

IV. SOIL WATER CONTENT IN RELATION TO NUTRIENT UPTAKE BY THE PLANT

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1. INTRODUCTION

Besides the fact that water is the main constituent of a plant it is also consumed in enormous quantities in the process of transpiration. As such large quantities of this substance are necessary as nutrient and as growth factor it is no wonder that it is often the primary limiting factor in growth of the plant. Water, however, is also of importance as a fluid transporting substance to the plant and in the plant. Also numerous characteristics of its medium, mainly the soil, are strongly influenced by its content and movement of water. In these two latter respects it can have a profound influence on mineral nutrition.

In this discussion an attempt will be made to elucidate the manners in which a number of interrelationships between soil water content and nutrient uptake are effected. In many cases no more can be done than to indicate along which lines progress has been made in obtaining further insight into the separate problems. No attempt has been made at completeness. Many parts of this discussion are due to contributions given by my colleagues of the Institute and its contributions in this field will be stressed.

The uptake of nutrients can be considered as an interplay between the amounts available and the possibilities of utilization of the stock by the plant. On these grounds the interrelationships with water content can be divided into three categories.

First of all we can consider in which manner water content influences the amount and the character of the available nutrients. A second aspect is the replenishment of nutrients at the root surface, where depletion occurs as a result of absorption. Modes of transport from source to sink will be discussed. In the third viewpoint the utilization will be stressed. Discussion will be focussed on the development of the absorbing root system, in its relation to water content of the soil. A few remarks concerning climatological effects which may affect nutrient uptake by different manners will also be given.

2. WATER CONTENT IN RELATION TO AMOUNT AND MODE OF OCCURRENCE OF READILY AVAILABLE MINERAL NUTRIENTS

The stock of available nutrients in the soil can be considered to occur in two

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fractions. One fraction consists of the nutrients "bound" in some way or other, either adsorbed, fixed, undissolved or unmineralized. The second fraction consists of the dissolved nutrients. No sharp distinction can be made on account of exchange processes. An important distinction between these two fractions is their difference in mobility, which is very restricted for the first and large for the second.

Except for the possibility of direct "contact exchange" (JENNY and OVERSTREET, 1939) contributing to uptake to some extent, the main primary source of the nutrients is the soil solution. Its reaction to changes in water content will be our first point for discussion.

As the water content of the soil increases the concentration of the soil solution will diminish. An almost inverse relationship between amount of water in the soil and concentration can generally be expected for the anions NO_3^- , SO_4^- , Cl^- , because almost the whole stock of these ions is in the solution. For the phosphate ions the situation is different. Here an intricate interplay of equilibria occurs with "bound" phosphate and the result will be that dilution is partly counteracted by release of phosphate ions (METWALLY and POLLARD, 1959).

In considering the behaviour of the cations of K, Na, Ca and Mg the situation becomes more complicated. More moisture in the soil will bring about a certain dilution. But the amount of dilution will differ according to the ion species. One of the main operating factors is the valency effect. This will result in a relative increase of the monovalent K^+ and Na^+ ions in the soil solution in comparison to the divalent Ca^{++} and Mg^{++} ions. This latter phenomenon can be described by a simplified equation derived from Eriksson's formulation. This relationship can be expressed by:

$$\frac{j^+}{j^{++}} = G \frac{C_o^+}{V C_o^{++}}$$

in which j^+ and j^{++} are the amounts of mono-, respectively divalent cations adsorbed (in m.e.); C_o^+ and C_o^{++} are the concentrations of these cations in the equilibrium solution (mol/liter) and G is the Gapon exchange constant. (VAN SCHOUWENBURG and SCHUFFELEN, 1963; LAGERWERFF and BOLT, 1959).

Recent data given by Moss (1964) show that the ratio $\text{K}/\text{Ca} + \text{Mg}$ in the soil solution decreases from 0.20 to 0.13 as the pF value rises from 0 to 3 for the soil used. This shift in the soil solution is also evident in the mineral content of the plants used in the experiments (radish and *Brassica sinensis*). Under field conditions the same effect may be detected (fig. 1). In elaborating the results of 71 experimental fields on clay soils in which K-fertilizing experiments on potato were performed, MES (personal communication) found that leaf K-content was positively correlated with the amount of rainfall preceding the data of sampling

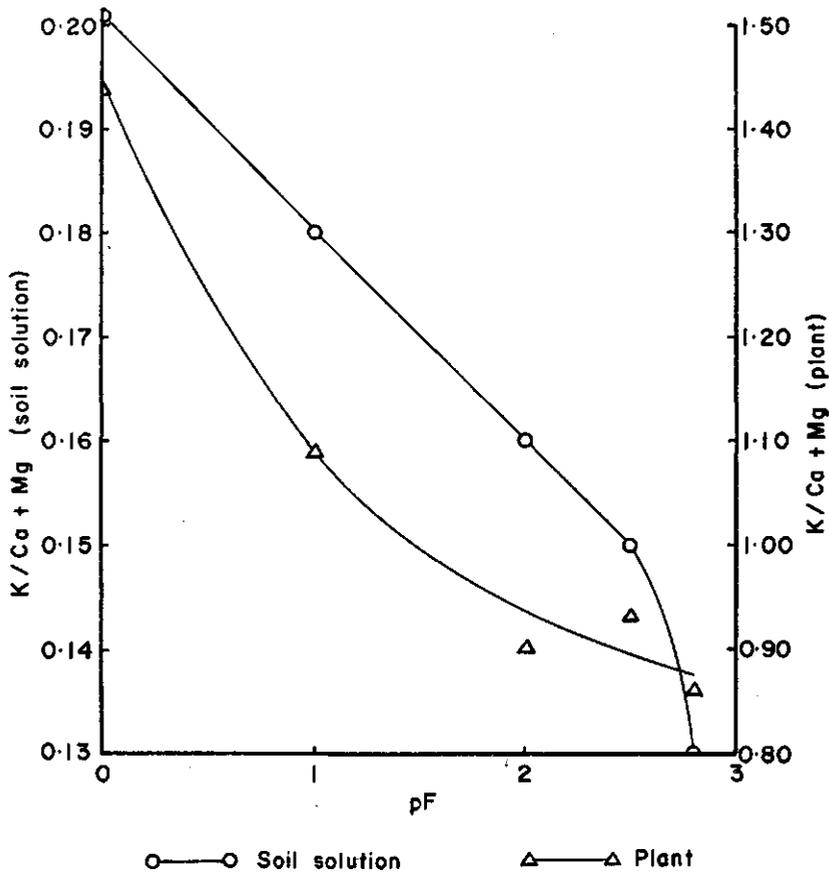


FIG. 1. The effect of dilution on the cation ratios of the soil solution and those absorbed by radish

up to a period of 45 days. Averaged over a period of 25 days each 10 mm rainfall effected a 0.25% increase in K_2O -content of the potato-leaves. The same type of response with potatoes has also been observed by VAN DER PAAUW (1958). It has also often been observed that Mg-deficiency is more liable to occur in wet years (BROWN et al., 1960).

Few data are available concerning variations in concentration of the minor nutrients along with moisture content of the soil in the range of pF 1 - 4.2. Results of OLIVER and BARBER (1966a) suggest that with increasing water content B concentration diminishes while Fe, Zn and Al concentration may rise. In a number of cases the interaction of water content and soil aeration becomes a decisive factor. As moisture content in the soil rises an increasing number of

the smaller capillary pores are filled with water. Also the thickness of the water films increases. As both diffusion of oxygen, and carbon-dioxide is enormously slowed down — O_2 by a factor 10^4 — in solution in comparison to in gas phase the $p O_2$ diminishes and bicarbonate content rises. The most extreme situation of reduction and high bicarbonate content will occur in flooded soil.

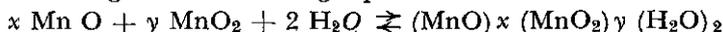
Taking the above-mentioned relations into consideration the question may be put what the requirements are for soil structure to allow a reasonable aeration at higher soil moisture contents, i.e. up to field-capacity (pF 2). This is the more important as lack of aeration does not only influence chemical soil equilibria but also profoundly effects root growth. If the air content at pF 2 decreases below 10, 15 or about 25 % for respectively heavy clays, silt soil, or sandy soils lower crop yields occur (BOEKEL, 1963; PATT et al., 1966). But if the water table is at a depth less than 100 cm these values may not be attained because of the lower pF and soil structure requirements are very high (BOEKEL, 1966). As these responses of the crop are effected by means of lack of optimal aeration of the root system this means that certain aspects of soil chemistry will also be affected.

Manganese availability may already be enhanced under conditions of low oxygen supply under normal moisture conditions (LABANAUSKAS et al., 1962).

Excess of water in the soil, however, can bring about far more important variations in availability of the minor elements. This excess of water is only important from an agricultural viewpoint for most crops if it only occurs incidentally, for a continuously anaerobic soil will not possess living roots. Temporary water saturation of the soil is, however, no uncommon feature.

The rise in bicarbonate content, especially in calcareous soil, can impede Fe absorption by the roots as a result of inactivation of enzymes.

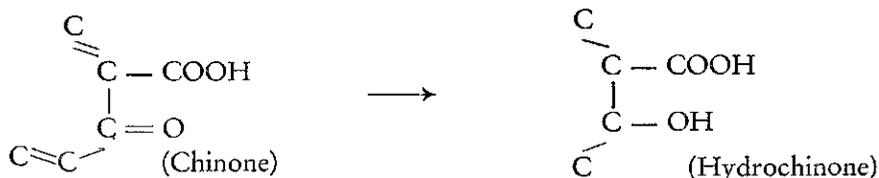
The anaerobic conditions result in reduction of MnO_2 to Mn^{++} , especially on acid soils (GRASMANIS and LEEPER, 1966). The amount of exchangeable manganese can increase enormously, resulting in toxicity (MIDDELBURG, 1967). According to GRAVEN et al. (1965) available Mn rises from 9 to 235 units after 144 hours of flooding on a Kellner loamy sand. However, there is another reaction, which may occur, and which has a contrary effect. The possibility of formation of a hydration complex, which is not plant available, also exists according to the following equation:



Especially in cold and wet soils the latter product can be formed and Mn absorption is disturbed. Evidence for reduced Mn availability if this type has been observed in pot experiments with clay soils taken from recent deposits in estuaries (DE GROOT, 1963).

The reduction that occurs in the soil under anaerobic conditions can give

rise to alterations in some organic compounds, resulting in enhanced chelate forming capacities. An example is the reaction:



If this occurs the solubility of Cu and Fe compounds is raised and availability is increased. Ultimately this may result in disturbances in the total minor element equilibria. For iron, however, the above mentioned possibility of toxic bicarbonate effects may counteract the result. Nevertheless the increase in soluble chelated Fe in the soil has been observed in pot experiments in wet soils (DE GROOT, personal communication). Under the anaerobic conditions due to water-logging the reduction processes may also affect NO_3^- and $\text{SO}_4^{=}$. Formation of toxic nitrite can occur but does not seem to be agriculturally important. Complete denitrification may effect important N losses. Sulphide, however, can certainly produce toxic effects. The formation of organic acids in general is not enough to be deleterious (FORD, 1965).

The rather complicated effects of very high moisture content on the chemistry and availability of the nutrient ions make it extremely difficult to forecast the result in a special case. In most cases survival of the root system is far more important so that the occurrence of these extremes should be avoided as far as possible.

3. SOIL WATER IN ITS FUNCTION OF ION TRANSPORTING MEDIUM

Although a very large volume of soil is permeated by the total root mass of a crop the volume of soil in direct contact with the absorbing root and its root hairs is nearly always small in comparison. Calculated estimates (WIERSUM, 1961) have given evidence that for a field crop this soil-root contact volume is usually less than 3% of the total. Of the total amount of available nutrients in the soil the same small percentage will thus be at immediate disposition of the plant. The amount of nutrition with which the root comes into contact by root-interception (BARBER et al., 1963) is even smaller.

The result is that most nutrients will have to migrate to the root surface. Contact-exchange and surface migration as postulated by JENNY can be consider-

ed of negligible importance. The only other way in which migration is possible is in solution, either by diffusion or by mass flow. Thus water has an indispensable function in the nutrition of a plant.

As a nutrient is absorbed by the root its concentration at the surface will be lowered and a diffusion gradient will be established. Ions will move along this gradient. The resulting decrease in concentration will also induce replenishment of the nutrients in solution either by desorption or by dissolving. This process of diffusion is necessarily restricted to small distances, 1-3 mm, to be of any worthwhile value.

The second mode of transport of ions is the passive movement along with the soil solution. This "mass-flow", first postulated by BRAY (1954), of the soil solution is induced by the water requirement of the transpiring plant. Except for some minor effects, this mass flow carries along all dissolved substances indiscriminately. By this means of transport much larger distances are involved. They are the same as the distances encountered in extraction of water from the soil, which means that most of the soil volume permeated by the root system is involved in the supply (HSIEH, 1964; RICHARDS and WEEKS, 1957).

a. *The process of diffusion in relation to the water content of the soil*

The amount of ion migration by means of diffusion is dependent both on the concentration gradient and on the total cross area of the pathways of transport. Variations in soil water content have a large influence on the total pathway available for diffusion.

In our own experiments (WIERSUM, 1958) excised root pieces were embedded in sand containing a fixed amount of nutrients. In this case mass flow is negligible, because no transpiring plant is attached to the roots. It was found that the uptake of several nutrients was positively correlated with increasing water content of the sand. Exactly the same type of relationship was established for the adsorption by pieces of embedded ion-exchange sheets. The relationship between water content and absorption tends to be linear. The steeper gradient for the ion-exchange sheets may be related to their high rate of fixation, which induces a steeper concentration gradient. As the water content of the substrate increases, more and more of the capillary spaces are filled with water and thus the total cross section of available pathway rises. Another factor facilitating diffusion is the decrease in tortuosity as the substrate contains more moisture.

Numerous investigators are involved in recent research on ion diffusion in soil as related to moisture content. It has now become evident that the volume percent of water in the soil is the decisive factor. The relationships with the pF value are more intricate and show much more variation according to the type of

soil (KEMPER and VAN SCHAIK, 1966). The speed with which diffusion occurs varies a lot for the different ions. The anions NO_3 , Cl , and SO_4 can be considered as fast moving, while phosphate is verly slow. As far as the cations are concerned K and Na seem to move faster and cover slightly larger distances than Ca and Mg (TEPE and LEIDENFROST, 1958; COOKE, 1966; VAIDYANATHAN and NYE, 1966).

The effect of water content on diffusion rate can be illustrated by results obtained by OLSEN et al. (1965). The porous system self-diffusion coefficient (D_p) ranged from 0.4×10^7 to 15.5×10^7 cm^2/sec . as the volumetric moisture content increased from 0.22 to 0.55. This is a nearly 40 times increase in rate of diffusion as soil suction is lowered from 6 to below 1 bar in a silty clay loam.

Generally a more or less linear relationship with soil water content is found (VAN SCHAIK and KEMPER, 1966; WESLEY, 1965; WIERSUM, 1958). Exceptions, however, have been found.

If, however, a higher water content of the soil results in a lowered concentration of a certain ion, e.g. Cl (PAUL, 1965), the enhanced possibilities for diffusion are more or less counteracted by a decrease in concentration gradient.

b. *The transport of ions by "mass flow"*

The water extracted from the soil by the plant carries along the substances dissolved in it towards the root surface. Interchange with adsorbed ions along the route will occur, but this has no influence on the overall process. If we conceive the soil solution as being in equilibrium with the solid phase of the soil, it is this solution that is transported.

If the amount of water consumed by a crop is known the amount of ions transported towards the root surface can be calculated if the constitution of the soil solution has been established. The amounts supplied are directly related to the amount of water transpired.

A generalized calculation (BARBER, 1962; WIKLANDER, 1965) immediately demonstrates the large differences in the amounts of the different ions transportable in this manner. Phosphate supply by this means is far below requirement, for potassium it is generally insufficient, while the amounts of Ca and Mg brought to the root surface are greatly in excess.

As the rate of uptake of any single ion is not directly linked with the rate of entry of water, this calculation of the contribution by mass flow is only of restricted value. However, nitrate is an exception. In the latter case we must regard the nitrogen supply of the plant to be dependent on this mode of transport. The distances involved are in the order of several centimeters.

An important consequence of this conception is that it has led us to the

realization that the ionic composition at the root surface may be widely different from that in the normal soil solution. Substances supplied in excess of uptake will accumulate at the root surface and its immediate vicinity. This may result in secondary interactions.

None the less it will be evident that the more water the plant can extract from the soil the higher the contribution by mass flow will be. Alterations in composition of the soil solution as discussed earlier will have to be taken into account however. A reasonably high moisture content throughout the soil can be considered favourable for this mode of supply. The results of recent investigations have given us an idea of the relative contribution of the two modes of transport.

Except for the quantities contained in the organic matter, which are only slowly released by mineralization the whole stock of available nitrate and sulphate is in solution. Nearly the whole stock contained in the soil volume contributing water to the plant is thus supplied to the roots. The depletion of soil nitrate under a crop in midseason (HARMSEN and KOLENBRANDER, 1965) is clear evidence of this occurrence. Chloride supply to the root surface occurs in the same manner.

OLIVER and BARBER (1966b) have investigated the mechanisms governing the supply of Ca, Mg, K and Na to soybean roots in a silt loam soil. A significant contribution to uptake of Ca and Mg was supplied by means of massflow. For potassium, however 87-96 % of the absorbed substance was calculated to have reached the root by diffusion. For sodium supply the mass flow was in excess of uptake.

The necessity for diffusion arises if supply by mass flow is insufficient. Besides for potassium, this is still more the case for phosphate. The result of supply by diffusion is clearly evident from the occurrence of thin depleted layers of soil along the roots as can be made visible by autoradiography.

The formulation of a relationship between uptake of ions and water content of the soil seems to be easiest in the case diffusion is the dominating factor. We then may expect an enhanced uptake along with a rise in moisture content. This kind of effect has been described by MEDERSKI and WILSON (1960) for P and K with corn. The Ca content was found to be independent of soil moisture content, which is not surprising if mass flow supplies excessive amounts.

A clear contrast in behaviour is also found in the results published by FLOCKER and TIMM (1966). The phosphate content in the petioles of potatoes rises as water tension in the soil is lower. The behaviour of the nitrate content is just the opposite.

If soil moisture decreases to values in the vicinity of wilting point ion transport is severely hampered. The possibilities for mass-flow approach zero and dif-

fusion becomes negligible. Maybe some contact-exchange absorption (JENNY and OVERSTREET, 1939) is still possible, but above pF 4.2 no significant uptake has ever been observed.

Summarizing we may come to the following general remarks.

It is evident that a high water content of the soil will be favourable as regards the supply of nutrients. In this respect we may refer to glass-covered horticulture where the growers aim at constant low water tensions in their soil. Of course leaching and development of anaerobic conditions must be prevented.

The question arises whether the discussed relationships can be formulated in a quantitative way. Here large difficulties are encountered. For the time being the most obvious way to tackle this problem seems to be the division of ions into two categories as regards their dominating mode of transport.

For those ions, such as phosphate, potassium, manganese, iron, and zinc, where diffusion is the main mode of supply a formula for diffusion process can be used. But the constant relating the diffusion rate to water content may vary for different ions.

When mass-flow accounts for the greater part of the supply water consumption by the crop is the regulating factor. This means that over a fairly large range of water contents the supply will be fairly constant. Only when transpiration is hampered in the dryer range the supply will decrease proportionally. But then the water itself will also become a very important factor.

Results obtained on corn under conditions of waterstress can illustrate this to some extent. The reduction in dry matter production (44 % of control) was accompanied by reduction of P content to 40 % and K to 71 %. Calcium however still accumulated to 93 % (JENNE et al., 1958). But in other research different results have been obtained. N content may be higher or lower.

4. THE ABSORBING ROOT SYSTEM IN RELATION TO WATER CONTENT OF THE SOIL

In more or less normal conditions growth of roots will occur during the greater part of the vegetative season. This continuous growth is more or less a necessity as the amount of easily extracted water and that of available but immobile nutrients in the root vicinity will become exhausted. Flow of water in unsaturated soil is mostly too slow to comply with plant requirements. To obtain a steady supply thus a continuous shift of the absorbing zones into fresh soil is needed.

Root growth in soil is possible up to the wilting point. (SALIN et al., 1965). The rate of growth increases, along with an increase in water content, which facilitates extraction. A number of investigators have published data on ob-

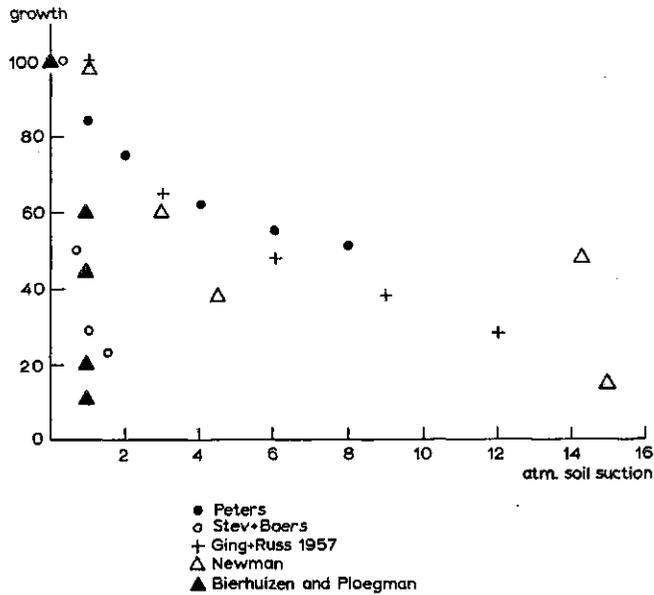


FIG. 2. Some of the data obtained on the relationship between soil water suction and root growth

served relationships between soil moisture tension and root elongation (GINGRICH and RUSSELL, 1957; PETERS and RUSSELL, 1960; RØNNIKE, 1957; NEWMAN, 1966; ROM and DANA, 1960; STEVENSON and BOERSMA, 1964; BIERHUIZEN and PLOEGMAN, 1958).

It is evident that the rate of elongation decreases as the water tension rises and that per unit of increase in tension the effects are usually higher in the range of low tension (PETERS, 1957). In figure 2 the results of a few investigations have been depicted to demonstrate the general trend.

The growth rate of a single root increases along with a rise in moisture content of the soil. This will go on till a condition is reached where lack of aeration becomes limiting (ROM and DANA, 1960). This lack of aeration is the result of decreased air-filled open pore space and also increase of waterfilm thickness on the roots (LEMON and ERICKSON, 1955). So in general roots will not penetrate downwards beyond the capillary fringe above the water table (WIERSUM, 1967). If the water table occurs at a shallow depth water suction in the soil will be less than pF 2. This will effect very poor aeration unless counteracted by a very favourable soil structure and a large total pore volume (BOEKEL, 1963).

Although rate of root growth is related to the ease of extraction of water the published results may partly be accounted for by an interaction with the pene-

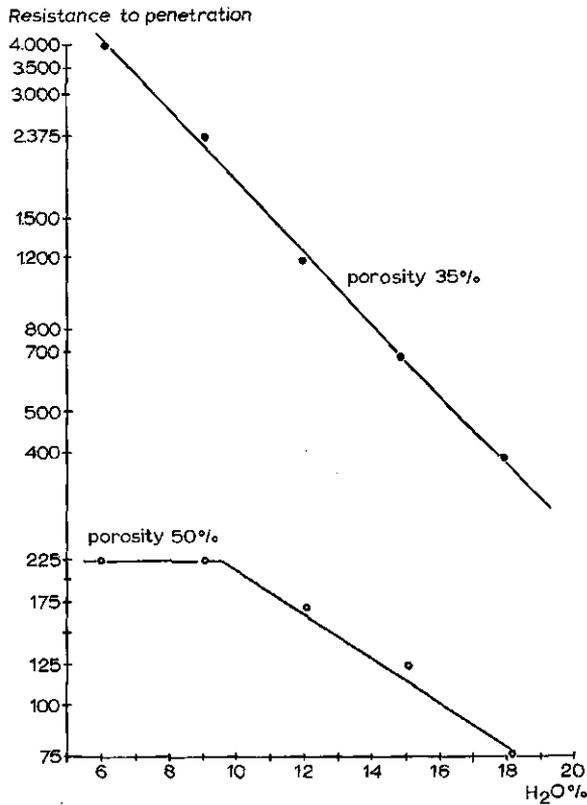


FIG. 3. An example of the relationships between penetrability of the soil and its moisture content at two different densities

trability of the soil. Penetrability of soil for roots is related to pore size (WIERSUM, 1957), density (SCHURMAN, 1965; BARLEY et al., 1965) and ease of displacement of soil particles (WIERSUM, 1957). The ease of displacement of soil particles is a factor, which is influenced by moisture content. That resistance to penetration in a soil decreases along with a rise in water content has been clearly demonstrated (MAERTENS, 1964; TAYLOR et al., 1966; fig. 3).

So in general it can be concluded that an increase in soil moisture content enhances root growth rate both by means of a direct and an indirect effect. Water contents higher than those at field capacity may, however, soon become deleterious on account of insufficient aeration unless a favourable soil structure occurs.

5. CLIMATOLOGICAL ASPECTS

Heavy rainfall in excess of evapotranspiration losses will result in loss of nutrients by percolation. The most important is the leaching of nitrate, of which process the characteristics have been dealt with by KOLENBRANDER (III). Losses of other nutrients, however, will also occur.

Another effect of periods of high rainfall may be the progressive destruction of soil structure. There are indications that the long lasting high moisture contents may result in reduced N mineralization. VAN DER PAAUW (1962) has clearly demonstrated that the cumulative depressing influence on yields of a sequence of wet years must be mediated by the soil.

6. GENERAL REMARKS

Having given this review of the manner in which way the water content of the soil effects the separate processes involved in nutrient extraction from the soil, the question arises if this knowledge can be of use to the agronomist. It is especially related to circumstances where regulation of water supply (drainage or irrigation) is of prime importance and chemical soil fertility has been taken care of.

What can be considered of general applicability?

Which soil moisture regime is to be considered best in relation to nutrition?

A continuous presence of available water in the whole rooted profile must be preferred. Loss of nutrients by leaching should be prevented. Keeping the soil as moist as possible, as long as aeration is sufficient to attain a sufficient depth of rooting. Then we may expect the most intensive utilization of soil nutrients, because of favourable conditions for mass flow, diffusion of ions, rate of root growth and mineralization.

We may have a look at management of soil moisture in protected horticulture. The rapid growth of the crops is facilitated by striving to obtain continuous very low soil moisture tensions.

What one should try to prevent is fluctuations of the groundwater level within reach of the root system. Roots will strive to penetrate downwards in periods of low water level, only to be killed by asphyxiation when it again rises. Another unfavourable condition to be aware of is temporary anaerobic conditions caused by pore saturation with water in the superficial layers as the result of heavy rains or irrigation.

If a subsoil occurs, which is penetrable for roots and which contains nutrients and sufficient moisture a temporary dessication of the topsoil need not be

deleterious to the crop and even enhance aeration of the subsoil. Own research (WIERSUM, 1967) has corroborated the fact that deeper situated roots can be as effective per unit of weight as the more superficial roots. A profile with these favourable characteristics will make water management easier.

On more or less saline soils one should be especially careful to avoid anaerobic conditions within rooting depth. Not only the roots may be impaired but low aeration may effect a loss in selectivity of the roots and a strong rise in sodium uptake (LABANAUSKAS et al., 1966).

The high moisture content leading to the poor aeration also results in a relative increase of the sodium concentration in relation to the divalent ions on account of the valency effect.

In some circumstances water management may have a profound influence on minor element nutrition. A too high moisture content could result in increased Mn availability and even toxicity. The other minor elements may also be effected, especially if the pH also changes.

At the end of this review it seems appropriate to mention the possible existence of relationships in this field, which would have general applicability. From the foregoing it will have become clear that water content of the soil can have an effect on nutrient uptake in quite a number of different manners. Soil chemistry, mode of supply and root behaviour are all involved.

The most clearcut relationship is that between moisture content and diffusion of ions in the soil. In this respect the available results of specialized investigations seem to offer good possibilities for a more generalized formulation.

Somewhat less strict is the relationship between rate of root growth and moisture content. Still all evidence shows that also in this case a higher moisture content is favourable, unless it leads to anaerobic conditions.

The relationship between water content of the soil and the ratio of mono-divalent ions in solution can also be expressed in an equation. A rise in moisture content of the soil will always favour a relative preponderance of the mono-valent ions in solution.

The supply of ions by mass-flow should be more dependent on the fertility level than on water content directly.

At this moment it seems impossible to suggest any more fundamental relationships of general applicability. But a better general understanding of the phenomena involved should stimulate further research. As more quantitative data become available more factors and parameters can be used in descriptive models, which would allow us to forecast the effects.

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