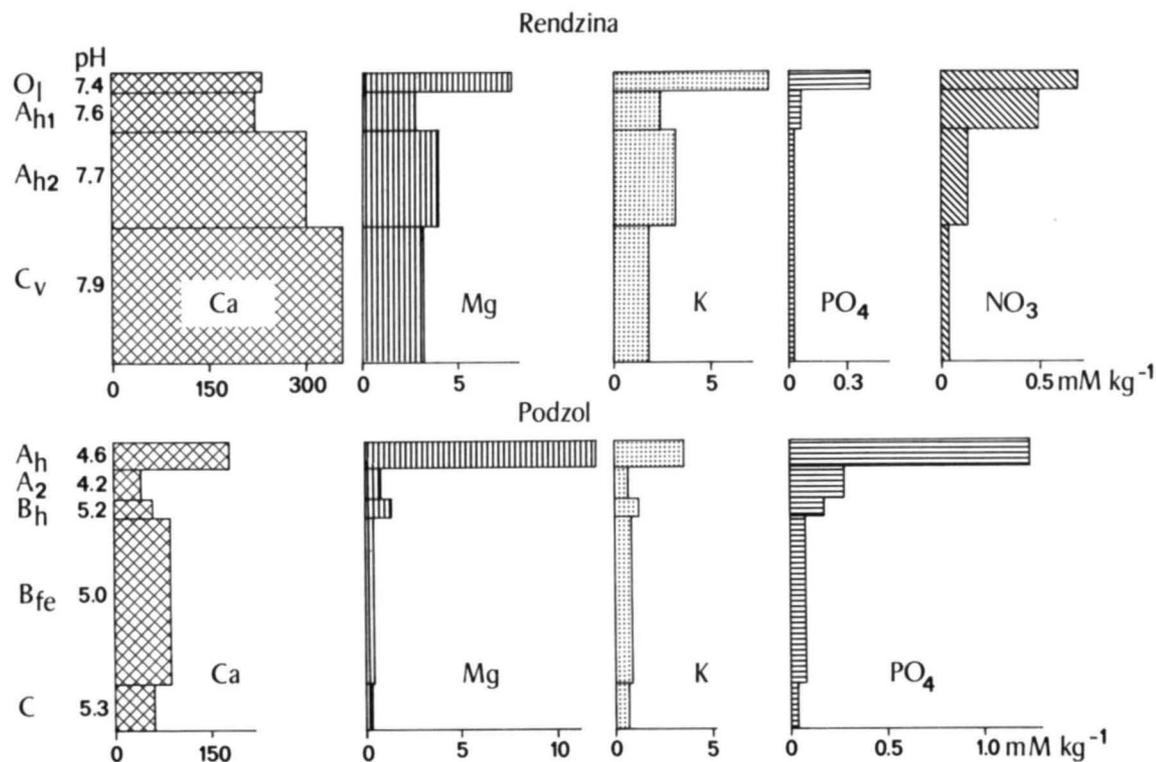


FIG. 6. Availability of nutrients in a rendzina soil profile on Cenoman chalkstone and of a podzol profile on Gault sandstone in the Teutoburg Forest near Brochterbeck. Availability was measured: for nitrate in an aqueous extract, for potassium and phosphorus on the basis of a lactic acid (pH 3.2) extraction, and for calcium and magnesium from exchange with 1 M ammonium acetic acid (pH 7.0)



PLATE 1. *Irregular distribution of humic and fulvic acid in the vicinity of roots of Betula alba in a podzol profile of the sand in the Veluwe area near Zwolle*

6.2. LOCALLY CONCENTRATED LEACHATES

Nutritional differentiation in plant communities is not only dependent on the soil situation, but can strongly be influenced by the plants themselves. One of the factors involved here is the canalization of water in a woodland system. Everyone knows the difference between the two sides of the trunk of a beech or oak, one exposed to the rain, the other in the rain shadow, both differentiated by their colonization with epiphytes. Besides water there is also a difference in nutrients, due to the input and output of leachates. Leaching is defined as the removal of substances from plants by the action of aqueous solutions such as rain, mist, dew, and fog. Most authors have losses of substances from foliage in mind (for a review see TUKEY 1970). Under the influence of the branching system of the tree, some part of the leachates collects on the trunk representing the stemflow. This water is considerably enriched with nutrients as compared with the normal rain water and throughfall (Table 4), as has been

TABLE 4. *Mineral content of water from rainfall, throughfall, and stemflow ($\mu\text{M l}^{-1}$) and of bark ($\mu\text{M g}^{-1}$ dry weight) from beech (*Fagus sylvatica*) and oak (*Quercus robur*) in the rain shadow (s) and rain channel (c). Site: calcareous woodland near Münster (Germany), 1972 (Data from SCHMITZ 1973 and ERNST unpublished)*

Element	Season	Rainfall	Throughfall	Stemflow		Bark			
				<i>Quercus</i>	<i>Fagus</i>	<i>Quercus</i>		<i>Fagus</i>	
						s	c	s	c
K	winter	14.1	75.7	260.9	69.3	11.4	7.5	22.6	36.7
	summer	20.9	63.9	339.4	94.6				
Na	winter	63.5	166.5	238.0	127.0	8.2	5.6	3.7	3.2
	summer	31.7	79.6	235.4	124.1				
Mg	winter	17.9	49.6	92.8	26.8	3.5	3.3	10.4	10.7
	summer	21.7	75.8	101.3	47.5				
Ca	winter	42.8	90.0	500.0	80.7	599	387	369	372
	summer	40.5	141.3	498.0	96.5				
P		-	-	-	-	4.8	6.7	12.2	13.9

described for mixed oak woodlands in Belgium (DENAEYER-DE SMET 1969) and England (CARLISLE *et al.* 1966). The stemflow of oak contains distinctly higher amounts of calcium, potassium, sodium, and magnesium than that of beech. Bark analysis of the rain channel and the rain shadow areas of beech and oak (0.5 m above soil surface) supported the suggestion that the leachates derive not only from leaves, but also from the bark itself (SCHMITZ 1973). This stemflow provides an appreciable source of nutrients for plant growth, for instance for mosses

beneath forest trees, but may also induce ecological disturbance lowering the pH and adding less favourable elements in the vicinity of the stems. The latter effect can be observed, if stemflow of trees is strongly channelled and a zone bare of herbs and grasses occurs.

6.3. DIFFERENTIATION OF LEAF LITTER IN SPACE AND TIME

One of the factors which builds up the local pattern of nutrients is the leaf litter of the various plant species. The divergent rooting behaviour of plants in a woodland leads to the exploitation of different nutrient pools. Most of the nutrients in the leaves of trees originate from a greater depth than those of the flat-rooted herbs. As a result, the annual supply of leaf litter, especially that of trees, has a strong impact on the herbs of the humus rich horizon (A_n). If we regard leaf litter as a form of fertilization of the herb layer, the seasonal litterfall may be compared with agricultural fertilization practices. In the beech woodland near Münster the dosage of nitrogen is equivalent to a grassland fertilization with 70 kg N/ha. Under favourable natural circumstances potassium too can reach usual agricultural levels. However, the annual addition of phosphorus to the herb layer (0.5 kg P/ha) is only a fraction of the amount given in normal agricultural practice which indicates that phosphorus may be a critical element in such woodlands. This situation is further complicated by the high amount of calcium, which is disadvantageous for the availability of phosphorus and sulphur (Table 5).

TABLE 5. *Nutrient contents of leaf litter in a calcareous beech woodland (Teutoburg Forest, 1970)*

Species	Dry matter ($g\ m^{-2}$)	Nutrient ($mg\ m^{-2}$)							
		N	P	K	Ca	Mg	Fe	Mn	Zn
<i>Fagus sylvatica</i>	251.1	5,400	221	1,255	5,650	276	50	63	11
<i>Carpinus betulus</i>	29.8	748	81	146	975	70	8	5	2
<i>Allium ursinum</i> (pure stands, June)	45.2	1,440	146	1,012	698	125	20	3	2
<i>Mercurialis perennis</i> (pure stands, Oct.)	32.0	918	68	808	1,280	117	11	1	2

Furthermore, there is a considerable local differentiation of fertilization in woodlands which is dependent on the plant species. The growth pattern of species such as *Allium ursinum* or *Mercurialis perennis* which are clustered in great patches creates a horizontal differentiation in the nutrient concentration, because the litter of *Allium* is rich in phosphorus, but poor in calcium, and

vice versa for *Mercurialis perennis*. This situation can be further stressed or equalized by the litterfall of the trees, dependent on the species composition and their abundance in these woodlands and on the climatic conditions at the time of shedding, especially on the wind velocity.

In contrast to the normal agricultural situation the plants of the herb layer are predominantly perennials and have mechanisms for the internal re-translocation of nutrients as demonstrated by the efficient translocation of phosphorus from leaves to rhizomes in *Anemone nemorosa* and other herbs as well as in trees (ERNST 1978), unlike potassium in herbs (Table 6). Furthermore, the well developed mycorrhiza of these species also aids in the phosphorus nutrition of plants (see MOSSE's paper in this volume), perhaps with the disadvantage of a too large supply of oligo-elements (ERNST 1978).

TABLE 6. Translocation of phosphorus from rhizomes to leaves and vice versa, in *Anemone nemorosa* in a calcareous beech woodland, as indicated by the concentrations of phosphorus and potassium ($\text{mM kg}^{-1} \text{ d.m.}$) during the growing season

		Developmental stage				
		Folded leaves	Unfolded leaves	Flowering	Fruiting	Leaffall
P	leaves	26 ± 1	61 ± 3	48 ± 1	27 ± 0.3	19 ± 1
	rhizomes	47 ± 1.5	34 ± 0.2	36 ± 1	51 ± 2	69 ± 2
K	leaves	132 ± 3	130 ± 3	136 ± 1	147 ± 9	137 ± 7
	rhizomes	110 ± 9	98 ± 2	96 ± 2	110 ± 3	110 ± 3

7. NUTRIENT AVAILABILITY IN TIME

7.1. MINERALIZATION

The input of nutrients by leaffall both at our research site and in other ecosystems (DUVIGNEAUD 1968; NIHLGÅRD 1972; GLOAGUEN & TOUFFET 1974) demonstrates not only the differentiation of nutrient input in space -horizontal as well as vertical- but also in time. In some of the geophytes such as *Ficaria verna* and *Allium ursinum* leaffall occurs as early as May or June, whereas herbs such as *Mercurialis perennis* shed in October together with the shrubs and trees.

Most of the nutrients in leaf litter, however, are not available just after shedding. Microorganisms act beneficially by transforming unavailable minerals and organic compounds of leaf litter into forms available for uptake by higher plants. The process is called (re)mineralization. The special effects of the soil microflora are highlighted in the paper by WOLDENDORP in this volume, so

that I can confine myself to some general statements. Moisture and temperature regulate mineralization, which is promoted by warm and moist conditions and retarded at low values of these abiotic factors. Let us turn now to the seasonal pattern of mineralization of nitrogenous compounds. There is a wide belief that nitrification is suppressed by temperatures below 5°C (ELLENBERG 1964; WILLIAMS 1968, 1969). This hypothesis is contradicted by the results obtained by ANDERSON *et al.* (1971), who demonstrated the adaptation of nitrifiers to low temperature. But there is also an ecological phenomenon that argues against it. In all of the ecosystems analysed, nitrogen mineralization was measured throughout the year and as can be seen from Fig. 7 the mineralization rate is not higher in warm and moist summers than in moist winter periods (see JANIESCH 1973; DAVY & TAYLOR 1974; DIERSCHKE 1974). In our calcareous beech woodland, mineral nitrogen accumulated in the soil more or less exclusively in the form of nitrate except at sites with much stemflow where ammonium-nitrogen was also present. This continuous mineralization in woodland soils was also

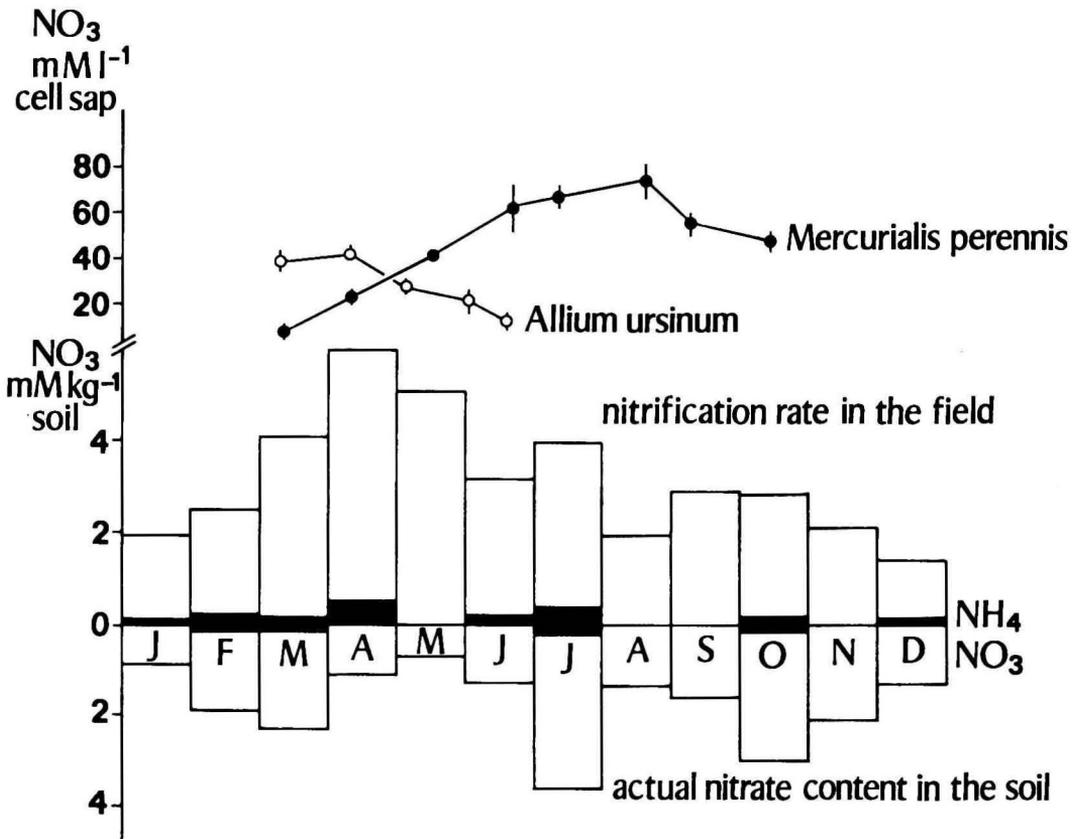


FIG. 7. Actual nitrate content (mM kg^{-1}) and nitrification rate in the field (3 weeks) of an A_0 -horizon of a rendzina beech forest in relation to the nitrate content of the cell sap ($\text{mM NO}_3 \text{ l}^{-1}$) from leaves of *Mercurialis perennis* and *Allium ursinum* during one year (January-December)

demonstrated for phosphate by SCHMIDT (1970). Incubation of soil samples under field conditions -in the absence of higher plants- yielded higher amounts of nitrate nitrogen than the actual soil content at sampling time. Perhaps the most significant feature observed was the pronounced actual concentration of nitrate in the soil, comparable with the values obtained for nitrophytic edge vegetations of Central European forests (JANIESCH 1973; DIERSCHKE 1974). These results seem to contradict the concept of a limited nitrogen supply in these ecosystems. It is conceivable that the species of these soils cannot compensate the nitrate production in the soil by nitrate uptake and that the herbs are not only nitrophytes, i.e. plants growing in a soil rich in nitrogen, but also nitrophilous, which indicates a tendency toward a high nitrogen demand. According to a general interpretation the growth of nitrophilous species is stimulated and optimized by at least 14.7 mM NO₃ (WALTER 1963) which is equivalent to the nitrate content of 1 litre of Knop's culture solution. The supposition on the nitrophilous nature of the above-mentioned species is based on the nitrate content of cell sap, which is a storage pool for nitrate within the plant. Nitrate uptake was found to be particularly strong so that a considerable amount of nitrate is present in the cell sap of herbs (NIESKE 1973; SUTTNER 1974; PLADEK-STILLE 1974), as shown in Fig. 7. However, the accumulation of nitrate in cell sap, i.e. in the vacuoles of the cell, cannot only be interpreted as a storage pool at times of luxury consumption, but it also suggests an ecological necessity for osmotic adjustment (JANIESCH 1973) or might be a sign of an inefficient activity of the nitrate reducing system, the nitrate reductase.

To elucidate the efficiency of nitrate reduction, nitrate utilization was assessed by the *in vivo* assay for nitrate reductase (STREETER & BOSLER 1972), which reflects the actual reduction of nitrate by the plant and its dependence on the nitrate supply (LEE *et al.* 1974), whereas the *in vitro* technique measures the potential activity of this enzyme and provides an indication for the nitrogen requirement of plants (BAR AKIVA *et al.* 1970). As far as *in vivo* activity of these woodland herbs is concerned, they show an appreciable actual activity which is comparable with that of other species thought to be nitrophilous (LEE *et al.* 1974). Therefore, the accumulation of nitrate in the vacuole might suggest a disturbance in the synthesis of nitrate reductase, which is dependent on the micronutrient molybdenum (NICHOLAS 1961), and might indicate a molybdenum deficiency in these habitats. To check this hypothesis seedlings of *Galium aparine*, a possibly nitrophilous plant of the edge vegetation of these woodlands (DIERSCHKE 1974), were grown in culture solution with increasing amounts of molybdenum (6-6,000 µM Mo). After 4 weeks of growth the activity of nitrate reductase and the nitrate accumulation in the cell sap were markedly affected by molybdenum concentrations higher than 60 µM Mo. Our results (Table 7) support previous reports of molybdenum sensitivity in the nitrophilous *Urtica dioica* and *Chenopodium album* (AUSTENFELD 1969). These results show that the marked accumulation of nitrate in these plants is not associated with and caused by

TABLE 7. Effects of increasing amounts of molybdenum on the growth, nitrate content of cell sap (shoots) and nitrate reductase activity of leaves of *Galium aparine* after 4 weeks of growth in a culture solution in a greenhouse at $20^{\circ} \pm 2^{\circ}\text{C}$ and 12 hours of light day⁻¹

Mo concentration in culture solution ($\mu\text{M.l}^{-1}$)	Dry matter (mg.plant ⁻¹)	Nitrate in cell sap ($\mu\text{M.ml}^{-1}$)	In vivo assay of nitrate reductase ($\mu\text{M NO}_2 \text{ g}^{-1}.\text{h}^{-1}$)
6	614 \pm 24	130 \pm 7	1.08 \pm 0.07
60	624 \pm 37	134 \pm 11	1.13 \pm 0.15
600	414 \pm 28	252 \pm 15	0.65 \pm 0.09
6000	180 \pm 18	306 \pm 13	0.35 \pm 0.05

a molybdenum deficiency, but is an index of luxury consumption.

It is also of interest that the mineralization of nitrogen yields not only nitrate, but also a reduced form of nitrogen, i.e. ammonia, depending on various edaphic factors. Although many laboratory experiments have been performed on nitrate and ammonium ions as nitrogen sources (see e.g. EVERS 1964; BOGNER 1968; GIGON & RORISON 1972; VAN ANDEL 1974; LEE *et al.* 1974) relatively few attempts have been made to compare the performance of plant populations adapted to soils with ammonium or nitrate as nitrogen sources. Populations of *Agrostis stolonifera* from soils with nitrate or ammonia did not differ significantly in the rate of ammonium assimilation, but differed slightly under a nitrate treatment (LEE *et al.* 1974). The experiments with populations of *Urtica dioica* and *Epilobium angustifolium* from acid (pH 3.8-5.7) and alkaline (pH 7.8-8.1) habitats (Fig. 8) revealed that growth of all populations given an $\text{NO}_3\text{-N}$ treatment at pH 6.4 was significantly better than in an ammonium-nitrate and a pure ammonium series, both at pH 5.8 (FISCHER 1977). Populations of *Scabiosa columbaria* sampled in different habitats (GIGON & RORISON 1972) also grew better in nitrate than in ammonium treatments. These results suggest the existence of different effects of ammonium and nitrate on plant growth, especially if a surplus of these nitrogen forms is present.

The generally higher susceptibility of plants to ammonium than to nitrate seems to be an ecophysiological paradox in view of the lower energy demand for the assimilation of ammonium. Ammonium ions can be directly incorporated into organic nitrogen compounds, whereas nitrate has to be reduced to ammonium by two enzyme systems (nitrate reductase and nitrite reductase). The nitrate pathway makes the plant dependent not only on the synthesis of these two enzymes, but also on the supply with certain micronutrients. However, in a situation of surplus, nitrate has the advantage of being able to form a storage pool in the vacuoles and of being metabolized on demand. In contrast, ammonium must be metabolized rapidly to prevent metabolic disturbance (see e.g. MATSUMOTO *et al.*

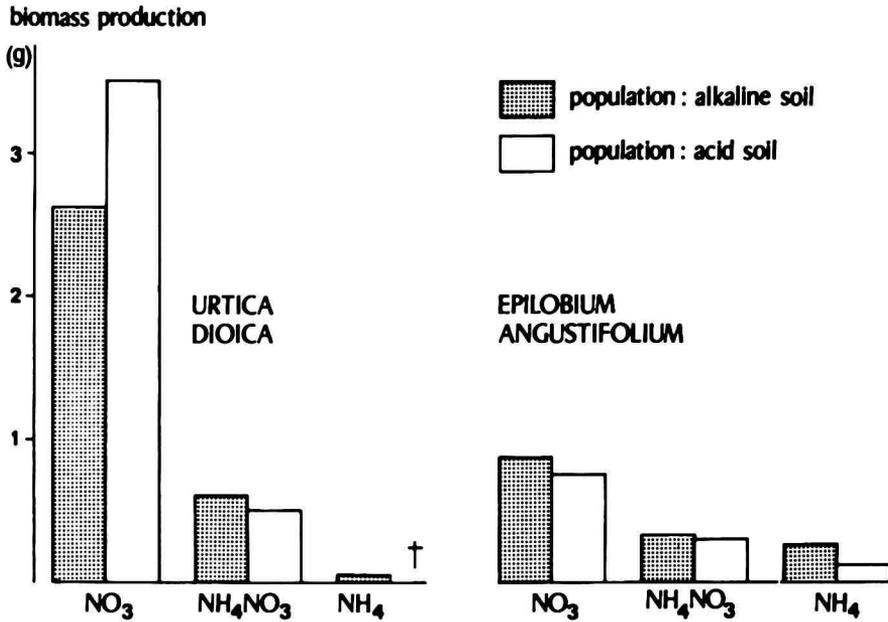


FIG. 8. Effect of the oxidation state of nitrogen on the biomass production of both an acid and an alkaline population of *Urtica dioica* and *Epilobium angustifolium* (FISCHER 1977)

1971). It is therefore of particular interest that the detoxification of ammonia via the formation of acid amides (asparagine, glutamine), ureides, and other compounds (for a review see MOTHES 1958) requires more energy and metabolic reactions than the transport of nitrate to the vacuole system. This aspect of the high susceptibility of many plant species to a surplus of ammonia should be given special attention in further ecological research (KIRKBY 1969).

At this point I wish to make some remarks on those plants which colonize or grow in habitats rich in nitrate. It seems that soils of woodlands and forest borders and skirts are sometimes characterized by such a high nitrification rate that the plants are unable to consume all the soil nitrate. The soil solution around the roots sometimes contains more than 10 mM NO₃, as has been shown for the plant communities *Agropyro-Aegopodietum* (JANIESCH 1973) and *Alliario-Chaerophylletum* (DIERSCHKE 1974). Despite the small number of soil analyses available for these environments, the conclusion of vegetation scientists has been that plants of these soils have a distinctly higher demand for nitrate. These plants can be expected to be nitrophilous. To verify this, I have compiled results on the growth behaviour of these species which are thought to be pronounced nitrogen indicators with an indicator value of 8 or 9 in the scale of ELLENBERG (1974). The behaviour of these N8 plants proved to be highly variable (Fig. 9). Some of the species such as *Rumex obtusifolius*

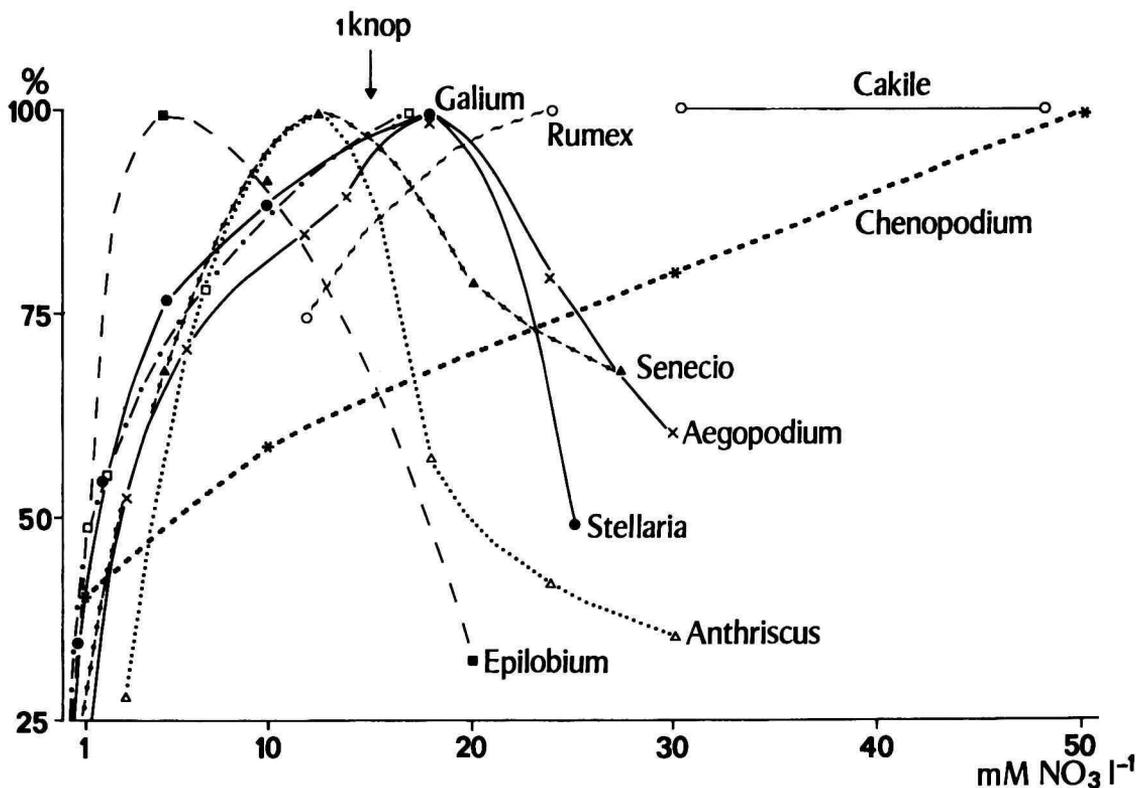


FIG. 9. Growth of "nitrophilous" species in water culture with increasing amounts of nitrate. Optimum growth is defined as 100%. Results for *Rumex obtusifolius* obtained by TIJBERG (1974), *Epilobium angustifolium* by VAN ANDEL (1974), *Aegopodium podagraria* and *Anthriscus sylvestris* by JANIESCH (1973), *Senecio sylvaticus* by VERA (1975), *Chenopodium album* by AUSTENFELD (1972), *Cakile maritima* by ERNST (1969), *Stellaria media* and *Galium aparine* by ERNST (unpublished)

(TIJBERG 1974) and *Cakile maritima* (ERNST 1969) have a splendid growth up to at least 25 mM NO_3 . Even higher concentrations are demanded by *Chenopodium album*, a N7 species (AUSTENFELD 1972). Other N8 species such as *Aegopodium podagraria* (JANIESCH 1973) or *Senecio sylvaticus* (VERA 1975) more or less tolerate a nitrate concentration of 14.7 mM, but at higher concentrations those species show a reduced biomass production. However, *Epilobium angustifolium* regarded as very nitrophilous (N8) is quite sensitive to this amount of nitrate (VAN ANDEL 1974, 1976). This situation underlines the unreliability of such speculations on the soil-plant relationship when the factor in question has not been measured.

7.2. SUCCESSION AND NUTRIENT AVAILABILITY

If forests are cleared by storms, fire or human activities, the microclimate is changed especially with respect to light and temperature. This generally causes stimulation of nutrient mobilization, in particular nitrification, with a special response of vegetation in these clearfelled areas. The pioneer vegetation establishing in this secondary habitat in western, central and northern Europe is characterized by *Epilobium angustifolium* which is associated with other typical species such as *Digitalis purpurea*, *Senecio sylvaticus*. Besides differences in the life cycle strategy of *Epilobium* and *Senecio* (VAN ANDEL & VERA 1977), these species also show a quite different response to the nutrient budget of the soil. *Senecio sylvaticus* as an annual species requires large amounts of nitrogen for optimal growth and seed production (12 mM N) and is less nitrogen efficient than *Epilobium angustifolium*, which does not need large amounts of nitrogen, but possesses a certain degree of tolerance against higher nitrogen concentrations. Both plants produce wind-spread propagules, the dissemination further reduces the nutrient budget of the soil (VAN ANDEL 1974), in addition to the removal of the felled trees, and leaching (TAMM *et al.* 1974). However, the loss of nutrients, especially of nitrogen in these clearings is not as dramatic as during the drainage of the Zuiderzee to form the IJsselmeerpolders, when there was an annual loss of nitrogen by fruits of the annual *Senecio congestus* amounting to 60 kg N ha⁻¹ (BAKKER 1960; VAN SCHREVEN 1963). In moderate situations as in these clearings, perennial plants such as *Epilobium angustifolium* conserve nutrients in their root stocks and therefore the nutrients of the mineralized leaf litter will be available to the next succession stage. However, our knowledge concerning this aspect of nutrient availability is less than scarce.

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10. DISCUSSION

In reference to the studies on nitrophilous plants, TROELSTRA (Oostvoorne) drew attention to the concept of the cation-anion (C-A) value of DE WIT *et al.* (1963). Some plants thrive better with a high (C-A) value (COIC *et al.* 1962). Therefore, TROELSTRA found it hard to accept the term ammonium toxicity. ERNST commented that the (C-A) concept is not very useful, because in most of the analysed examples (e.g. DIJKSHOORN 1957; MENGEL 1965) the value of C is only estimated as the sum of the macronutrients, which was not the intention of the initiator of this concept (BEAR 1950). This is also done in such plants where other elements, such as silicium, contribute more than 50 per cent to the ion content of the plants (LEWIN & REIMAN 1969). On the other hand, there are plants where the (C-A) value is not disturbed, but increased ammonium uptake is the cause of a decrease in growth rate (e.g. INGESTAD 1976). All in all, the concept may perhaps be relevant for plants where K^+ has antagonistic effects to NH_4^+ (BARKER *et al.* 1967; NELSON & HSIEH 1971; PATNAIK *et al.* 1972).

GRIME (Sheffield) then discussed the mechanism of the positive growth response to increasingly low concentrations of micronutrients such as zinc or even oligo-elements such as aluminium. ERNST pointed out that in low concentrations most of the elements may have a stimulating effect on growth, although they are by no means essential. The absence of these elements may cause metabolic disfunction. CHAPHEKAR (Bangor) emphasized this aspect once more by mentioning the plant populations which are tolerant for heavy metals such as lead and copper.

KINZEL (Vienna) then referred to his idea of the physiotypes of plants (KINZEL 1971). He thought that at the moment the study of the soil-plant relationship is characterized by a relatively good amount of knowledge about well-defined soil types but a sparse knowledge of metabolic types of plants. Research on the latter should be encouraged because it can help us to understand the ecology of plants.

With respect to the mineral cycling in ecosystems, BARKMAN (Wijster) then drew attention to the current practice in national forestry in The Netherlands of decortivating trees before their removal and using the peeled bark to cover sandy paths. ERNST agreed with BARKMAN's suggestion that it would be worthwhile

to scatter the bark throughout the forest and thus keep the minerals in the ecosystem. PERSSON (Uppsala) remarked that the discussion on mineral cycling should put more emphasis on the turnover of the below-ground biomass, especially the fine roots, because they contribute twice as much as the leaf litter to the organic matter of forest ecosystems (PERSSON 1975).

There was some argument between MINDERMAN (Arnhem) and ERNST about whether the quality of chemicals in the soil can be determined. ERNST did not share MINDERMAN's opinion that there is only certainty about the total amount of minerals within the plant, but he believed that by using KINZEL's concept of physiotypes, knowledge about root exudates and new techniques for chemical soil analysis sufficient progress in the future will be made.

WHITE (Dublin) shifted the discussion to another ecological subject. He asked whether the distinction between ecological and physiological amplitude, which according to ELLENBERG is almost a tenor of contemporary ecology, was really more a distinction made by investigators than by nature, as suggested by ERNST, or is a general principle. ERNST denied the latter, because in most of the re-analyzed examples the published differences are due to an omission of important abiotic factors or to neglecting of the physiological differentiation of plant species in ecotypes. He considered the great discrepancy between the two amplitudes to be a symptom of our ecological ignorance. WOLDENDORP (Arnhem) pointed out that the comparison is useless, because in the physiological experiment only the dry matter is compared with the factor in question, whereas in the field the total fitness of the population can be studied. ERNST commented that this is only partially true, because in good physiological experiments the fitness of a population, too, can be elucidated with respect to its reproduction, genetic structure, competitive ability, and other fitness parameters.

In answer to a question on the necessity to extend the physiological experiments to mycorrhiza, ERNST replied that this should be done, especially where phosphorus nutrition must be taken into consideration (see the paper by MOSSE in this volume). However, besides the beneficial aspect of phosphorus supply by mycorrhiza, it must be kept in mind that via mycorrhiza the input of other elements, especially oligo-elements, is also stimulated, as has been shown for *Neottia nidus-avis* and *Monotropa hypopithys*, which are completely dependent on mycorrhiza.

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