Nutrient availability and yield formation

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Summary

Available macronutrients located in the direct vicinity of the plant root (root hair cylinder) contribute only to a minor degree to the total amount of nutrients required by the plant. Thus the bulk of macronutrients has to be transported towards the plant roots. Nutrient mobility in the soil therefore is an essential factor of nutrient availability. The rates of nutrient translocation either by diffusion or mass flow depend on the nutrient concentration in the soil solution. For this reason the nutrient level of the soil solution is of higher importance for the nutrient availability than the quantity of exchangeable or easily soluble plant nutrients.

Soil moisture is a further important factor of nutrient availability, as with an increase in water content, diffusion and mass flow rates generally are improved. A third component of nutrient availability is the root system. The more a soil volume is penetrated by plant roots the shorter are the mean distances nutrients have to be translocated in order to reach the plant root.

The nutrient concentrations of the soil solution can be determined by suitable techniques. Soil test methods based on the nutrient concentration of the soil solution mostly yield better correlations with plant growth than methods based on the pool of soluble and/or exchangeable nutrients.

Introduction

The problem 'nutrient availability and yield formation' has engaged the attention of many researchers ever since it has become known that soil minerals play a major part in plant growth, but so far it has not been possible to build up from the vast amount of data obtained a general theory elucidating the partly conflicting findings. During the last decade new concepts based on experimental results were developed which may open up new ways in this field of research and therefore deserve critical discussion. An approach to that is made in the present paper.

Principal processes affecting nutrient availability
After the publication of Jenny & Overstreet (1938) had appeared contact axchange has since been regarded as an important process involved in nutrient availability. Contact exchange in simple terms means that ions at the outermost surface of plant roots exchange for ions adsorbed to soil colloids. The rate of this exchange depends on the quantity or density of exchangeable ions both present at the root surface and adsorbed to the soil colloids. It is expressed by the following equation:

$$r = k(i_r) \times (i_s)$$

r = exchange rate (meq/unit time)

(i_r) = density of exchangeable ions at the root surface (meq/unit area)
surface (meq/unit area)
(i_s) = density of exchangeable ions adsorbed to the soil colloid (meq/unit area)
k = coefficient

The exchange rate further depends on temperature, adsorption strength and distance between both adsorption layers. These parameters, however, will not be discussed in detail as they do not contribute essentially to the derivations and conclusions presented in this paper.

The density of ions adsorbed to the root surface depends on the plant species, on the age of the root tissue and also on root metabolism. The respective factor (i_r) of the above equation is therefore determined by plant morphology and metabolic activity and not by soil properties. It is assumed that the density of exchangeable ions at the soil colloids is the major factor controlling nutrient availability. This deduction, however, is only correct in the event that contact exchange actually occurs and that the bulk of nutrients is taken up by the plant roots in this way.

Contact exchange occurs when the ions adsorbed to soil colloids are reached by root growth. According to investigations by Barber et al. (1963), only about 20 % of the phosphate and 7 % of the potassium required by the plants are present in the immediate vicinity of plant roots and thus can be reached by 'interception'. Blanchet (1965) and Mengel et al. (1969) came to similar conclusions. Drew & Nye (1969), in experiments wiht young ryegrass *(Lolium multiflorum),* found that the potassium present in the soil volume penetrated by a root hair cylinder only accounts for 0.8 to 6.3 % of the total potassium requirement of the plant. For phosphate similar results were obtained (Drew & Nye, 1970). It therefore appears that the bulk of potassium and phosphate needed by the plant is not available in the immediate vicinity of the root but has to be transported over longer distances to the plant roots. This statement implies that contact exchange plays only a minor part, if any, in nutrient availability.

Contact exchange will only occur if the surfaces of soil colloid and plant root are close to each other. Only ions with overlapping oscillation spaces will give rise to exchange. This means that the distance between two ions capable of contact exchange must be in the range of 1 to 3 nm. Ions that have shifted by contact exchange from the soil colloid to the root surface adhere to the outermost surface of the cell wall at a distance of about 1 μm from the actual ion uptake mechanism located in the plasmalemma. Therefore ions adsorbed to plant roots by contact exchange are far from being taken up. They still have to cover a considerable distance by diffusion or mass flow via the free space of plant roots to reach the plasmalemma (Mengel, 1974). This will only be achieved after the ion adsorbed to the outermost surface of the root has been exchanged again and thus can move freely in the water-filled pores and spaces of the cell wall, the socalled free space. This demonstrates that contact exchange is only of minor importance in nutrient availability.

As already outlined above the largest proportion of potassium and phosphate has to move from the soil medium towards the plant roots. This is also true of nitrate which is not adsorbed to soil colloids and thus not liable to exchange processes. Experimental data have substantiated the above statement. Von Braunschweig & Mengel (1971), in experiments with 20 various soils differing widely in clay content and exchangeable potassium, found a fair relationship between K uptake by oats and the diffusion rates of potassium in the soil medium, whereas K uptake and the content of exchangeable K in the soil showed a poorer correlation. K uptake also affected grain yield, and thus a
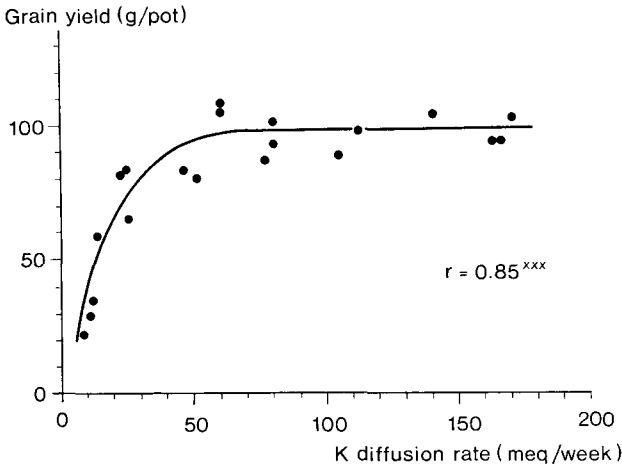
Grain yield (g/pot)

Fig. 1. K diffusion in the soil vs. grain yield of oats.

good correlation between the K diffusion rates in the soil and grain yield was observed (Fig. 1).

Active uptake of macronutrients seems to occur at a higher rate than diffusion, provided that plant metabolism is not impaired by low temperature, oxygen deficiency or other inhibiting conditions. This means that the nutrient concentration of the soil solution close to the root surface is rather low and increases with increasing distance from the root surface, since the root is a physiological sink for plant nutrients depleting the adjacent soil of nutrients. With highly diffusive ion species, such as nitrate and chloride, this depletion zone is rather large, whereas phosphate has only a small depletion zone due to the low diffusion rate of this nutrient. With K^+ it is intermediate (Nye, 1969). Kauffman & Bouldin (1967) found maximum diffusion lengths for K^+ of 6 to 7 mm/74 h, which are in good agreement with those measured by Grimme et al. (1971). Kauffman & Bouldin
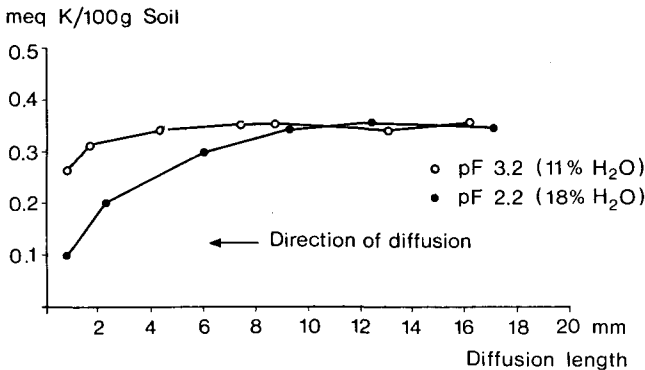
meq K/100g Soil

Fig. 2. Depletion of K^+ due to diffusion to a sink at two moisture levels.

(1967), in experiments with young maize roots, also succeeded in demonstrating that in fact the root vicinity is depleted of K+ due to uptake by the plant.

Fig. 2 shows such a depletion zone or depletion profile found by Grimme et al. (1971) in model experiments with a cation exchanger as a K+ sink. In these experiments the diffusion was studied at two soil moisture levels (pF 1.8 and pF 3.2). It appeared that the depletion zone was much larger in the soil with the lower pF, which indicates that soil moisture exerts a considerable influence on K diffusion. Soil moisture is therefore a major factor controlling actual nutrient availability. The effect of soil moisture on K+ diffusion as well as on Mg^{2+} diffusion was also shown by Mengel & von Braunschweig (1972) and Grimme (1973).

Although only a small portion of macronutrients required by the plant is reached by 'root interception' (Barber et al., 1963), the importance of plant roots to explore the soil volume for nutrients should not be underestimated. The larger the soil volume penetrated by the roots the shorter are the mean diffusion distances which have to be covered by the plant nutrients to reach the root. This relationship is shown in Fig. 3. Supposing only one root (left root in Fig. 3) were present, the nutrient (indicated by an arrow) would be far-off from the root. The diffusion rate depends on the concentration gradient of the respective nutrient and is expressed by the following equation:

$$r = k \frac{dc}{ds}$$

where r = diffusion rate; c = concentration; s = distance; k = coefficient.

In the example shown in Fig. 3 the nutrient is not subject to a concentration gradient, and at this far distance from the root consequently not yet available to the root by diffusion. Supposing the plant had a denser root system and another root extended closer to the location of the nutrient (right root in Fig. 3), the nutrient would already be in the depletion zone. This means that there is a concentration gradient and the nutrient is therefore exposed to diffusion towards the plant root. This example is to demonstrate that nutrient transport to the plant roots is favoured by a dense root system.

Assessment of the importance of the root system for nutrient availability in quantitative terms meets with difficulties due to the heterogeneity of the root material, and therefore often poor relationships between the total root matter and nutrient uptake are found. Particularly in the presence of moribund and collapsed outer cortical cells,
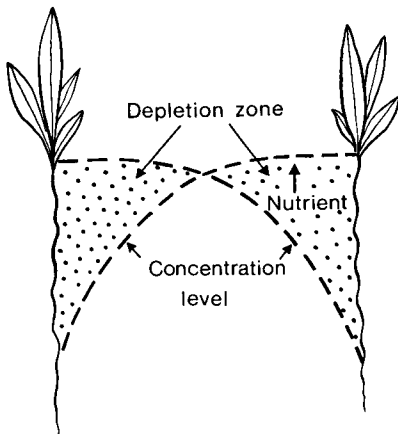

Fig. 3. K diffusion in relation to root density.

frequently found under field conditions, nutrient absorption is impaired (Clarkson et al., 1968). Russel & Clarkson (1971) report that usually nutrient absorption is more closely related to root volume than to root length or root surface. Since ions can enter deep into the cortical tissue of roots and the cortical cells by nature are favourite sites of ion uptake it is assumed that rather the root volume than the outer surface of the roots determines nutrient absorption.

Provided that the nutrient concentration of the soil solution is sufficiently high the ion uptake capacity per unit young root matter is very high as has been proved by Maertens (1971) with young maize plants. In Maerten's case 30 to 35 g of fresh root matter were sufficient to take up the amount of nitrogen, phosphate and potassium needed by the whole plant. As total root matter amounted to about 500 g fresh matter, it appears that a rather small portion of the root system is able to absorb sufficient amounts of nutrients to ensure a satisfactory supply to the upper plant parts. This example shows, that an extensive root system is rather needed for exploring the soil for nutrients than for increasing the nutrient uptake capacity. The larger the soil volume penetrated by plant roots, the more nutrients have the chance to reach the roots by diffusion or mass flow. Newman & Andrews (1973) found that the uptake of potassium and phosphate by young wheat plants was closely related to the soil volume available to the plants. The treatments with small soil volume showed a rather dense root system, but in the case of potassium, this did not result in satisfactory K uptake. It is assumed that in this case the depletion zones of K are overlapping and thus a competition for K+ of the neighbouring roots occurs. Such a competition was not observed with phosphate due to the smallnes of the phosphate depletion zones. The importance of the root system for nutrient availability is the higher, the poorer a soil is in nutrients. This was demonstrated by Chloupek (1972) in pot experiments with wheat. In the treatments without nitrogen, phosphate and potassium grain yield increased with increasing amount of root matter, whereas in the treatments with fertilizer the extension of the root system was of minor importance for grain yield. Also deeper soil layers (100 to 150 cm) contribute to the nutrient supply of plants and the roots of the deeper layers are often highly efficient in nutrient uptake (Nye, 1969; Ogus & Fox, 1970). Nutrient absorption from these deeper zones, however, requires sufficient oxygen in these layers (Wiersum, 1967).

Soil solution
Soil moisture and root extension are important factors in nutrient availability. The assessment of both meets with difficulties as they are largely dependent on weather conditions, which usually cannot be forecast exactly. The nutrient flow towards plant roots is further influenced by the nutrient concentration of the soil solution. This is defined as 'the aqueous liquid phase of the soil and its solutes consisting of ions dissociated from the surfaces of the soil particles and of other soluble materials' (Adams, 1974). In the 1920s and 1930s American soil scientists paid considerable attention to the soil solution and a lot of highly valuable experimental data were gathered, in particular by Burd & Martin (1924). Then, with the consept of 'contact exchange', the interest in soil solution problems declined. If, however, it should be true that the movement of macronutrients toward plant roots is the most important process in nutrient availability as outlined above, the concentration of plant nutrients in the soil solution would be a major factor controlling the translocation of nutrients in the soil. It does not matter whether this nutrient movement is due to diffusion or mass flow, the rate of movement in both cases depends largely on the ionic concentration of

the respective plant nutrient in the soil solution. This is the reason why paramount attention should be attached to the soil solution and its composition when studying nutrient availability problems.

Investigations into the soil solution meet with two major difficulties: firstly, it is difficult to abtain true soil solution, and secondly the composition of the soil solution can change rapidly due to variations in soil moisture, leaching, nutrient uptake by plants and also microbiological processes. The latter especially affect the nitrate concentration which can change considerably during the growing period (Harmsen, 1959). As to cations and phosphate, on the other hand these changes are not so spectacular, as the concentrations of these nutrients in the soil solution are 'buffered' due to exchange reactions and solubility. These reactions are of a physico-chemical nature (Schuffelen, 1971); they are subject to the laws of thermodynamics, and for this reason they can be evaluated, provided that the most important reaction factors and processes are known. With phosphate these are above all the solubility products of the various more or less crystalline or amorphous phosphates; with potassium and other cations, the exchange reactions and the greater or lesser selectivity of soil colloids for cation adsorption mainly control the cation concentration in the soil solution. These processes tend to establish an equilibrium between the free ions of the soil solution and the adsorbed or precipitated ones. Although this equilibrium is not always obtained, due to the involvement of other processes, such as leaching or nutrient uptake by the plants, the concentration of the equilibrated soil solution is a reproducible 'level', which is of utmost importance for nutrient availability. If this equilibrated concentration of a plant nutrient is rather low, this nutrient will be sparingly available.

The equilibrium depends also on soil moisture. To obtain comparable values, soil solution concentration should therefore be referred to the respective soil moisture. A suitable 'standard moisture' is field capacity. The equilibrated ion concentrations at this moisture level is of particular importance because it indicates the nutrient level reached by equilibration. To obtain soil solution at field capacity requires more sophisticated techniques, of which the displacement technique seems to be most reliable (Parker, 1921). The soil is placed into a column. The displacing liquid is then poured on top of the soil column, and when penetrating into the soil column it displaces the soil solution by hydrostatic pressure. The soil solution is collected at the outlet of the column. The critical point of this technique is that it is not suitable for routine analysis.

A further approach to obtain soil solution by an easier technique than that described above was made by Magistad et al. (1945). These authors added water to soil samples and mixed both until maximum water capacity was nearly reached. Affter 20-hour incubation of the samples the soil solution was drawn off by means of a Büchner funnel. Solutions obtained by this technique are not true soil solutions as the water content of the samples is usually higher than that found under field conditions. According to investigations by Reitemeier (1946), solutions at maximum water capacity contain larger amounts of dissolved cations than soil solutions at field capacity. At higher water levels, in particular more carbonates and gypsum are dissolved thus increasing the amount of soluble Ca^{2+}. This exchanges in part for K^+, Na^+ and NH_4^+ so that also an increase in dissolved univalent cations is observed. In soils devoid of carbonate and gypsum, a higher level mainly results in enhanced dissolution of univalent cations according to the Donnan distribution (Schuffelen & Bolt, 1958). If increased water content should not affect solution and exchange processes, the quantity of dissolved ions would remain unchanged. This is obviously not the case. Especially water extracts with soil: water ratios of 1 : 1 or wider do not give ion con-

centrations similar to those found in the true soil solution.

On the other hand, the difference between the water content of soil samples at field capacity and that at maximum water capacity is not very large. Eaton et al. (1960) reported that sandy soils contain about twice as much water at maximum water capacity as than at a soil moisture level of pF 2. In heavier soils this difference in water content was about 1.5-fold. At pF 2 the ion concentrations in the soil solution were about 1.5 to 2 times higher than at maximum water capacity. These data show the ionic concentrations measured at maximum water capacity do not differ widely from those found at field capacity, and for this reason also the concentrations found in the saturation extract, as described by Magistad et al. (1945), yield ion concentrations which give reliable information on the ionic composition of the true soil solution. Németh (1971, 1972) found that the first fractions obtained by means of the electro-ultrafiltration technique are in good agreement with the ion concentrations found in Magistad's saturation extract.

Soil tests and crop response
The correlations found between the data of soil tests and yield responses are usually poor. This is by no means surprising as most soil test methods rather measure the solubility or exchangeability of plant nutrients than the composition of the soil solution. According to Adams (1974), 'the extractants remove arbitrary and undetermined amounts of solid phase electrolytes and ions' which are of minor importance in plant nutrition. By Adam's opinion 'the emphasis on solid phase soil properties obviously results from the ease and convenience with which these data can be obtained and correlated with observed plant growth'. On the other hand, it must be admitted that the composition of the soil solution is subject to considerable changes, mainly due to nutrient uptake by the plants. In pot experiments with fallow soils, Mengel & Aksoy (1971) found that the K concentration of the soil solution remained nearly constant over a period of about two months, whereas an increase in the concentration of Ca^{2+} and Mg^{2+} was observed in some of these soils.

For crop production not only the momentary level of plant nutrients in the soil solution is of importance but also the rate at which this level is declining during the growing season. For this reason soil tests should not only inform about the level of plant nutrients present in the soil solution, but also indicate the degree to which the level of a nutrient is 'buffered'. A well buffered nutrient solution means that this level is declining slowly. The water extraction method for the determination of phosphate, developed by Sissingh (1969), takes into consideration both factors, i.e. the soil solution and the quantity of easily soluble phosphates which replenish the soil solution. This method therefore yields satisfactory relationships between the soil test data and yield response (Van der Paauw, 1969). The same is true of Németh's electro-ultrafiltration technique. The phosphate values obtained by this method are in good correlation with the data obtained by Sissingh's water extraction. Fig. 4 shows the correlations found between the grain yield of winter wheat and the electro-ultrafiltration values as well as phosphate contents determined by the lactate extraction method, respectively. These data were obtained by Németh & Harrach (1974) in field experiments carried out on loamy soils. In further investigations by Németh (not yet published) highly significant correlations were found between the phosphate uptake by various crops under field conditions and the phosphate content of the soil determined by the EUF (electro-ultrafiltration) method.

The buffering of potassium in the soil solution depends essentially on the clay content

Grain yield $r = 0.62^{xx}$
in t/ha $y = 2.6 + 39.3$

Grain yield $r = 0.31$
in t/ha $y = 0.38x + 37.53$

• Pararendzina

○ Grey brown podsolic

P-EUF-fraction

(mg P/100 g soil)

Lactate soluble phosphate
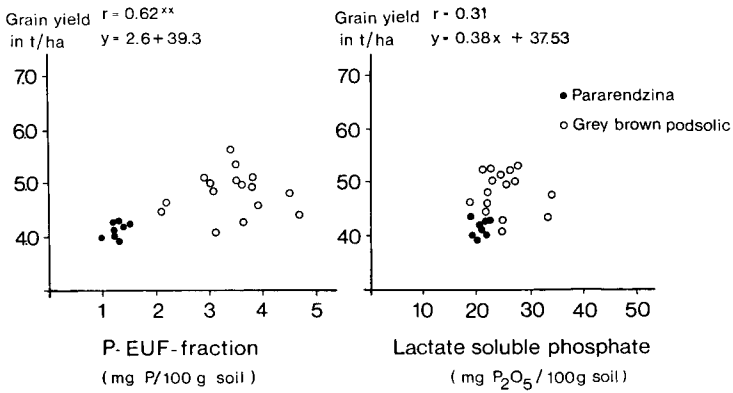
(mg P_2O_5 / 100g soil)

Fig. 4. Grain yield of winter wheat related to the P status of the soil.
Left hand: P obtained by the EUF technique.
Right hand: P obtained by the lactate extraction.

and on the type of clay minerals present. Fig. 5 informs about this relationship. In contrast to the loamy soils, the light-textured soils show a steep decline in K concentration. The data of Fig. 5 originate from a pot experiment with oats (von Braunschweig & Mengel, 1971). The decline in the K concentration during the growing season may probably be less under field conditions since a larger volume of soil per unit root matter is available. Soils with a clay content of about $> 12 \%$ generally have a suffi-

meq K/l

% exch. K/
Clay 100g Soil

25 | 26
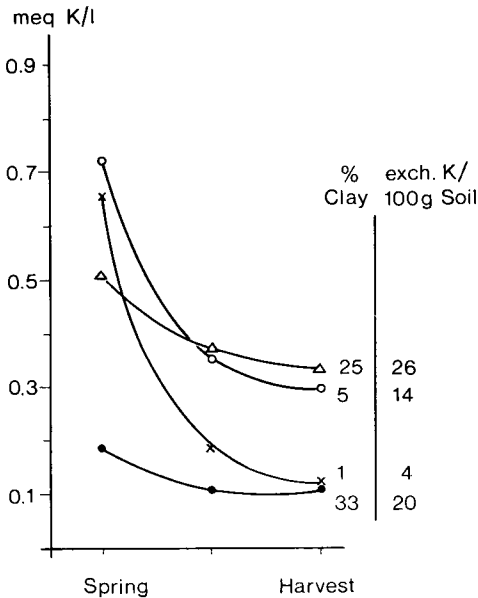5 | 14

1 | 4
33 | 20

Spring   Harvest

Fig. 5. Decline of the K concentration in the soil solution during the growing season in four different soils.

ciently high K buffer capacity. In this case K concentrations in the soil solution ranging from 0.7 to 1.0 meq K/1 are sufficient to produce grain yields of 6 to 7 t/ha. Soils with higher clay contents often have relatively high contents of exchangeable K^+, but rather low K concentrations in the soil solution (< 0.2 meq K/litre). These soils generally possess a very good K buffer capacity. All K concentration values cited above refer to a soil moisture level of nearly maximum water capacity. The data obtained by this Magistad's extraction method are in good agreement with the first fractions determined by EUF. The EUF desorption curves inform not only about the K concentration of the soil solution but also about the K buffering and the K fixation or K release capacity of a soil (Németh, 1972).

One might think that the nutrient composition of the soil solution on principle should exert the same influence on plant growth as does the nutrient composition in solution culture. Howard and Adams (1965) found that root growth of young cotton plants was closely related to the '$a_{ca}/\Sigma a_{cation}$' ratio of the nutrient solution. The critical ratio for optimum growth (0.2) was the same, no matter whether the plants were grown in nutrient solution or in soil. This demonstrates that the calcium activity of the soil solution (a_{ca}) referred to the total cation activity of the soil solution (Σa_{cation}) determined by appropriate techniques actually is an indicator of the true soil solution. A similar example is cited by Bennett & Adams (1970) who showed that NH_4OH will become toxic as soon as the critical level of 0.2 mM has been exceeded. This critical level is valid for solution culture as well as for the soil solution. Wild et al. (1969) found satisfactory correlations between the K concentration of the nutrient solution and the growth and K uptake of flax and ryegrass, whereas only poor correlations were observed between the activity ratio ($K/(Ca + Mg)^{1/2}$) and growth because this ratio is not a reliable indicator of the true K concentration of the nutrient solution (von Braunschweig & Mengel, 1971).

As already outlined above, nitrate does not tend to reach an equilibrium in the soil solution since nitrate consumption and production is mainly controlled by biological processes and not by physical-chemical reactions. In the major part of arable soils nitrate is the most important nitrogen component of the soil solution, because NH_3 is rapidly oxidised to nitrate (White & Greenham, 1967). The nitrate concentration in the soils is subject to considerable changes (Weller, 1971). High nitrate contents are especially observed during dry periods since mineralisation of organic nitrogen is still going on whilst nitrate diffusion towards plant roots is impaired considerably (Casper, 1973).

Although these findings are a drawback to using the nitrate concentration in the soil solution as an indicator for the availability of nitrogen, it seemed worthwhile to study the nitrate dynamics of various soils under different climate conditions more in detail. First results of these investigations show that high soil nitrate contents in spring affect growth and yield of cereals (Braun, 1974) and that high nitrate contents in late summer are prejudicial to the quality of sugar beets (Bronner, 1974).

The question of the limiting factor in crop production plays a major part in intensive crop cultivation aiming at maximum yields as practised in Central Europa. This question in most cases cannot be answered by simple soil tests but needs more comprehensive study of the soil and, in particular, of the soil solution. In a first approach of this kind, Németh (unpublished data) investigated the soil solution of eight different sites in Schleswig-Holstein where spring wheat of the same variety with uniform nitrogen fertilizer treatment was grown. The results of these investigations together with the respective grain yield are shown in Table 1. It appears that the data of the soil solution

Table 1. Available nutrients obtained by the EUF technique related to the grain yield of spring wheat.

Loc. No	Grain yield (kg/ha)	K (meq/litre solution)		P (mg/100 g soil)	Mg (mg/100 g soil)	Mn (mg/kg soil)	Zn (mg/kg soil)	Fe (mg/kg soil)	Cu (mg/kg soil)
1	5970	0.7	(0.3)	1.5	4.0	0.5	0.7	1.8	0.3
2	5310	0.6	(0.15)	1.5	2.0	1.0	2.2	9.5	0.2
3	4940	0.4	(0.14)	1.0	2.0	2.0	2.4	14.0	0.2
4	4660	0.4	(0.03)	0.9	3.0	0.1	3.6	0.1	0.5
5	4480	0.8	(0.1)	0.5	2.0	14.0	2.5	9.0	0.3
6	4130	0.5	(0.1)	0.9	2.0	1.5	1.8	3.0	0.6
7	3850	0.5	(0.1)	0.4	2.0	9.0	2.4	55.0	0.5
8	3700	0.02	(0.05)	0.3	1.8	0.5	2.4	1.0	0.1

largely explain the yield level obtained. The data for K are expressed as meq K/litre soil solution at nearly maximum water capacity. The values presented in brackets indicate the K buffer capacity. High values mean high K buffering whereas low values stand for low K buffer capacity. The phosphate fraction comprises the phosphate of the soil solution and the easily soluble phosphates. This fraction is in close correlation with the values obtained by the water extraction technique of Sissingh (1969). The data for Mg and heavy metals refer to a fraction of the EUF technique, which is closely related to the ion concentrations of the respective ion species in the soil solution.

The first site, a polder soil of the Western coast, was well supplied with all nutrients and thus showed a satisfactory yield level. The soil of the 2nd location had a poor K buffer capacity, and this might have been the factor limiting yield. The same applies to the 3rd and 4th soil, but here also the K concentration of the soil solution was too low. The same holds true of the soil of location No 6. On the location No 5 obviously phosphate availability limited the yield. In this case the Mn concentration was high, so that also toxic Mn effects might have injured yield formation. The soil of location No 7, too, contained large amounts of soluble Mn and also Fe. The low grain yield obtained at this location might be ascribed not only to the low phosphate level, but also to the high Fe and Mn contents. The poor yield of location No 8 is due to the low K and phosphate availability.

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