Crop response to the supply of macronutrients

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Abstract

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The response of a number of field crops (small grains, potatoes and sugar-beet) to the availability of nitrogen, phosphorus and potassium is described. For each combination of crop and nutrient element a generally applicable relation between economic yield and nutrient uptake can be described based on the minimum contents of the element in the principal crop organs. The wide variability in crop response to fertilizer application resulted mainly from widely varying relations between fertilizer application and nutrient uptake by the canopy. The application of this concept for the prediction of crop yield under nutrient limiting conditions is discussed.

Free descriptors: small grains, potatoes, sugar-beet, nitrogen, phosphorus, potassium, fertilizer, nutrient supply and uptake, potential production.

Contents

1 Introduction

In the last decade much attention has been paid to the calculation of weather-dependent potential production possibilities on both regional and global scale (Buringh et al., 1975; de Wit & van Heemst, 1976; Alberda, 1977). It has become clear however, that in many cases neither the available radiant energy, nor the amount of precipitation dictates the present level of productivity, but the supply of plant nutrients (Harpaz, 1975; van Keulen, 1977b; Penning de Vries et al., 1981). To analyse the present situation and to assess the prospects for improvement it is necessary therefore to gain insight in the quantitative aspects of plant nutrition and its influence on yield. Quantitative relations could be derived from dynamic production models which take into account physiological, physical and biochemical processes in more or less detail (de Wit et al., 1978; Seligman et al., 1975).

Such models are useful for integrating research results, for directing research efforts, for analysing the relation of production to nutrients under well defined conditions. However for analysis of agricultural production and planning, such models have several shortcomings:

- Our understanding of the basic principles is at present hardly sufficiently rigid to permit application under a wide range of conditions (de Wit et al., 1978).
- The required input data are more, both in quantity and quality than can be expected to be available for most situations of interest.
- The models are usually far too complex to be incorporated in models, aimed at planning agricultural production and so would lead to highly unbalanced combinations in terms of accuracy and detail.

For the purpose of agricultural planning, output should thus be described by a number of schematic functions, sufficiently general to be applied under a wide range of conditions and not requiring too much detailed input. This publication describes a method to arrive at such functions for the inputs of the major plant nutrients, illustrated for several field crops.

2 General considerations

The relation between the amount of a certain input applied (for instance water or a nutrient) and yield for a given crop, may vary considerably under different circumstances (Fig. 1). A rice crop (Fig. 1A) responded much better to nitrogen application in the dry season with high irradiance than in the wet season (Tanaka et al., 1964); the production of the plant mixture of the natural vegetation (Fig. 1B) may vary threefold under identical annual rainfall (Tadmor et al., 1974); the ryegrass (Fig. 1C) still responded with increased yields to the highest level of applied nitrogen under the 'wet' irrigation treatment, but not under the 'dry' treatment (Nielsen, 1963).

Determination of such 'input-output' relations does not increase our understanding of the basic causal relationships and are therefore difficult to use for extrapolation and prediction. It should be realized that to achieve a higher yield level from the application of increased amounts of input:

- the plant must take up the input, which may be inhibited by an inadequate application method (wrong time, place or form), so that the input remains in the soil (phosphate fixation) or leaves it without passing the plant (leaching of nitrogen, evaporation from the soil surface.
- after being taken up by the plant, the input must be utilized to produce economically useful material, such as dry matter for grass, grains for cereals of sugar for sugar-beet. This process may be hampered or completely inhibited by other growth limiting factors than the one tested such as low irradiance, lack of water or inadequacies in the supply of nutrients other than the one applied.

From a presentation as given in Fig. 1, it cannot be concluded which of the two processes was responsible for an observed lack of response, or what their relative contribution was to a positive response. To distinguish between both processes such input-output experiments must be combined with measurements that allow the calculation of the amount of input utilized by the plants. Fertilizer experiments should be accompanied by chemical analysis of the different plant parts, while in irrigation experiments measurement of the various terms in the water balance greatly increases their explanatory value. When such data are available, the results are most conveniently presented graphically as suggested by de Wit (1953). The method is illustrated in Fig. 2, using the same data sets as in Fig. 1.

The constructed diagrams consist of three graphs: one giving the relation between economic yield and the total amount of an input taken up by the crop, the second the relation between the amount of the input applied and the amount taken up, and the third graph, not repeated here, the relation of input applied and yield.

Figure 2A (graph a) shows that the curve relating nitrogen uptake and grain yield passes through the origin. Since total uptake, by both grain and straw is used here,

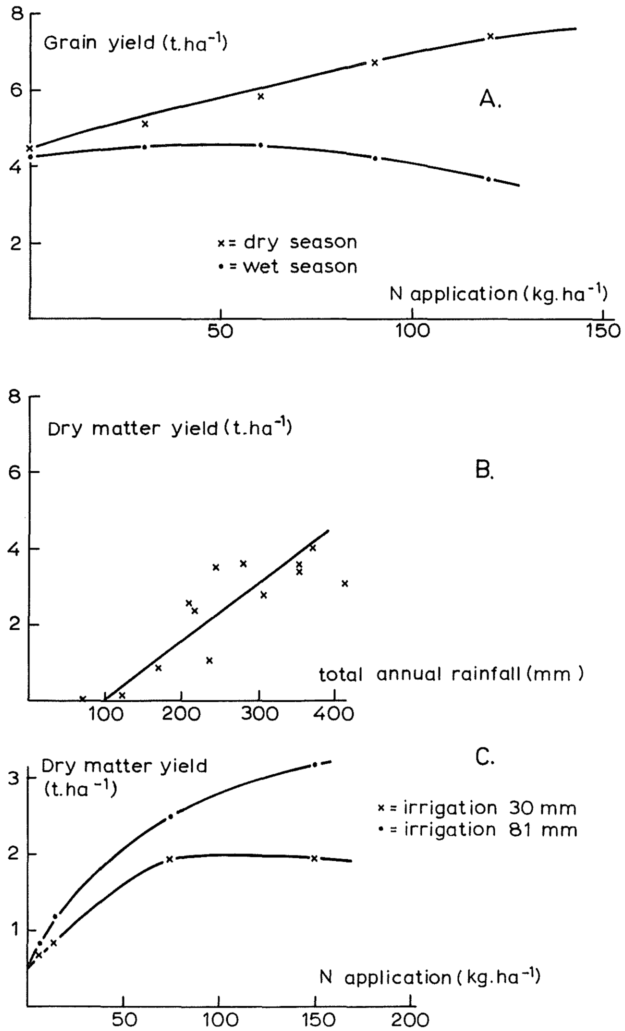


Figure 1. Relation between the amount of an input applied and crop yield for
A. Rice (Tanaka et al., 1964).
B. Herbaceous natural vegetation (Tadmor et al., 1974).
C. Perennial ryegrass (Nielsen, 1963).

it could theoretically be possible, that only vegetative material had been formed. For practical purposes, however, such situations are of little interest. In the region of limited nitrogen availability, a proportional relation exists between uptake and yield. Each unit of nitrogen taken up is converted to grain with equal efficiency. So the nitrogen in the tissue is diluted to a minimum level, below which a further increase in dry weight is inhibited. With higher uptake the linearity disappears, reflecting increased contents of nitrogen in the harvested material. Finally the curve reaches a plateau where increased uptake of nitrogen does not lead to higher grain yields. This is often called the region of 'luxury consumption'. The additional nitrogen partly increases the protein

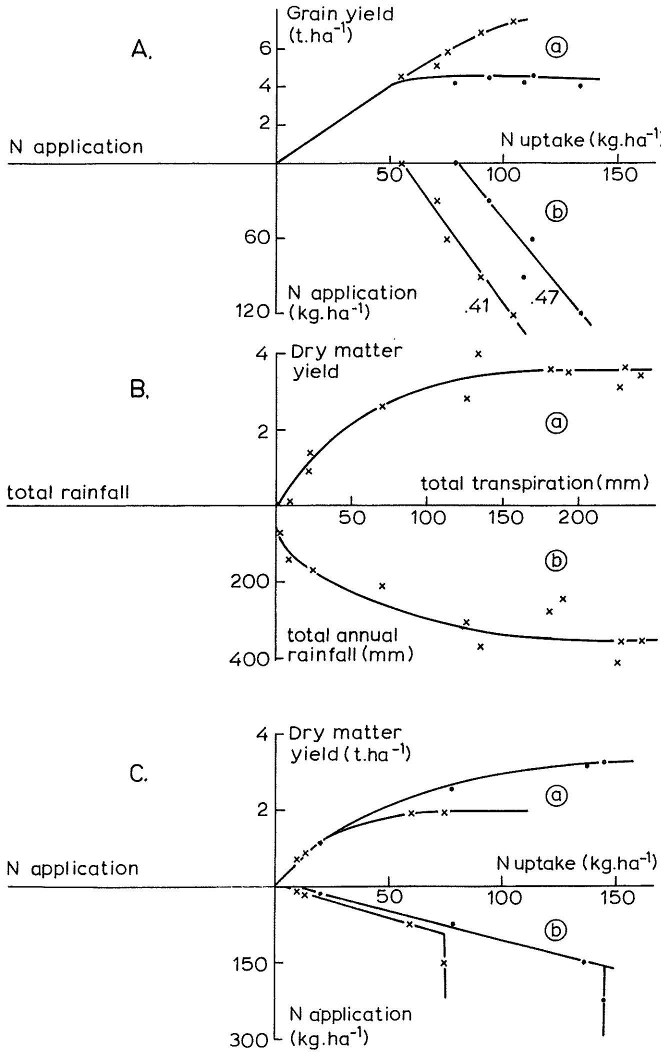


Figure 2. Relation between the amount of an input utilized and crop yield (a) and between the amount of an input applied and the amount utilized (b). (Data from same sources as Fig. 1.)
A. Nitrogen application on rice.
B. Water on natural vegetation.
C. Nitrogen application on perennial ryegrass.

content of the grains and partly remains in the straw. The level of the plateau is determined by the growth factor that is in short supply. Under conditions where water and nutrients are adequately available, it is a function of incident radiant energy (de Wit, 1965). The difference between the wet and the dry season for nitrogen application to rice was due to cloudy weather with low irradiance during the wet season (van Keulen, 1976). Shortage of other mineral elements or of water results in plateau-levels which are well below the one determined by radiation, as is shown by van Keulen (1977a) for phosphorus. Analysis of yield-uptake curves for nitrogen in small grains (van Keulen, 1977a) and for other major nutrients in various crops (de Wit, 1953) showed that these relations are in general independent of the type of fertilizer and the method of application, provided there is no serious deficiency at any stage.

The relation between amount of fertilizer applied and uptake (Fig. 2A, graph b) is almost always a straight line over the full range of applications. Uptake and losses from the soil are apparently proportional to the concentration of the element in the soil solution. The line is characterized by two parameters: the intercept with the horizontal axis and the slope with respect to the vertical, the first representing the inherent soil fertility with respect to the element for a given crop, the second the efficiency of fertilizer uptake. Both parameters will be treated in more detail.

The total amount of water transpirated during a growing season by herbaceous vegetation in a semi-arid environment (Fig. 2B), was obtained from a simulation model (van Keulen, 1975). In the model optimum nutritional conditions were assumed throughout, though that was not the case in the experiments. Soil moisture measurements in fertilized and non-fertilized fields suggest however, that there is not much difference in water loss between the two situations. The relation between total transpiration and dry matter yield has the same shape as that between nitrogen uptake and yield. At low levels of moisture availability, yield is proportional to the amount of water used. This reflects the fact that exchange of CO_2, necessary to maintain photosynthesis, and of water vapour are governed by the same physical principles (de Wit, 1958). Deviation from the straight line and the existence of a plateau indicate the transition from the situation where water is the main limiting factor, to one where other growth factors are limiting. The plateau level in this case was determined by the amount of nitrogen available from natural sources (net mineralization, fixation by both symbiotic and free-living micro-organisms and supply by rain (Harpaz, 1975)), the maximum value of about 3500 kg dry matter.ha^{-1}, reflecting a total amount of about 30 kg N.ha^{-1}. Even under the semi-arid conditions of the northern Negev, the production is not limited by moisture availability in more than half the years (van Keulen, 1975).

The relation between total rainfall and total transpiration (Fig. 2B, graph b) is curvilinear and shows considerable scatter, mainly because availability of water to the plants is governed not only by total amount of precipitation but also by its distribution. The erratic nature of rainfall in semi-arid regions means that the same amount of water may result from widely varying numbers of showers. A larger number of showers leads to longer periods of wetness of the soil surface and hence to larger losses by direct evaporation from the soil surface. When physiological ageing of the vegetation as a result of temperature or daylength prevents further uptake of water, one may encounter situations where moisture remains in the profile, especially at higher levels of precipitation.

The uptake-yield relation of Fig. 2C refers again to nitrogen. The shape is similar to that of Fig. 2A: a proportional relation at low nitrogen supply, gradual deviation and finally a plateau. The level of the plateau is determined by available moisture in this irrigation experiment. The application-uptake curve (Fig. 2C, graph b) is again a straight line at low nitrogen supply, but shows a breakpoint in both treatments. Depletion of water from the profile renders the nitrogen in the soil unavailable to the plant, because it cannot be transported to the root system. In this situation water not only influences the uptake-yield relation, but also the application-uptake curve.

It may be concluded therefore that in the study of input-output relationships a distinction between an application-uptake relation and an uptake-yield relation thus leads to a better understanding of the relevant processes and improves the prospects for prediction and extrapolation.

3 Quantitative aspects

3.1 THE UPTAKE-YIELD FUNCTION

3.1.1 Initial efficiency

3.1.1.1 Small grains

a. Nitrogen

In an extensive analysis of yield-uptake curves for nitrogen in small grains with emphasis on rice (van Keulen, 1977a) it was shown, that under most conditions the initial slope was constant, at a value of about 70 kg of grain (at a moisture content of 0.15 $kg.kg^{-1}$) produced per kg of N taken up (Fig. 3). The explanation of this value is, that the minimum content of nitrogen in the grain is 0.01 $kg.kg^{-1}$, that in the straw about 0.004 $kg.kg^{-1}$, and the grain to straw ratio is in general around unity. Variations in the slope may be the result from deviations in one of the above mentioned numerical values. Especially the grain/straw ratio may deviate substantially from one, as in the typical monsoonal climates, where rice requires a long vegetative period in order to mature during the dry season (de Wit, 1957). The slope may change then to values around 60, but this can be taken into account when the growing conditions and hence the grain/straw ratio are known.

The picture is more complex under arid and semi-arid conditions. Water shortage, particularly at the end of the growing season, that is during grain filling, may cause accelerated senescence of the leaves and hence reduced rates of photosynthesis. Nitrogen is in general incorporated preferentially in the young tissue and diluted during further development. Interruption of the flow of carbohydrates to the filling grain due to inhibited assimilation, then results in grains with a high protein content and the efficiency of nitrogen utilization decreases considerably, even under limited supply. This is clearly illustrated for wheat grown in Australia and India for wich initial efficiencies of about 40 result (Figs. 4A and 4B). In such situations it is therefore much more difficult to predict the effect of nitrogen uptake on grain yield.

Another situation in which the initial efficiency may deviate from the "normal" value is when a large proportion of the total uptake occurs after flowering. If the rate of uptake of nitrogen from the soil at that stage can keep up with the potential rate of grain filling (which may be determined either by the photosynthetically active leaf area or by the number of grains), again grains are produced with a high nitrogen content, while also in the straw the nitrogen content remains high. This effect is illustrated in Fig. 5: the slope is about 42.5 for nitrogen uptake at maturity, but is about 65 when the N-uptake at heading is used. The nitrogen taken up after that time did apparently not influence yield potential, which must have been fixed at an earlier stage. Under conditions where

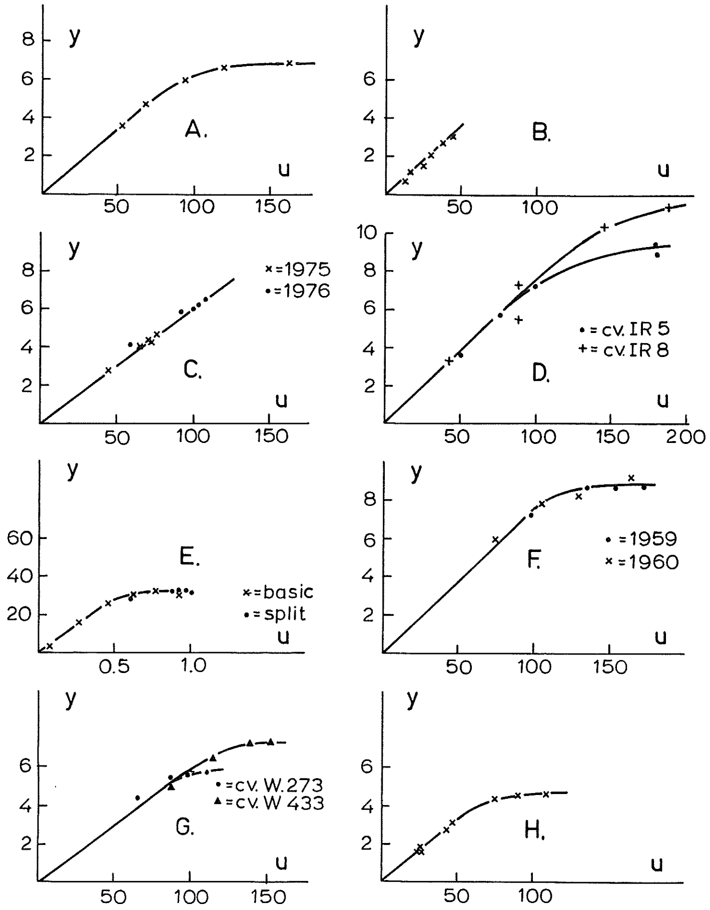


Figure 3. Relation between total nitrogen uptake (u in kg N.ha^{-1}) and grain yield (y in t.ha^{-1}, at 15% moisture content), except in E., u and y in g.pot^{-1}.
A. Winter wheat, the Netherlands (Dilz, 1971).
B. Wheat, India (Sarkar et al., 1975).
C. Rice, United States (Reddy & Patrick, 1978).
D. Rice, Peru (Sanchez et al., 1973).
E. Oats, in a pot experiment (Selke, 1940).
F. Sorghum, United States (Herron at al., 1963).
G. Maize, United States (Jung et al., 1972).
H. Barley, Great Britain (Widdowson & Penny, 1972).

nitrogen is in limited supply, however, its uptake after flowering is generally negligible and the phenomenon discussed here is then of little practical importance.

So for the construction of uptake-yield functions for small grains an initial slope of 70 can be used.

b. Phosphorus

In Fig. 6 the relation between phosphorus uptake and grain yield is given for a number of experiments with small grains. It may be concluded that also for phosphorus a

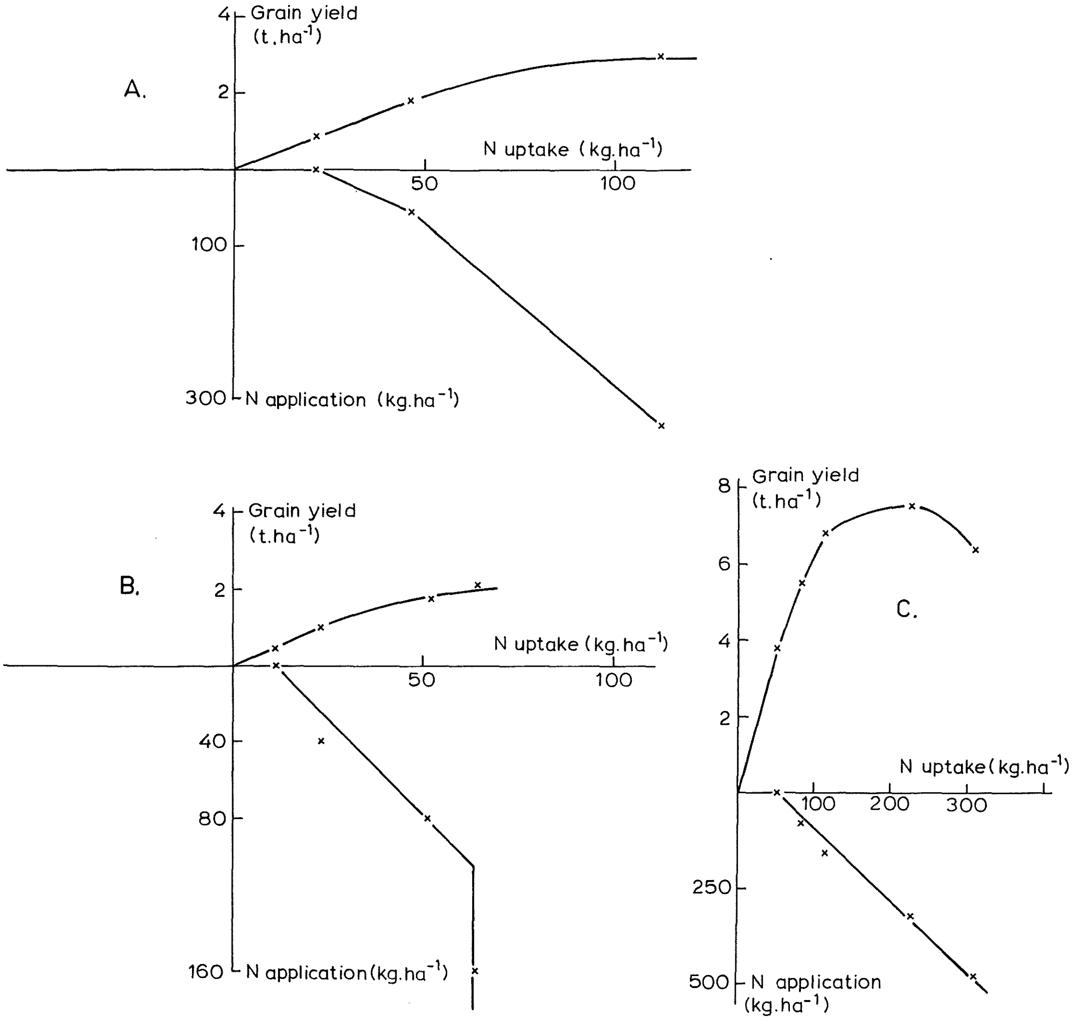


Figure 4. Relation between nitrogen uptake and grain yield, and that between nitrogen application and nitrogen uptake.
A. Wheat, Australia (Halse et al., 1969).
B. Wheat, India (Khetawat et al., 1972).
C. Rice, Peru (Sanchez et al., 1973).

minimum content in grain and straw exists. Examination of the phosphorus contents in limiting situations shows that these values in grain and straw are 0.0011 and 0.0005 $kg.kg^{-1}$ respectively. Applying the same reasoning as in the case of nitrogen would lead to a slope of 600 kg of grain per kg P taken up (or equivalent to about 250 kg of seed per kg P_2O_5 absorbed). The slopes in Fig. 6 seldom exceed the value of 450, since in virtually all cases the grain/straw ratio was well below 1. Most of the phosphorus taken up by the plant also ends up in the grains and therefore small variations in the grain/straw ratio do not affect the slope too much.

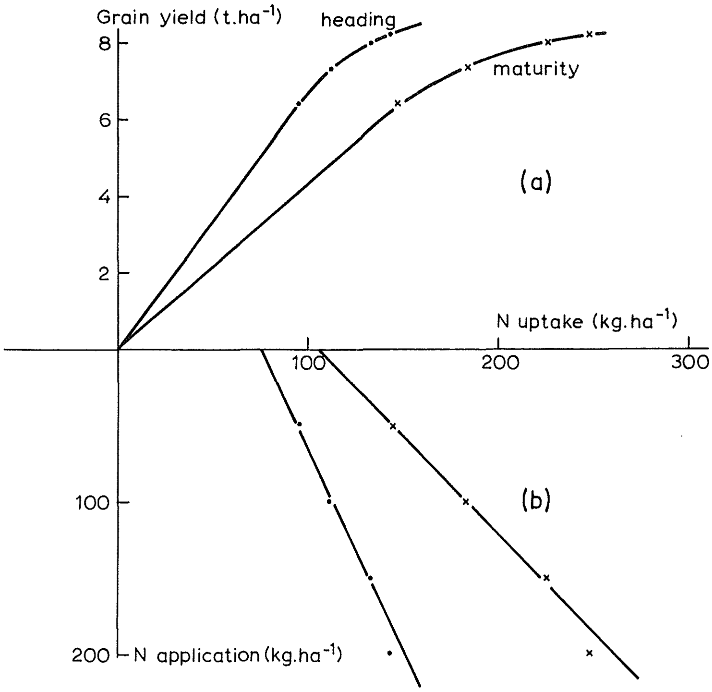


Figure 5. Relation between grain yield and nitrogen uptake (a) and that between nitrogen application and nitrogen uptake (b), at maturity and at heading for wheat in the Netherlands (Spiertz & Ellen, 1978).

In situations where nitrogen and phosphorus are both available in limited amounts, the P/N-ratio may be a more reliable indicator for the actual limitation than the absolute content of either element (Penning de Vries et al., 1981). That ratio varies from 0.04 under phosphorus limiting conditions to 0.15 if nitrogen is in short supply (W. Dijkshoorn, CABO, pers.comm.). The range between the two extreme values may be passed fairly quickly when either element is supplied to correct a limitation.

Considering the available evidence, it should thus be possible to predict the yield of grain from phosphorus uptake, if that element is limiting. The total amount of the element available to the plants during the growing season should then be known. This calls for a method, in which both the inherent fertility of the soil and the recovery of fertilizer can be estimated.

c. Potassium

In Fig. 7 yield-uptake curves for potassium in small grains are presented for situations where a pronounced effect of potassium uptake on yield was observed.

The variation in the initial slope of the curves presented, is much larger than for nitrogen and phosphorus. One of the reasons is that, at harvest the larger part of the potassium is found in the straw, since K is not a component of the plant proteins. Therefore normal variations in grain/straw ratio have a much greater impact on the initial

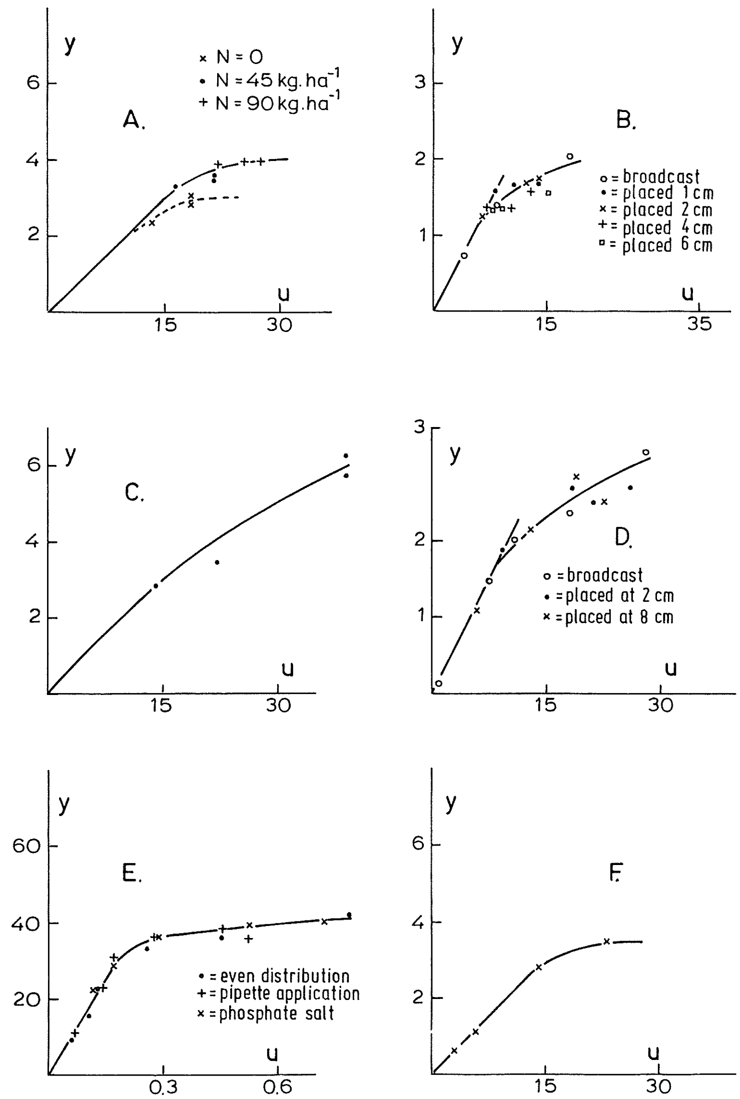


Figure 6. Relation between total phosphorus uptake (u in kg $P_2O_5.ha^{-1}$) and grain yield (y in $t.ha^{-1}$, at 15% moisture content), except in E, u and y in $g.pot^{-1}$.
A. Rice, Nigeria (Bredero, 1965).
B. Oats, the Netherlands (Prummel, 1950, cited by de Wit, 1953).
C. Rice, Mali (Traoré, 1974).
D. Oats, the Netherlands (Prummel, 1950, cited by de Wit, 1953).
E. Oats, in a pot experiment (Rauterberg, 1937).
F. Maize, Mali (Traoré, 1974).

slope. Another reason for the larger variation may be the fact that potassium has a double function in the plant, partly being a necessary nutrient as such, partly serving as a positive charge accompanying organic anions. As a balancing ion it can almost completely

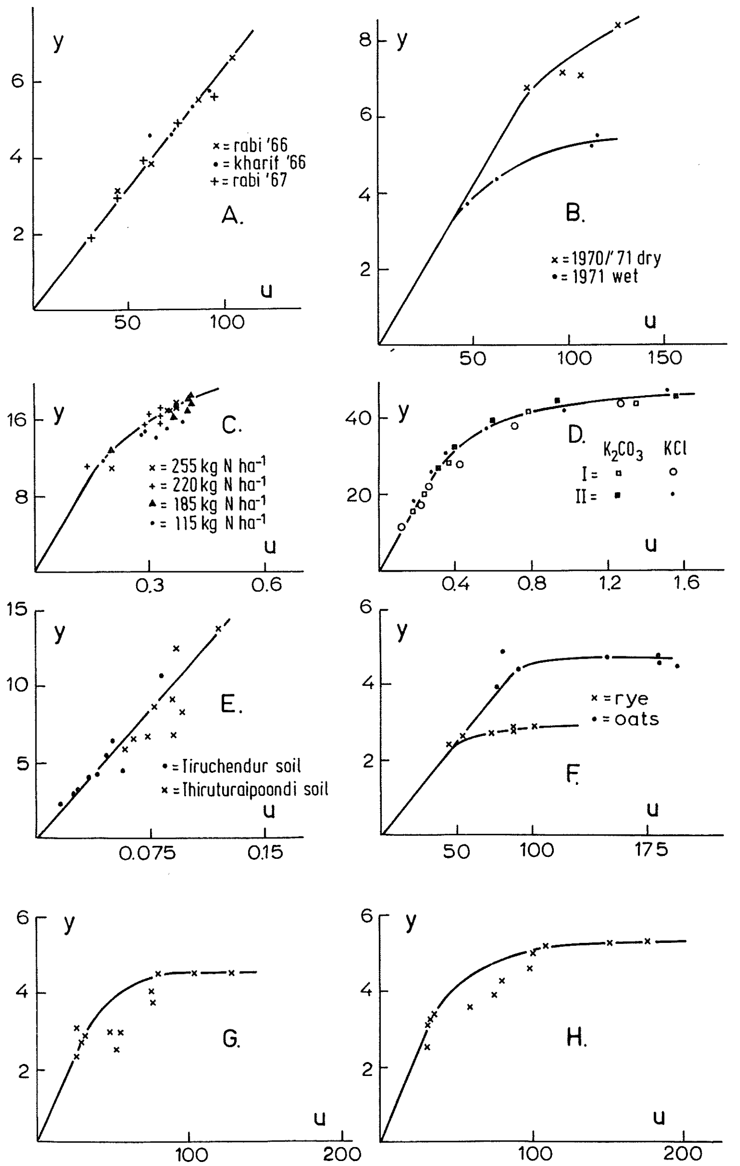


Figure 7. Relation between total potassium uptake (u and grain yield (y, at 15% moisture content). In A, B, F, G and H, u in kg $K_2O.ha^{-1}$ and y in $t.ha^{-1}$. In C, D, E, u and y in $g.pot^{-1}$.

A. Rice, India (Mahapatra & Panda, 1972).
B. Rice, Mali (Beye, 1974).
C. Rice, in a pot experiment (Esakkimuthu et al., 1975).
D. Oats, in a pot experiment (Rauterberg, 1937).
   I. Absolutely evenly distributed. II. Solution applied with pipette.
E. Millet, in a pot experiment (Kanaka Doss et al., 1975).
F. Barley, Great Britain (Widdowson et al., 1959).
G. Barley, Great Britain (Widdowson & Penny, 1973).
H. Wheat, Great Britain (Widdowson & Penny, 1973).

be replaced by other positive ions, if available in sufficient amounts (de Wit et al., 1963). The minimum and essential content required for vegetative growth is of the order of 200 $mmol.kg^{-1}$ (dry matter) (van Tuil, 1965) or 0.008 $kg.kg^{-1}$. In the grains the limiting potassium content is between 0.0025 and 0.005 $kg.kg^{-1}$. The combination of these two values with a grain/straw ratio of one, yields an initial slope for potassium of 55-80 kg of grain per kg K. Most of the curves presented in Fig. 7 are within this range, except those in 7F. The rye and oats had grain/straw ratios around 0.5 and accordingly initial slopes around 40.

It may be concluded that when the amount of potassium available for plant growth during the growing season can be determined, it is possible to predict the yield potential of small grains as determined by this element.

3.1.1.2 Potatoes

The fairly consistent results obtained so far with small grains provide an attractive basis for examination of other crops for their nutrient requirements. As a first example potatoes have been selected, this being another crop grown over a wide geographic range and for which many experimental data were available.

a. Nitrogen

The results of a selection of N-fertilizer experiments, covering a wide geographic and varietal range are given in Fig. 8. The yield is expressed as tuber dry matter, that being the variable most often reported. When only fresh tuber yields were given, dry matter was estimated, using a conversion factor of 0.22 kg dry $matter.kg^{-1}$ (fresh weight).

Examination of the various curves shows again that under conditions of limited nitrogen supply a proportional relationship between N-uptake and tuber yield exists. Comparison of the slope from the different curves indicates also for this combination of crop and nutrient a striking consistency. The slope amounts to about 100 kg of tuber dry matter per kg of N taken up (which is, at a dry matter content of 0.22 $kg.kg^{-1}$ equivalent to the production of about 450 kg of fresh tubers per kg of nitrogen). At harvest, about 80% of the total dry matter formed during the season is in the tubers, which have a limiting nitrogen content of 0.008 $kg.kg^{-1}$ (Vertregt, 1968). The haulm contains at harvest between 0.01 and 0.015 kg $N.kg^{-1}$, when grown under nitrogen-deficient conditions. Variations in any of the parameters may result in deviations from the value of 100 kg of dry tubers per kg of N taken up, but such variations do not generally exceed 10%.

A phenomenon regularly observed in experiments with potatoes is that the peak accumulation of nitrogen falls before the moment at which peak biomass is reached (Feigin, 1977; Carpenter, 1963). Closer examination of the data shows that only part of the losses can be explained by leaf fall. Some other processes must also play a role, such as direct leaching of the element from the leaves by rain, or transport of nitrogenous compounds to the roots and subsequent exudation. In most cases this phenomenon is more pronounced at the lower levels of nitrogen availability, so that malfunctioning of the membranes causing leakage from the cells at inadequate nutritional levels seems more likely than active excretion of the element. This phenomenon should be taken into account, when constructing

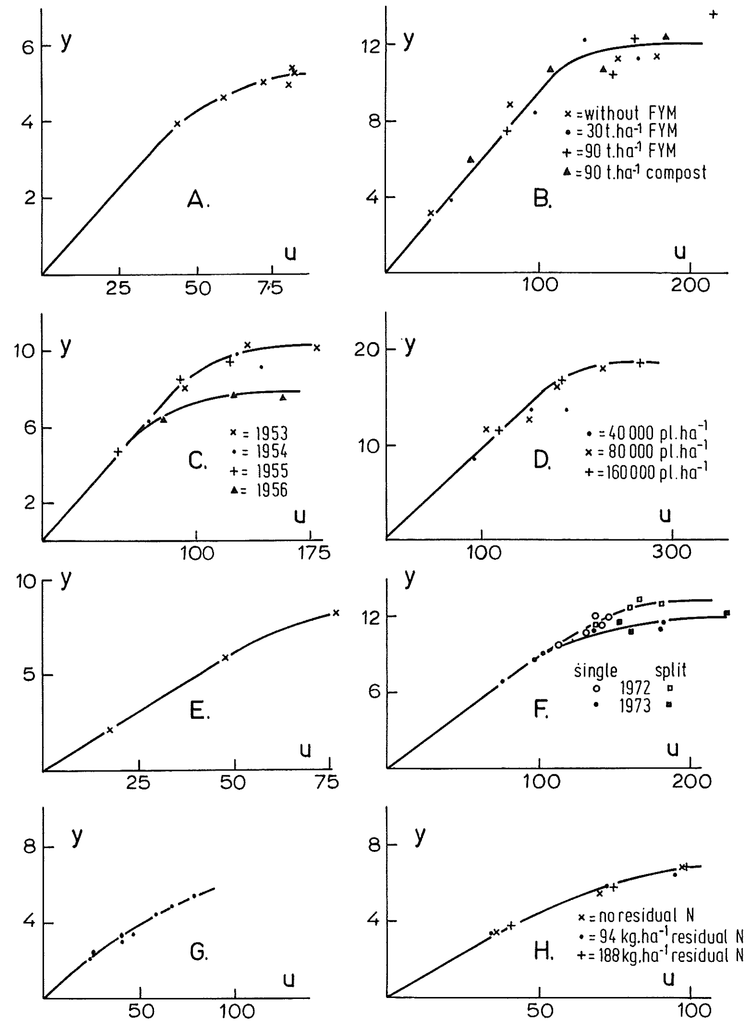


Figure 8. Relation between total nitrogen uptake (u in kg N.ha^{-1}) and dry tuber yield of potatoes (y in t.ha^{-1}).
A. Germany (Selke et al., 1963).
B. Israel (Feigin, 1977).
C. The Netherlands (de Haan, 1970).
D. The Netherlands (Bodlaender, exp. IBS 1056/1967).
E. Peru, *Solanum andigena* (Ezeta & McCollum, 1972).
F. United States (Liegel & Walsh, 1976).
G. Great Britain, u in tubers only, (Mattingly, 1974).
H. Great Britain (Widdowson & Penny, 1965).

uptake-yield curves as measured efficiency is otherwise too high, the lost nitrogen having contributed to the production process.

b. Phosphorus

Yield-uptake curves for phosphorus on potatoes are given in Fig. 9, for situations

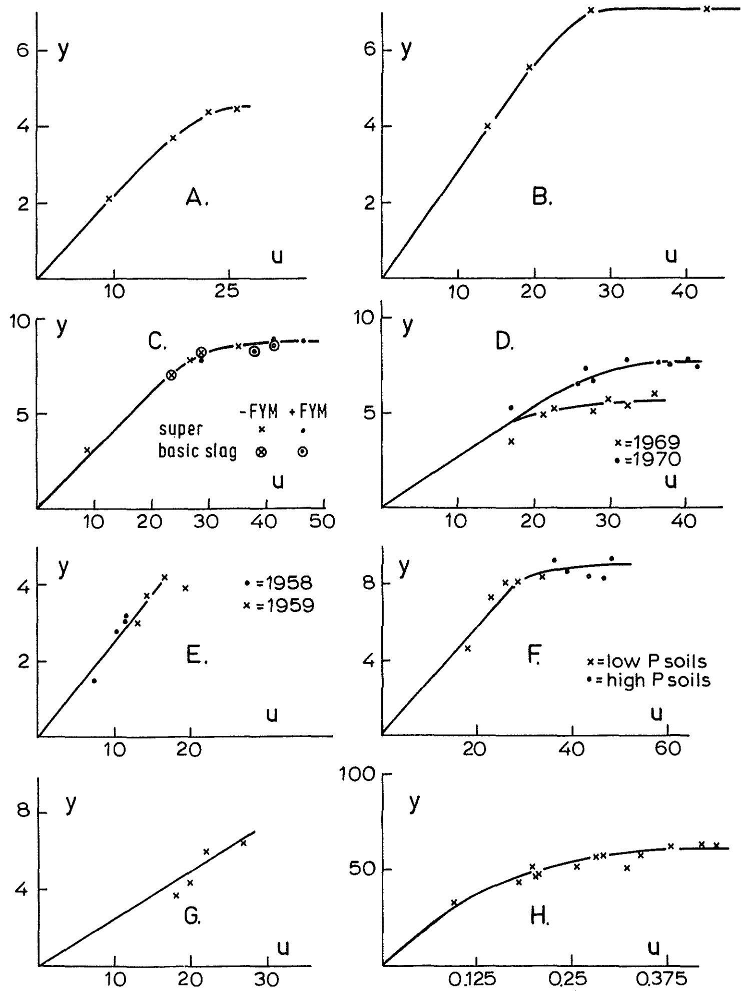


Figure 9. Relation between total phosphorus uptake (u in kg $P_2O_5.ha^{-1}$) and dry tuber yield of potatoes (y in $t.ha^{-1}$). Except in H, u and y in $g.pot^{-1}$.
A. United States (Jacob et al., 1949).
B. The Netherlands (van der Paauw, 1948).
C. The Netherlands (van der Paauw, 1950).
D. United States (McCollum, 1978).
E. United States (Carpenter, 1963).
F. Great Britain (Dainty et al., 1959).
G. United States (Krantz et al., 1949).
H. In a pot experiment (Selke et al., 1963).

where this element apparently limited production. There is almost always a linear relationship between total uptake and dry tuber yield in the lower part of the curve. The average slope of the experiments reported here, was 600 kg of of dry tubers per kg of P taken up (or about 2700 kg of fresh tubers at a dry matter content of 0.22 $kg.kg^{-1}$), the minimum contents in tubers and tops being 0.0013 and 0.0011 $kg.kg^{-1}$ respectively.

The phenomenon of losses in the later stages of growth also occurred for phosphorus

(Knowles & Watkin, 1940) but was less pronounced than for nitrogen, perhaps because of much lower contents in the tissue, or of lower mobility of phosphorus. The consequence is however, that the danger of introducing error in uptake-yield curves of phosphorus is not so great.

c. Potassium

Experiments in which potassium was presumably the limiting element for the production of potatoes were rather scarce. In Fig. 10 some of these have been summarized, showing again the familiar pattern. The initial slope of these averaged 80 kg of dry tubers per kg K absorbed. The minimum potassium contents in the economic plant parts (tubers) and in the haulms, were 0.012 and 0.0033 $kg.kg^{-1}$ respectively. The amount removed with the tubers is therefore high because of the generally high yields. For nutrition of potatoes potassium is very important from a qualitative point of view, although it does not generally have a quantitative aspect (as demonstrated by the limited number of suitable experiments). Low potassium contents in the tubers make these very susceptible to blackspot (Vertregt, 1968) which is a disadvantage in handling. Although quality is important in potato production, it is beyond the scope of this paper to treat its quantitative implications. The results of this survey would, however, suggest again that potassium shortage is not a very widespread phenomenon.

3.1.1.3 Sugar-beet

As another example sugar-beet was chosen, mainly because this crop was used in an earlier analysis of Dutch agriculture (van Heemst et al., 1978).

a. Nitrogen

In Fig. 11 yield-uptake curves for nitrogen applied to sugar-beet are presented, yield being expressed here as sugar, calculated from root yield and sugar content of the roots. The initial efficiency of nitrogen utilization was 80 kg of sugar produced per kg of nitrogen taken up. A numerical calculation of this value is somewhat more complex than for the previous crops, as it not only requires minimum contents of the element in the tissue, but also an estimate of the sugar content of the beets. Reported minimum values are 0.005 $kg.kg^{-1}$ in the roots and 0.02 $kg.kg^{-1}$ in the leaves at harvest. If it is assumed that 75% of the total dry matter produced is in the roots (taking into account leaves shed during the later stages of growth) and that the sugar content of the root is 0.8 $kg.kg^{-1}$ (on a dry weight basis) efficiencies of about 80 kg of sugar per kg of nitrogen absorbed will result.

Because of the same complex relation there is generally a fairly narrow plateau if sugar yield is plotted against nitrogen uptake. Higher uptake of nitrogen may lead to higher dry matter production, because the longevity of the leaves increases and their condition improves. Very often this results in a simultaneous decrease in sugar content of the roots, as photosynthates are used for growth and maintenance of the tops. The result is that at high uptake of nitrogen, the sugar yield may decline rather drastically as is illustrated in Fig. 11D. Moreover amino acids and other undesirable nitrogenous compounds

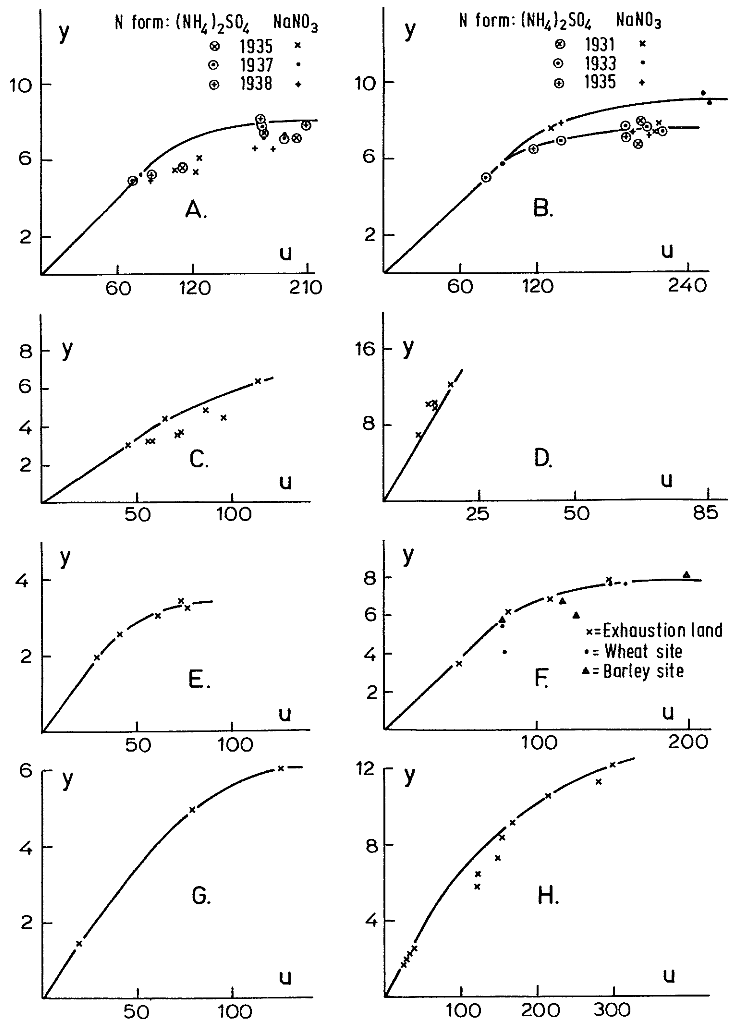


Figure 10. Relation between total potassium uptake (u in kg $K_2O.ha^{-1}$) and dry tuber yield of potatoes (y in $t.ha^{-1}$). Except in D, u and y in g (16 plants)$^{-1}$.
A. The Netherlands, u in tubers only (van der Paauw, 1942).
B. The Netherlands, u in tubers only (van der Paauw, 1942).
C. Germany (Amberger & Gutser, 1976).
D. Great Britain (Knowles & Watkin, 1940).
E. Germany (Görlitz & Specht, 1974).
F. Great Britain, u in tubers only (Johnston et al., 1976).
G. Great Britain, u in tubers only (Bolton, 1973).
H. Great Britain, u in tubers only (Widdowson & Penny, 1973).

may accumulate in the roots, to such an extent that they interfere with the crystallization of sugar during refining (noxious nitrogen). Such effects are however absent below uptakes of about 100 kg N ha^{-1} so that, in that range, sugar yield may be predicted from nitrogen uptake using the above given efficiency.

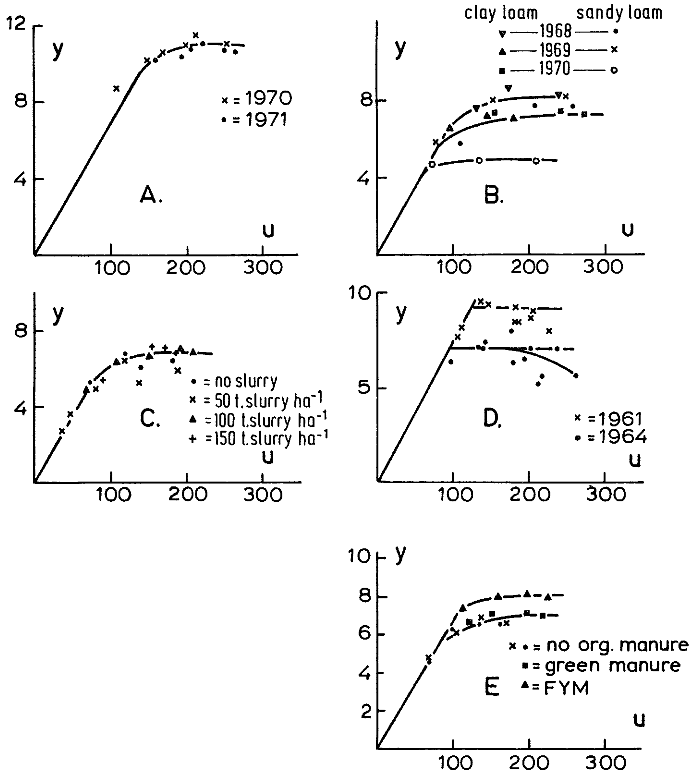


Figure 11. Relation between total nitrogen uptake (u in kg N.ha^{-1}) and sugar yield of sugar-beet (y in t.ha^{-1}).
A. United States (Smith et al., 1973).
B. Great Britain (Last & Draycott, 1975).
C. The Netherlands, Proefnr. AGM 155 (Proefboerderijen, 1976).
D. Czecho Slovakia (Strnad, 1972a).
E. Great Britain (Mattingly, 1974).

b. Phosphorus

In Fig. 12 the relation between phosphorus uptake and sugar yield is given for a number of experiments in which there was a response to application of that element. Unfortunately only a limited number of such experiments was available for analysis. The results suggest an initial slope of about 400 kg of sugar per kg of P taken up by the crop. The minimum contents reported are about 0.001 kg.kg^{-1} in the roots and 0.0025 kg.kg^{-1} in the leaves in terms of P in dry matter. Application of the same parameters as used for nitrogen then leads to the production of 430 kg of sugar per kg of P taken up, which is close enough to the value of 400 kg per kg P taken up to be used for yield predictions. Contrary to what is found for small grains there is almost as much P in the crop residues (leaves) as in the economic plant parts.

There is a need for more data to establish the phosphate requirement of sugar-beet more accurately, but the values reported here may serve as a first approximation.

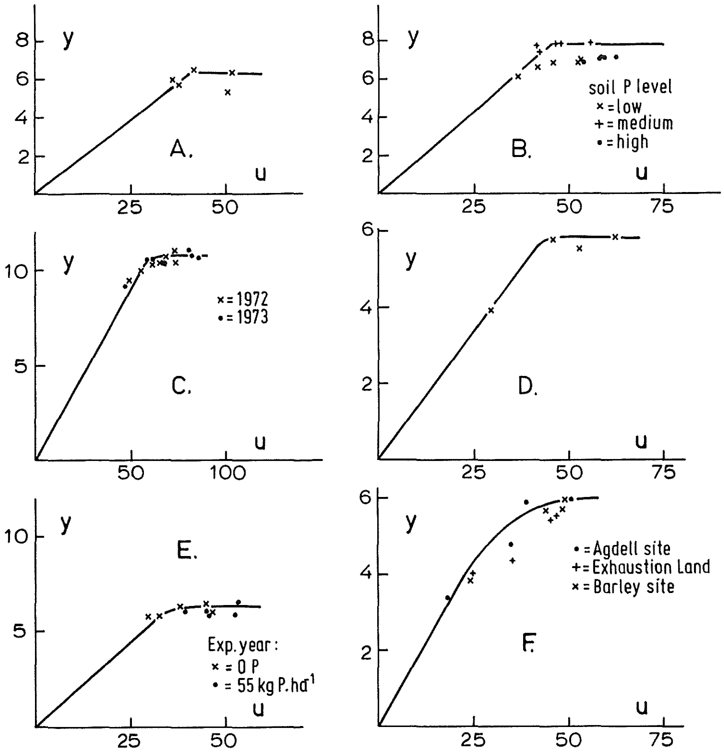


Figure 12. Relation between total phosphorus uptake (u in kg $P_2O_5.ha^{-1}$) and sugar yield of sugar-beet (y in $t.ha^{-1}$).
A. Czecho Slovakia (Strnad, 1972b).
B. Great Britain (Draycott & Durrant, 1976a).
C. United States (Westermann et al., 1977).
D. Great Britain (Draycott et al., 1978).
E. Great Britain (Johnston et al., 1976).
F. Great Britain (Johnston et al., 1970a).

c. Potassium

The role of potassium in sugar-beet nutrition is more difficult to assess than that of the other two elements. The interaction between potassium and sodium is so prominent in this species, that the two elements can hardly be treated separately (James, 1972). The available experimental evidence suggests that at least part of the functions of K in the plant may be taken over by Na (Schmehl & James, 1971), which does not seem unreasonable as far as it concerns the maintenance of electroneutrality in accompanying inorganic anions necessary for growth. That process holds in principle for all plant species and the more conspicuous role of sodium in sugar-beet would be the result of the fact that far larger amounts of this element are being taken up by this species.

Whatever the reason is for the strong interaction of K and Na in the sugar-beet plant, a practical way of treating the phenomenon has to be found. Two possible treatments suggest themselves: the first one is to disregard the interaction, hoping that an absolute

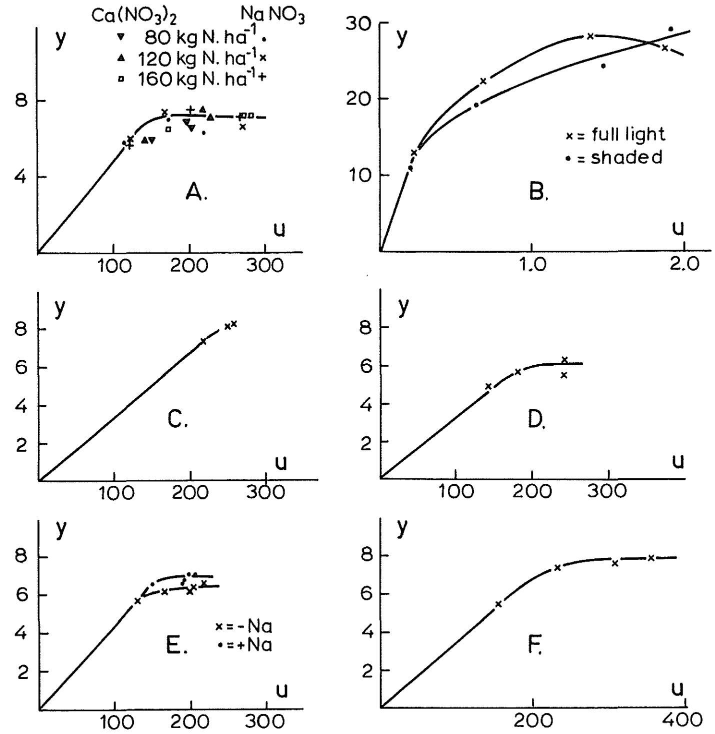


Figure 13.1. Relation between total potassium uptake (u in kg $K_2O.ha^{-1}$) and sugar yield of sugar-beet (y in $t.ha^{-1}$). Except in B, u and y in $g.pot^{-1}$.
A. The Netherlands (Jorritsma, 1956).
B. In a pot experiment (Warcholowa & Koter, 1970b).
C. Great Britain (Draycott et al., 1974).
D. Great Britain (Johnston et al., 1970b).
E. Great Britain (Draycott & Durrant, 1976b).
F. Great Britain (Draycott et al., 1972).

minimum content of potassium in the plant organs can be established, and a unique yield-uptake curve constructed. This procedure has been followed in the analysis presented in Fig. 13.1.

The minimum K-contents found in these experiments were 0.0067-0.0083 $kg.kg^{-1}$ in the root tissue and values between 0.0125 and 0.0187 $kg.kg^{-1}$ for aerial parts. Application of the parameters outlined in Section 3.1.1.3a (i.e. 75% of the total dry matter in the roots and a sugar content of 80%) results in an efficiency of about 60 kg of sugar produced per kg K taken up. The overall efficiency is in this case rather sensitive to changes in the weight ratio between tops and roots, as illustrated in Figs. 13.1C and 13.1D, where this ratio is about 0.6, and the efficiency declines to about 42 kg of sugar per kg of K taken up.

Another possibility would be to aim for a combined minimum content of (sodium + potassium), thus assuming a great deal of interchangeability between the two elements. In Fig. 13.2 this approach has been followed, expressing the uptake of the two elements in

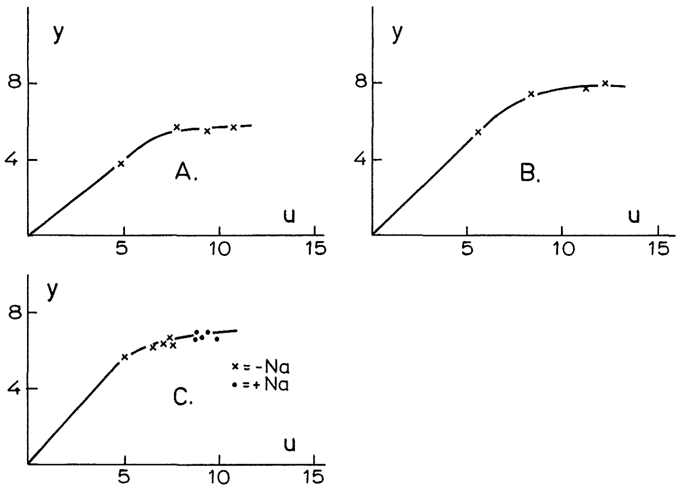


Figure 13.2. Relation between total uptake of potassium plus sodium (u in kmol (K+Na).ha^{-1}) and sugar yield of sugar-beet (y in t.ha^{-1}).
A. Great Britain (Draycott et al., 1978).
B. Great Britain (Draycott et al., 1972).
C. Great Britain (Draycott & Durrant, 1976b).

kmol. The minimum contents reported in these data range for dry tops from 1.0-1.5 mol (K+Na) .kg^{-1} and for dry roots from 0.2-0.5 mol.kg^{-1}. These values lead to utilization efficiencies of about 1000 kg of sugar per kmol of (Na+K) taken up.

From the limited number of data available for comparison of the two methods, it is not possible to conclude any advantage for one of the two. It seems at this point necessary to collect more information on the effects of potassium and sodium on sugar-beet production.

In this context, it is also of interest to pay attention to the recycling of potassium. Under conditions where potassium is readily available, its content in the above ground plant parts of the sugar-beet is fairly high (Shepherd et al., 1959), so that most of the element is in the crop residues. If these are left in or returned to the field, they may become a major source of potassium for the following crop.

3.1.2 The plateau level

As shown in Fig. 2, the uptake-yield curves deviate from a straight line at higher uptakes of the element. The actual value at which the deviation occurs may vary, since it depends not only on the total amount of the element available, but also on the exact timing of the availability. Finally the uptake-yield curve reaches a plateau. The level of the plateau is determined by the growth factor in short supply. Under conditions of optimum availability of moisture and nutrients other than the one considered, the maximum level is determined by the available radiant energy, as was illustrated in Fig. 2A. The value of the plateau may be calculated, when the level of irradiance is known, taking into account the length of the growing period and the proper partitioning factors for distribution of dry matter between vegetative and reproductive plant organs. To account for the distribution a harvest index may be used to obtain economic yield from total dry matter production at maturity (Sibma, 1977; van Heemst et al., 1978). A more realistic approach would probably be to consider separately the different phenological stages of the canopy and to apply the partitioning factors directly to production in each of these periods (van Keulen, 1976). Such a method would also facilitate the introduction of limiting factors (e.g. water shortage) during specific growth periods, which may have a much more pronounced effect on economic yield than on total dry matter production.

To determine what growth factor determines the yield potential in a given situation, the various 'potentials' represented by energy, moisture availability and nutrient availability may be compared to decide which one forms the minimum factor under the conditions at hand. (This of course still assumes the absence of pests and diseases). In such an approach the existence of interactions between the various growth factors becomes evident, as the effect of for instance phosphate application is different with low or high levels of nitrogen availability.

3.1.2.1 Influence of moisture availability

In Section 3.1.2. the specific role of water in determining production potential was mentioned. Construction of a relation between water uptake and economic yield is more difficult than for nutrients. There is, in broad terms, a good correlation between dry matter production and total water use, if differences in environmental conditions that determine the evaporative demand are taken into account (de Wit, 1958). However, the yield of a specific plant part may be affected by water stress in a particular period like flowering or fruit setting. The timing of the availability seems for water much more important therefore than for plant nutrients, the more so since plants cannot build up a buffer on which to rely for later use. A possible solution to this problem could be a stepwise calculation of yield potential in which, during each period, the relation between actual and potential transpiration is used as a correction factor, the value of that factor being dependent on the phenological stage of the canopy. The ratio between actual and potential transpiration may be calculated in a Thornthwaite-type approach (Arbab, 1974), in which the storage capacity of the soil is taken into account. Whether such an approach is feasible must be tested in more detail. Another important aspect of the moisture balance is that shortage of water may affect the yield-uptake relations notably that of nitrogen, as was shown earlier (van Keulen, 1977a). Whether the two aspects can be treated separately, or some sort of interaction has to be taken into account will have to be examined in more detail.

3.1.2.2 Complicating factors

A special case is application of (very) high amounts of inputs, as these may have an adverse effect on yield. This is illustrated in Fig. 4C for application of nitrogen to rice. The variety involved is a tall (almost 150 cm at harvest) traditional locally grown cultivar. The uptake of large amounts of nitrogen leads to excessive vegetative growth and subsequently to lodging, which adversely affects grain yield, because photosynthesis is hampered and grain may be lost. Moreover, lodging may cause management problems, as harvesting becomes increasingly difficult either by hand or by machine.

A similar effect, with other causes was shown in Section 3.1.1.3a for nitrogen applied to sugar-beet.

3.2 THE APPLICATION RATE-UPTAKE CURVE

If the yield potential for a given crop is to be estimated from the amount of nutrients utilized by the vegetation, it is necessary to estimate uptake as a function of application rate. In this section, the relation between these two variables will be treated for the three macro elements.

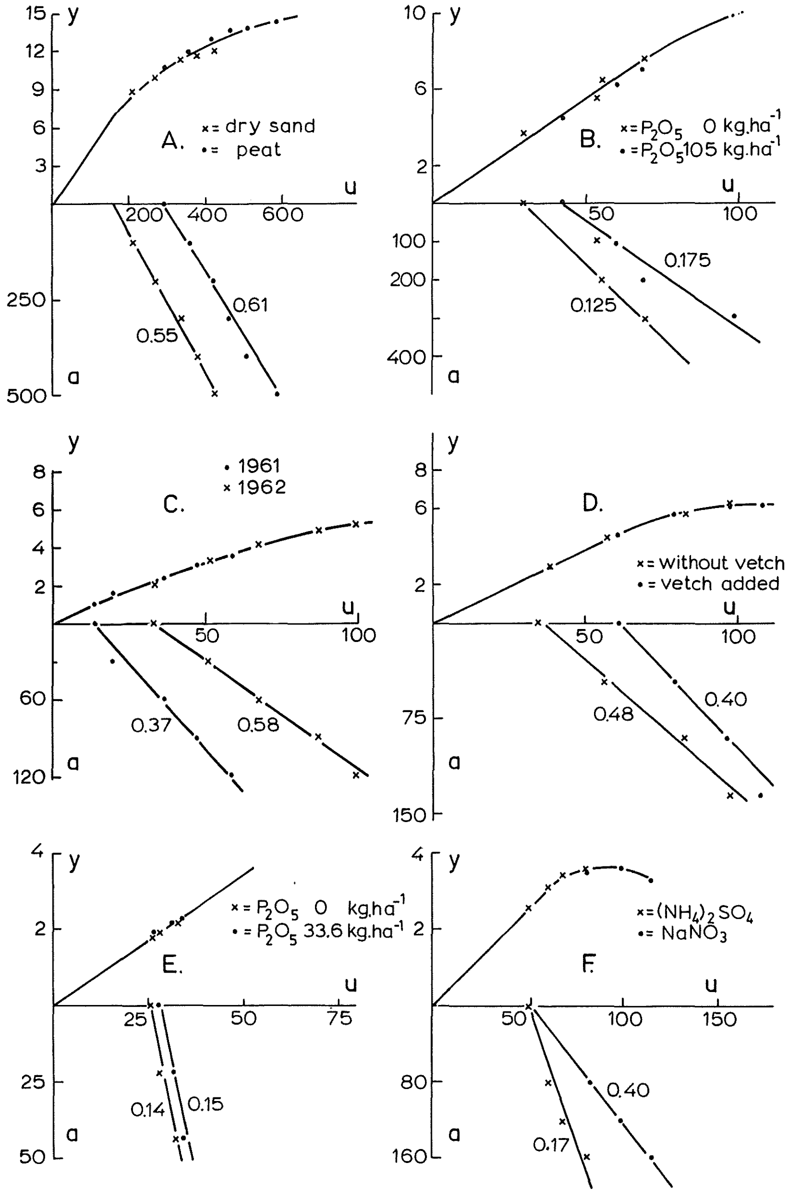
3.2.1 Nitrogen

For nitrogen the relation between the rate of application of fertilizer and the uptake by plants is in most cases a straight line, characterized by its intercept with the horizontal axis (uptake) and its slope with respect to the vertical axis (van Keulen, 1977a; Section 2).

3.2.1.1 Uptake at zero application (zero-nitrogen level)

The intersection of the application rate-uptake curve with the uptake axis represents the inherent fertility of the soil for the element with a given crop i.e. the amount available without fertilizer application. This value is partly a soil characteristic, depending on the mineral composition of the soil and the content and quality of its organic matter, as illustrated in Fig. 14A for permanent pasture in the Netherlands. The sandy soil, supplied 160 kg $N.ha^{-1}.year^{-1}$ (in itself a considerable amount) but was by far exceeded by the peat soil, with a supply of almost 300 kg $N.ha^{-1}.year^{-1}$. These high levels of nitrogen supply in the unfertilized situation must partly be attributed to the continuous application of excess nitrogenous fertilizers and large amounts of farmyard manure in the years before the experimental period. Such high rates of application cannot be fully utilized by the vegetation and lead to continuous improvement in the quality of the organic material in the soil (i.e. low C/N-ratios) and hence to high rates of mineralization. Especially for the peat soil, improved drainage conditions in the last decades may also have contributed to the high supply of N. Lowering of the water table leads to improved aeration conditions, which in turn cause accelerated breakdown of organic matter. This breakdown does not take place in an equilibrium situation and it leads to depletion of the soil N-store in the long run (Schothorst, 1978).

To estimate the zero-N level, it is important to know wether or not an equilibrium situation approximately exists. Reclaimed mineral soils, for instance, may also supply considerable amounts of nitrogen by breakdown of organic material accumulated in the unreclaimed situation. Such behaviour leads to high yields directly after reclamation, which gradually decline when a new equilibrium is approached, which may take 30-50 years



A. × = dry sand
• = peat
0.55
0.61
B. × = P_2O_5 0 kg.ha^{-1}
• = P_2O_5 105 kg.ha^{-1}
0.125
0.175
C. • 1961
× 1962
0.37
0.58
D. × = without vetch
• = vetch added
0.48
0.40
E. × = P_2O_5 0 kg.ha^{-1}
• = P_2O_5 33.6 kg.ha^{-1}
0.14
0.15
F. × = $(NH_4)_2SO_4$
• = $NaNO_3$
0.17
0.40
y
u
a

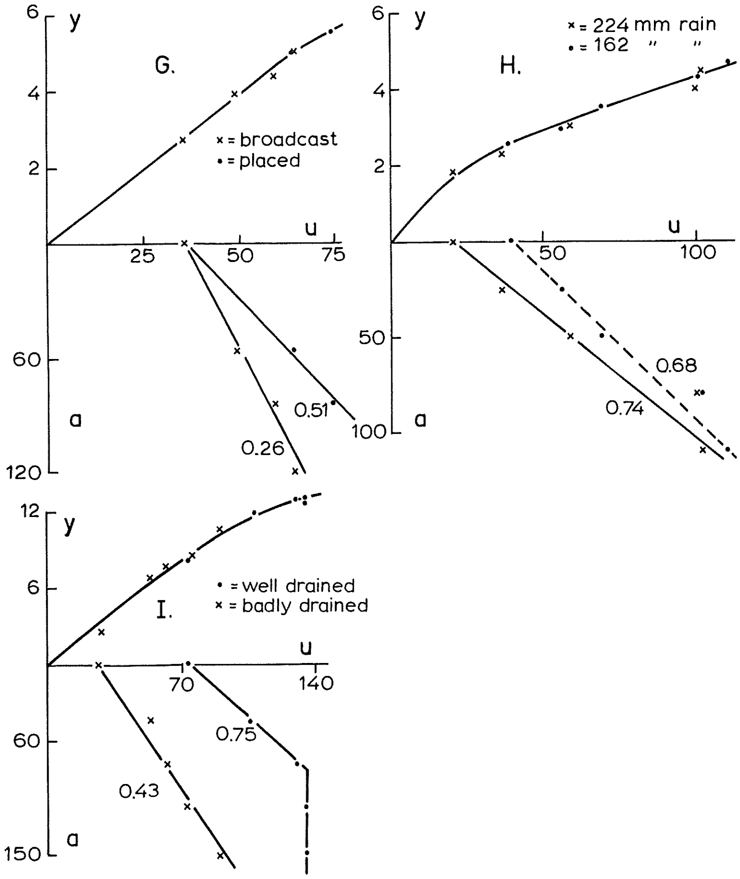


Figure 14. Relation between uptake of nitrogen (u) and yield (y) and that between application of nitrogen (a) and uptake.

A. Permanent pasture, the Netherlands (van Steenbergen, 1977); y in t.dry matter.ha^{-1}, u and a in kg N.ha^{-1}.
B. Unimproved pasture, Kenya (keya, 1973); y in t.dry matter.ha^{-1}, u and a in kg N.ha^{-1}.
C. Permanent pasture, the Netherlands (Oostendorp, 1964); y in t.dry matter.ha^{-1}, u and a in kg N.ha^{-1}.
D. Rice, United States (Williams et al., 1972); y in t.grain.ha^{-1}, u and a in kg N.ha^{-1}.
E. Rice, Burma (de Wit, 1957); y in t.grain.ha^{-1}, u and a in kg N.ha^{-1}.
F. Wheat, the Netherlands (Lehr, 1950); y in t.grain.ha^{-1}, u and a in kg N.ha^{-1}.
G. Rice, Indonesia (Ismunadji & Sismiyati, 1976); y in t.grain.ha^{-1}, u and a in kg N.ha^{-1}.
H. Winter rye, the Netherlands (van der Paauw, 1962); y in t.grain.ha^{-1}, u and a in kg N.ha^{-1}.
I. Winter wheat, the Netherlands (Sieben, 1974); y in t.dry matter.ha^{-1}, u and a in kg N.ha^{-1}.

(Baars, 1973). A similar effect is to be expected when management practice changes from the use of large amounts of chemical fertilizers to one virtually without. The yields achieved if nitrogen fertilizer is withheld for one year are not indicative for the expected yield level obtained in the continuous non-fertilizer situation.

Environmental factors, notably temperature and rainfall also have a distinct influence on the zero-N level. Temperature influences microbial activity and so for instance the rate of mineralization. Rainfall may have various effects on the N balance: it supplies nitrogen to the soil from atmospheric sources and, through its effect on the moisture balance in the soil, it also influences the rate of mineralization (Kononova, 1961) and the magnitude of losses by leaching and by denitrification. The variations due to environmental conditions are illustrated in Fig. 14C, referring again to permanent pasture in the Netherlands. The data were obtained from the first seasonal cut of grass, after an early application of nitrogen. In 1961 the spring was unusually warm, with about normal precipitation, whereas in 1962 it was a cold spring with about 25% more rainfall than normal. The low temperatures, hampering decomposition and the high rainfall, favouring leaching and denitrification, resulted in a zero-N level of less than half that of the other season. The effect of rainfall alone on the zero-N level is illustrated in Fig. 14H, referring to an experiment with rye in the northern part of the Netherlands, where part of the winter rainfall was intercepted by covering the crop. The decrease in percolation of water beyond the rooting zone resulted in a 50% increase in N uptake from the unfertilized plots. Presumably a substantial proportion of the nitrogen mineralized during the previous autumn was washed out under the high rainfall conditions.

During decomposition of organic material release and immobilization of inorganic nitrogen may proceed simultaneously, so that the amount of nitrogen available for plant uptake is the net result of both processes. Which of the two processes predominates at any moment depends on the composition of the organic material being decomposed, particularly on its C/N-ratio (van Veen, 1977). Under semi-arid conditions with a distinct rainy season, there is usually net mineralization from humus, the more resistant organic matter, at a low rate, at the beginning of the growing season, and concurrently decomposition of fresh organic material results in immobilization. Later on, the situation is reversed. If moisture availability or photoperiodic influences lead to cessation of growth before this 'turning point' has been reached, the mineralized nitrogen may not be available for plant growth at all. The time course of mineralization and immobilization is therefore also important in determining the zero-N level. An accurate prediction of the total amount of nitrogen mineralized during a growing season and the timing of that mineralization requires, however, detailed knowledge of the soil, the quality of its organic components and the prevailing environmental conditions (van Veen, 1977).

A striking phenomenon in the analysis of fertilizer rate-uptake curves is the effect of phosphorus on the zero-N level. In experiments with rice, de Wit (1957) already noticed that the yield-increasing effect of phosphate application was in fact a 'disguised' nitrogen effect (Fig. 14E), which was confirmed by observations of Brederq (1965). The explanation of these phenomena for flooded rice was thought to be the role of the blue-green algae in the nitrogen balance. Application of phosphates improves the growing conditions for these organisms and hence their ability to fix nitrogen from the atmosphere, part of which is available to the rice crop in the same season. This explanation does not hold, however, for the observations in Kenya (Fig. 14B) on natural pasture or those in Mali (J. Krul, pers. comm.) in pot experiments on local soils, with species from the natural vegetation. Also in these situations application of phosphate increased the zero-

N level though growth was still limited by N-shortage as may be concluded from the fact that all observations are situated along the same yield-uptake curve. Three processes could be responsible for the observed phenomenon.

In soils very low in phosphorus, decomposing micro-organisms are completely dependent on organic P for growth, so this element may be the limiting factor. Addition of this element then leads to improved growing conditions for the microbes and hence to increased decomposition of organic material.

Application of phosphorus stimulates root development, so that a larger volume of soil can be explored by the roots. This process seems less likely for pot experiments where both with and without phosphate application, root density was high. Moreover, theoretical considerations (van Keulen et al., 1975) suggest that even at relatively low root densities, virtually all the nitrogen in the bulk soil is available for uptake, either by mass flow or by diffusion. The data of Fig. 14B could nevertheless be interpreted in this way, since the recovery of the applied nitrogen fertilizer was also somewhat higher in the +P treatment. The results of recent field experiments (Penning de Vries et al., 1981) suggest yet another process although nitrogen is available in the soil in sufficient amounts, it cannot be utilized by the plants because of lack of phosphorus. Presumably a minimum P/N ratio cannot be passed in the tissue without upsetting plant metabolic processes. Whether in that case accumulation of inorganic nitrogen in the plant tissue takes place, which cannot be transformed into proteins and thus inhibits further uptake of N from the soil, cannot be concluded. Without additional experimental evidence, it is difficult to judge the relative importance of the various processes under different conditions, and even more difficult to predict their effects quantitatively.

Different management systems may also influence the zero-N level. Improved drainage conditions may change the nitrogen supply from the soil by its influence on aeration and hence microbial activity. This affects the net rate of mineralization of the soil organic matter and the potential loss of already mineralized nitrogen by denitrification. The effect is illustrated in Fig. 14I, for winter wheat in East Flevoland, one of the polders reclaimed from lake IJssel (Sieben, 1974). Appreciably more N is supplied from a well drained plot, where the watertable was always lower than 30 cm, than from the plot where the watertable was less than 10 cm below the surface from October till April.

A conspicuous effect arises from the introduction of green manures, especially legumes in the rotation, which may increase nitrogen availability for the following crop, as illustrated in Fig. 14D. How much additional nitrogen is available depends on the growing conditions for the legume, the effectiveness of nodulation and fixation, and the decomposition in the subsequent growing period.

In conclusion it may be stated that although qualitatively a great deal of knowledge is available with respect to the factors influencing nitrogen availability at zero-fertilizer application, reliable quantitative predictions are still difficult. In situations where such information is not available, an alternative procedure may be the analysis of yield data at low input levels, from which the nitrogen uptake may be derived, via the constant slope of the yield-uptake curve (van Keulen, 1977a).

3.2.1.2 Recovery of fertilizer

The slope of the application-uptake curve represents the efficiency of uptake of fertilizer, in other words the fraction of that fertilizer recovered in the (mostly above ground) plant material. As this determines how much of the often expensive input is really utilized, it is a parameter of prime importance, for the decision on economically feasible fertilizer application rates.

Large variations in this slope are observed when analysing data from fertilizer experiments. The main processes responsible for losses of nitrogenous compounds from the soil system are denitrification, volatilization and leaching. A process which should also be taken into account, especially when nitrogen is applied to previously unfertilized land is that of immobilization in the organic material. This may temporarily lead to low recoveries during which period the 'quality' of the organic matter is improved, until a new equilibrium is reached. Under anaerobic conditions, denitrification takes place in which the nitrates are used by micro-organisms as terminal electron acceptors. It is especially important in rice culture, where flooding of the soil invariably causes long periods of anaerobiosis. Nitrates applied as such or formed by nitrification from ammonium sources end up in the reduced zone, either by mass flow or by diffusion. They disappear within a very short time. The recovery of nitrogen fertilizers applied to rice, is therefore in general low especially when applied at the beginning of the growing season, when the requirements of the crop are low and the roots are in a weak competitive position. This is illustrated in Fig. 14E, where not more than about 10% of the applied fertilizer is taken up by the crop. Split applications may improve the situation, since later in the season the rates of uptake are higher and hence the residence time of the fertilizer in the soil shorter. But even when applied during the period of maximum growth and uptake more than 40% may be lost (Koyama et al., 1973). An effective method to minimize denitrification losses is placement of ammoniacal fertilizers directly in the reduced soil layer. The absence of oxygen prevents nitrification and hence the subsequent transformation into gaseous compounds. The advantages of this method are illustrated in Fig. 14G, where incorporation of a basal application doubled the recovery fraction in comparison to the normal practice of broadcasting. So much higher yields could be obtained, not by increasing the amount of input applied, but by adopting management practices, which lead to a more efficient use of those inputs. The same phenomenon is also shown in Fig. 14I where improvement in the drainage conditions increased the recovery fraction from 0.6 to almost 0.75. Why the application-uptake curve in the latter case levels off at higher application rates is not clear. The amounts of about 120-140 kg $N.ha^{-1}$ seem too low to exept 'nitrogen saturation' of the material.

Whether denitrification also plays an important role in nitrogen losses under 'upland' conditions is still a subject of much debate. Traditionally nitrogen balance studies have ascribed unaccounted fractions to denitrification losses. Direct measurements of denitrification under field conditions are, however, scarce. Recent theoretical work (Leffelaar, 1977) indicates that anaerobiosis may indeed occur under upland conditions, especially when respiratory activity is locally concentrated (within structural elements, around plant roots) and the diffusion of oxygen is impaired by water layers around these spots. Reliable quantitative estimates of the importance of the process under 'aerobic' conditions are however difficult to obtain. In view of the crucial importance of the denitrification term in the nitrogen balance, more emphasis on the subject seems warranted.

Weather conditions during the growing season also play a role in determining the efficiency of fertilizer uptake. As for the availability of soil nitrogen, conditions that favour denitrification and leaching decrease the fraction of the applied fertilizer recovered. This is illustrated in Figs. 14B and 14C where lower availability of soil nitrogen coincides with a lower recovery. The same phenomenon was also observed by Brockman et al. (1971) in their analysis of nitrogen fertilization experiments in grass swards. There again utilization of the applied chemical fertilizer could be improved by improved management: application at the proper time in amounts that can be utilized by the crop within a short time might reduce losses from leaching and denitrification. Under conditions where these processes are relatively unimportant, as in semi-arid regions, an inverse relation between the zero-N level and recovery seems to exist (Penning de Vries et al., 1981). The reason for this phenomenon is not yet clear.

Volatilization of nitrogen, particularly from ammoniacal sources may be an important source of losses. This process takes place when the fertilizers are applied superficially, in particular on soils with a high pH. The effect on the recovery is shown in Fig. 4F, for spring wheat in one of the reclaimed Polders in the Netherlands. The pH of the soil before the nitrogen dressing was 8.2 (Lehr, 1950). At such a high value, most of the ammonium sulphate which had been broadcast, disappeared within one month of the dressing, indicating high rates of volatilization. Similar results were obtained by Sahrawat (1978) who reports volatilization losses of 5-15 kg $N.ha^{-1}$ in the first days after broadcasting $(NH_4)_2SO_4$ to flooded rice. In the soil pH was between 7.5 and 8.6 and in the flood water between 8.5 and 9.5, the latter as a result of CO_2-depletion by the photosynthetic activity of blue-green algae. Indications for losses of ammonia through volatilization were also obtained in experiments in the northern Negev Desert of Israel (van Keulen, 1975). The phenomenon seems thus fairly widespread and should be taken into account in estimating recovery fractions.

Whether it will be possible to obtain accurate estimates of recovery fractions from independent data, such as composition of the soil including its organic components, normal rotation, method of fertilizer application and prevailing wheather conditions, remains to be tested.

3.2.2 Phosphorus

In large parts of the world crop production under natural conditions is limited by phosphorus availability. This observation and the increase in the price of phosphate fertilizers in recent years are sufficient reason for a closer look at phosphate fertilizer application.

Phosphorus may be present in the soil in various forms. For a review of the extensive literature on this subject see Beek & van Riemsdijk (1979). Here, some attention is needed however, both to increase insight in the relations presented and to hint at gaps in the knowledge where further research may be helpful.

In contrast to nitrogen, a major part of the total store of phosphorus in the soil may be present as inorganic compounds of low solubility, notably aluminium, iron and calcium compounds. The proportion of P present in these forms in virgin soils varies between 10 and 80%. This wide variation probably mainly reflects differences in local conditions governing the formation and breakdown of organic phosphorus compounds. Under intensive agriculture, where phosphatic fertilizers have been used for a long time, the organic store is relatively unimportant (Beek, 1979). The organic and the inorganic pool of phosphorus each have their own cycle and interact through their influence on the composition of the soil solution. For any given situation, which is not too far from equilibrium, that is either the natural situation where exploitation is negligible or intensive agriculture with a regular supply of phosphate fertilizers, only one of the cycles may be of practical importance. In non-equilibrium conditions, for instance when exploitation starts, it seems likely that the interaction between the two cycles becomes important. But to estimate the availability of phosphorus, a quantitative description of both the organic and the inorganic cycle is necessary. Despite the vast amount of experimental work on phosphorus fertilizers, such descriptions have only recently become available (Beek, 1979; Cole et al., 1977) and they have not been thoroughly tested.

3.2.2.1 Uptake at zero application ('zero-phosphorus level')

As for nitrogen, the intersect of the fertilizer rate-uptake curve with the uptake axis represents the inherent soil fertility for phosphate for a given crop. It is on the one hand a soil characteristic determined by mineralogical composition and organic matter content and composition as illustrated in Fig. 15J, where a sandy soil and a reclaimed soil of mixed peat and sand ('dalgrond') from the Netherlands are compared, the latter supplying more than double the amount of phosphorus in the same year to the same crop. Differences between crops also exist, associated with differences in rooting pattern and root growth rates (Cole et al., 1977; Powel, 1977), since a substantial proportion of total phosphorus uptake is due to interception.

The concentration of phosphate ions in the soil solution, which is a major determinant for uptake by the plants, is the net result of chemical and biological transformations of P in the soil (Beek & van Riemsdijk, 1979). Retention, desorption and dissolution proceed concurrently, thus continuously changing the concentration of P in the soil solution, which in turn influences the rate and direction of these processes. The exchange rates between the various components of soil P and between those components and the soil solution are influenced by environmental conditions in the soil, such as moisture content, temperature and pH. The influence of pH is illustrated in Fig. 15I, where liming of an acid lateritic soil considerably increased the zero-P level. A pronounced effect of pH could also be expected in soils where most of the phosphorus store is present in organic forms. The availability of P in such soils is determined mainly by the decomposition rate of the organic material and hence by microbial activity, which is strongly pH-dependent (Webber, 1978; van Veen, 1977).

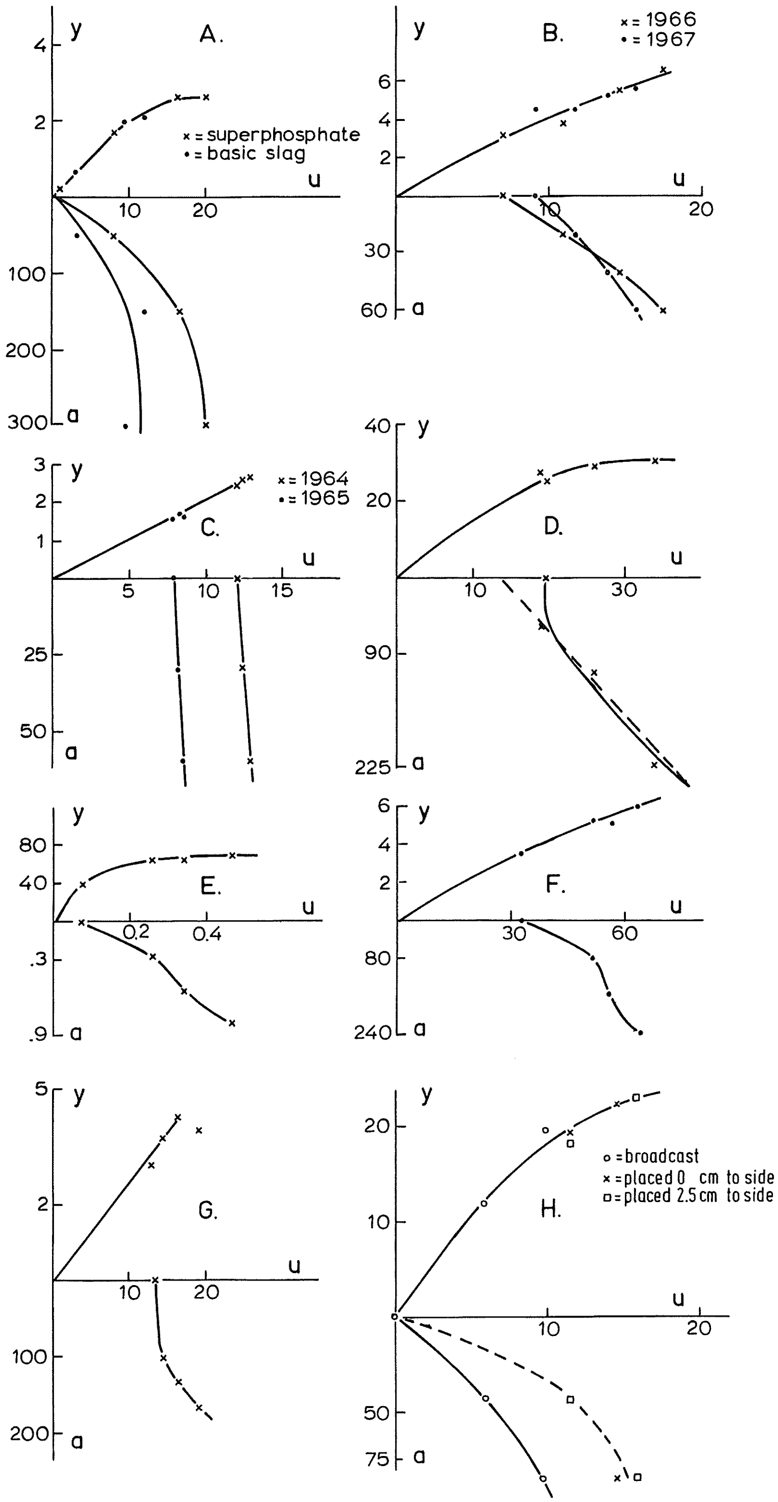
Differences in phosphorus availability from year to year (Figs. 15B and 15C) could be associated with temperature differences (affecting again the rate of decomposition of organic material) and with varying soil moisture conditions (affecting microbial activity an the solubility of inorganic phosphorus compounds). Other environmental conditions (freezing, thawing, heating) or management practices (soil tillage, addition of chemicals) also influence the phosphorus availability (Russell, 1973).

The phosphate status of soils, in terms of available phosphorus for plant uptake, is generally assessed by chemical extraction. A wide variety of extractants is available, some of these being especially suitable for soils of certain chemical and mineralogical composition. In general, values obtained in this way for a given soil, correlate reasonably with uptake of phosphorus from the same soil. However, the proportion actually taken up from the potentially available store depends on root growth characteristics. These characteristics may vary as a result of conditions other than the phosphorus status of the soil (Powell, 1977). To predict yield the absolute amount of phosphorus available to the plant during its growth cycle, or that part of the cycle in which the yield capacity can be influenced, is necessary. As far as we know, none of the presently used extraction methods is suitable for that purpose. To obtain estimates of that value it may be necessary to analyse data from experiments carried out on sites, where phosphorus limits crop production and to use the uptake-yield curve to calculate the amount of phosphorus taken up.

3.2.2.2 Recovery of fertilizer

The relation between application rate and uptake is much more complex for phosphate fertilizers than for nitrogen as illustrated in Fig. 15. In some experiments the relation is a straight line (Fig. 15C), but recovery is so low here, that not too much importance can be attached to that result. The complexity is to be expected, since the reactions between phosphates in the soil solution and the solid phase of the soil are not of simple first-order kinetics over the full range of concentrations (Beek, 1979). The main reasons are the dynamics of phosphates in the soil system. The processes of adsorption, precipitation and immobilization efficiently remove phosphate ions from the solution, so that the concentration there is not proportional to the amount applied to the soil (Beek & de Haan, 1974). The recovery of phosphate fertilizers is therefore in general low. It decreases with increasing application rates (Figs. 15A, 15B), since the longer residence time of the phosphates in the soil leads to a larger proportion of the fertilizer being effectively immobilized by adsorption, precipitation or incorporation in the organic material of the soil. In such situations, where recovery of applied fertilizer is low, more efficient utilization can be achieved by fertilizer placement that is concentrating the fertilizer in a limited soil volume, as illustrated in Fig. 15H. A theoretical background for this increased availability and its practical consequences is provided by de Wit (1953). As for nitrogen, a different management system could thus lead to more efficient fertilizer use.

Some 'special' cases may be encountered. Figs. 15D and 15G show that the efficiency of uptake increases with higher applications of fertilizer. This situation is typical for soils having phosphate-fixing properties, that is the ability to form chemical bounds between particles of the solid phase (clay minerals, sesquioxides) and phosphate ions. In


A.
B.
C.
D.
E.
F.
G.
H.
x = superphosphate
• = basic slag
x = 1966
• = 1967
x = 1964
• = 1965
o = broadcast
x = placed 0 cm to side
□ = placed 2.5 cm to side

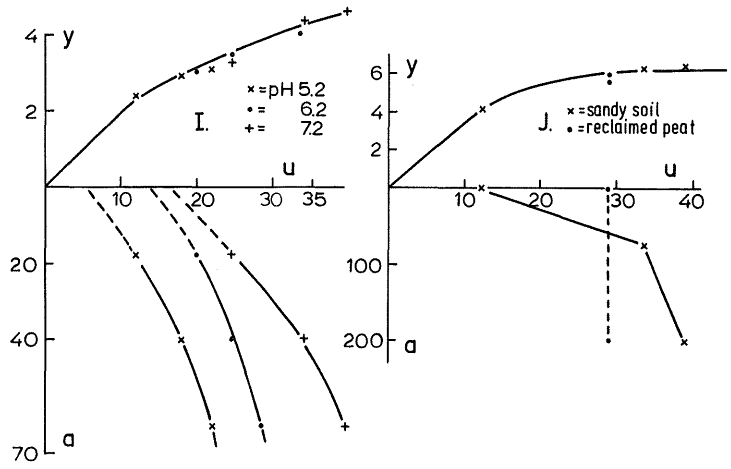


Figure 15. Relation between uptake of phosphorus (u) and yield (y) and that between application of phosphorus (a) and uptake.

A. Oats, the Netherlands (van der Paauw, 1948); y in $t.grain.ha^{-1}$, u and a in kg $P_2O_5.ha^{-1}$.
B. Rice, India (Mahapatra & Panda, 1972); y in t.grain ha^{-1}, u and a in kg $P_2O_5.ha^{-1}$.
C. Rice, India (Majumdar, 1973); y in t.grain ha^{-1}, u and a in kg $P_2O_5.ha^{-1}$.
D. Potatoes, United States (Jacob et al., 1949); y in t.fresh $tubers.ha^{-1}$, u and a in kg $P_2O_5.ha^{-1}$.
E. Red clover, (pot experiment) Israel (Hagin, 1957); y in g.dry $matter.pot^{-1}$, u and a in g $P_2O_5.pot^{-1}$.
F. Rice, India (Motsara & Datta, 1971); y in $t.grain.ha^{-1}$, u and a in kg $P_2O_5.ha^{-1}$.
G. Potatoes, United States (Carpenter, 1963); y in t.dry $tubers.ha^{-1}$, u and a in kg $P_2O_5.ha^{-1}$.
H. Swedes, Great Britain (Cooke, 1951, cited by de Wit, 1953); y in t.fresh roots ha^{-1}, u and a in kg $P_2O_5.ha^{-1}$.
I. Wheat, India (Tripathi & Pande, 1971); y in $t.grain.ha^{-1}$, u and a in kg $P_2O_5.ha^{-1}$.
J. Winter wheat, the Netherlands (van Itallie, 1939); y in $t.grain.ha^{-1}$, u and a in kg $P_2O_5.ha^{-1}$.

such soils the potential adsorption sites are first 'saturated' with phosphate ions. At higher application rates the concentration in the solution increases, and so the efficiency of uptake. It is often difficult if not impossible to distinguish between chemical binding and precipitation especially if high amounts of Al- or Fe-ions are also present in the soil (Beek, 1979). Still a different shape of the relation is shown in Figs. 15E and 15F, in which there is first a decrease in recovery and then an increase at higher application rates. The same phenomenon was reported by de Wit (1953, Fig. 10) for an experiment with oats. A possible explanation is, that precipitation takes first place, increasing with increasing concentration of phosphates and at the highest application rate all free cations (Fe^{3+}, Al^{3+}, Ca^{2+}) available for the formation of insoluble phosphate compounds are exhausted. Phosphate concentrations in the soil solution will then rise and increased uptake of fertilizer phosphates will result.

Similar behaviour would result if the phosphorus fertilizer is adsorbed on components of the solid phase. The most conspicuous difference from precipitation would be the time constant of removal from the solution, which is much larger for precipitation (Beek, 1979). That distinction cannot be made in this approach since it does not consider the dynamics of phosphorus in the soil. In any case such shapes could be considered as extended forms of the one presented in Fig. 15H.

From the results, presented in Fig. 15 we conclude, that the behaviour of phosphates in the soil and the availability to the plant root system is complex. Quantitative prediction based on measurable chemical or mineralogical properties of the soil is not yet feasible, despite the vast amount of experimental data on phosphorus application. It seems necessary therefore to formulate a sound theoretical model, in which the mechanisms important in the phosphorus dynamics in the soil are incorporated. Combination with relevant plant characteristics may lead to a better understanding of the experimental data and provide a basis for prediction. For the moment however, the best way of predicting phosphorus availability seems to be by analogy related to soil properties determined in soil surveys.

3.2.3 Potassium

Generally the potassium content in plants is high, of the same order of magnitude as nitrogen. Under intensive agriculture, aiming at high yields, therefore, large amounts of potassium are removed from the field at harvest. The situation may be somewhat more favourable than for nitrogen, since often the major part of the potassium is in the vegetative parts of the plants, which are partly or completely left in the field or returned later. The evidence presented in Sections 3.1.1.1c, 3.1.1.2c and 3.1.1.3c indicates that the potassium-supplying power of most soils is such that shortage of the element is rare. However if constraints imposed by nitrogen and phosphorus availability are removed and crop yields increase consequently, the removal of potassium will also rise considerably. To sustain high production levels, sufficient potassium fertilizer must then be supplied to compensate for that removal. Examination of application-uptake curves for this element is therefore essential for a description of the agricultural production system.

3.2.3.1 Uptake at zero application ('zero-potassium level')

The potassium-supplying capacity of the soil is mainly determined by its mineralogical composition. The main source of the element is minerals like micas and feldspars, which under influence of weathering may supply substantial amounts of potassium. So clay soils, having a higher proportion of these minerals as a rule, will supply larger amounts of potassium than sandier soils (Mengel & Haeder, 1973). The reactions involved in supplying potassium from the soil store to the plant roots are again equilibrium reactions, governed by the relative concentrations of the various forms of potassium which are ions in the soil solution, ions adsorbed in exchangeable form on the negatively charged clay and organic matter particles and potassium chemically bound in the clay minerals (van Diest, 1978). Thus conditions changing these concentrations influence the zero-K level. Of such conditions, weather may be of importance: higher temperatures and moisture contents favour weathering of minerals, and increase potassium availability. Differences between years may therefore be considerable (Figs. 16B and 16C).

Different crops also show striking differences in their ability to extract potassium from a soil. An example is given in Fig. 16I, which refers to a longterm (about 60 years) fertilizer experiment with various potassium fertilizers in West-Germany. Potatoes were grown in 11 years, barley in 13 years and sugar-beet in 5 (Amberger & Gutser, 1976). Sugar-beet absorbed by far the greatest amount of K from the unfertilized soil, and the difference between potatoes and barley in uptake of K_2O was still about 35 $kg.ha^{-1}$. The differences seem to be related to the demand of the crop for potassium, sugar-beet can utilize large amounts of this element. There is a similar positive correlation, however, with the length of the growing period, so it is uncertain which process is responsible for this phenomenon.

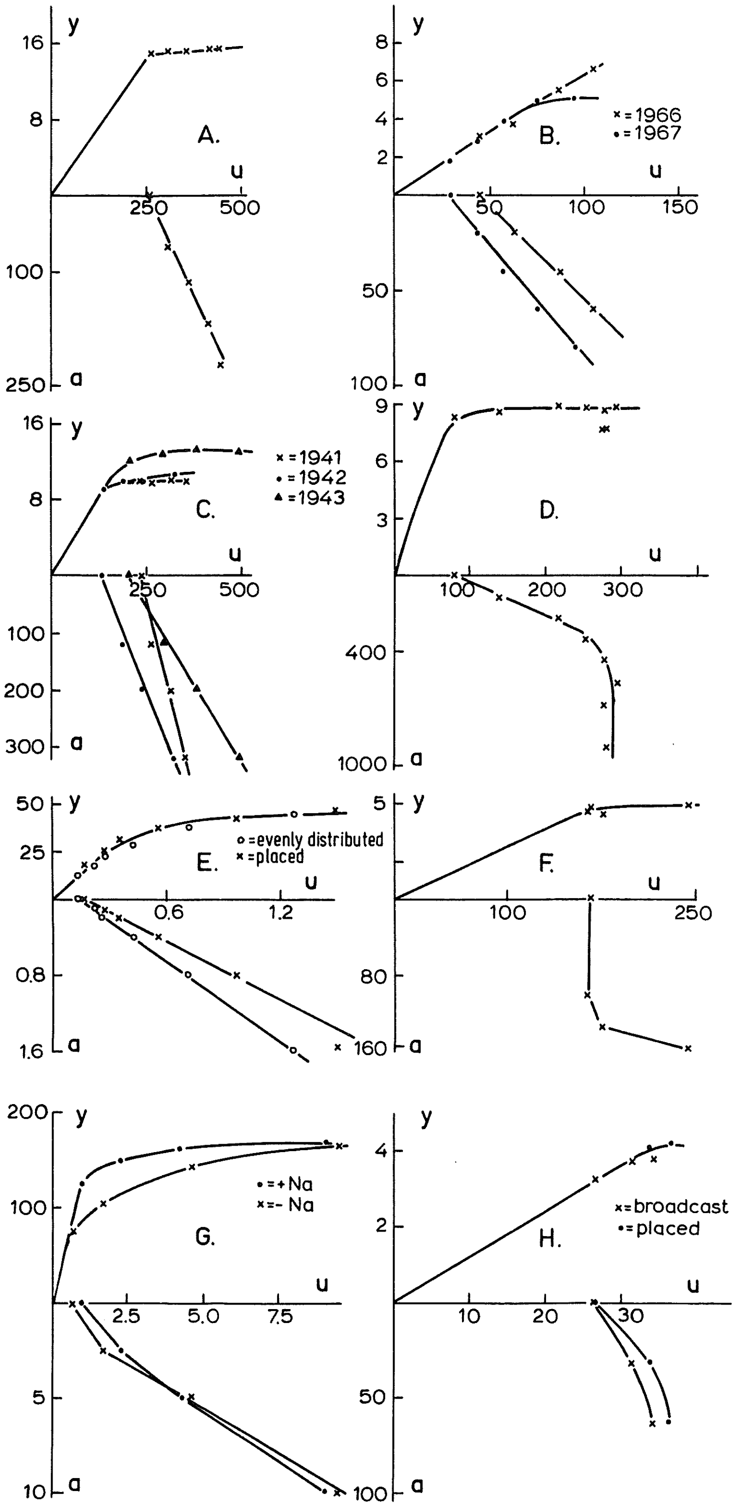
Data from chemical extraction methods used to assess the potassium status of soils generally relate reasonably to the uptake without fertilizer (Grimme & Nemeth, 1978). Because of great difficulty in using these for prediction of uptake during the growth period, analysis along the lines proposed for nitrogen and phosphorus may therefore also be preferable for potassium, although there are probably far less data available for such an analysis.

3.2.3.2 Recovery of fertilizer

Two main processes influence the efficiency of uptake of fertilizer potassium. In soils with a low adsorption capacity (sandy soils) potassium ions are very mobile and may easily be lost by leaching beyond the rooting zone. Clay soils, however, with a high proportion of 2:1 clay minerals (illite, vermiculite) may fix potassium. In these minerals potassium is absorbed selectively at specific sites in the clay lattice, rendering it unavailable for plant uptake (Temme & van der Marel, 1952). Such absorption, though chemically different in nature from phosphate fixation, results in a similar shape for the application rate-uptake curve (Figs. 16F and 16G). At low application rates, most or all of the potassium ions are removed from the soil solution and built in the clay lattice, and, at higher application rates proportionally more of the ions remain available for plant uptake.

If potassium fixation does not play a role however, recovery of potassium fertilizers is fairly high (Fig. 16). As for nitrogen, the fraction taken up is independent of the amount of fertilizer applied. The major process responsible for losses is thus leaching, its magnitude being proportional to the concentration in the soil solution. Differences from year to year (Fig. 16C) would thus be mainly associated with differences in rainfall.

The levelling off, of the rate-uptake curve at high application rates (Fig. 16D) must thus be attributed to active exclusion of potassium ions by the plant at high concentrations in the solution. When the content of the element in the tissue is close to maximum, further uptake is apparently inhibited. This will however only happen at very high levels, as 'luxury consumption' is apparent in several experiments presented in Fig. 16 (A, C, D and E). Decreasing recovery at increasing rates of application may occur, however also at much lower rates (Fig. 16H) and apparently below the level of luxury consumption. Here again, chemical reactions must render the potassium unavailable for the plant, as confirmed by the fact, that local placement (i.e. concentrated application) leads to increased


A.
B.
×=1966
•=1967
C.
×=1941
•=1942
▲=1943
D.
E.
o=evenly distributed
×=placed
F.
G.
•=+Na
×=- Na
H.
×=broadcast
•=placed
y
u
a

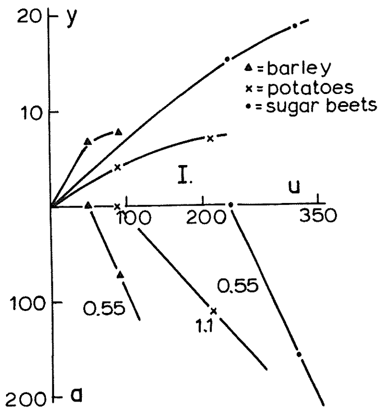


Figure 16. Relation between uptake of potassium (u) and yield (y) and that between application of potassium (a) and uptake.
A. *Cynodon dactylon*, Nigeria (Chhedda & Saleem, 1973); y in t.dry matter ha^{-1}, u and a in kg $K_2O.ha^{-1}$.
B. Rice, India (Mahapatra & Panda, 1972); y in t.grain.ha^{-1}, u and a in kg $K_2O.ha^{-1}$.
C. Permanent pasture, the Netherlands ('t Hart, 1948); y in t.dry matter.ha^{-1}, u and a in kg $K_2O.ha^{-1}$.
D. Red clover, United Stated (Smith & Smith, 1977); y in t.dry matter.ha^{-1}, u and a in kg $K_2O.ha^{-1}$.
E. Oats in a pot experiment (Rauterberg, 1937); y in g.grain.pot^{-1}, u and a in g $K_2O.pot^{-1}$.
F. Potatoes, United States (Carpenter, 1963); y in t.dry tubers.ha^{-1}, u and a in kg $K_2O.ha^{-1}$.
G. 'Weidel grass' in a pot experiment (Gutser & Teicher, 1973); y in g.dry matter.pot^{-1}, u and a in g $K_2O.pot^{-1}$.
H. Barley, Great Britain (Widdowson et al., 1959); y in t.grain.ha^{-1}, u and a in kg $K_2O.ha^{-1}$.
I. Germany (Amberger & Gutser, 1976); y in t.dry matter.ha^{-1}, u and a in kg $K_2O.ha^{-1}$.

recovery. Presumably there is competition between the soil system and the roots for available potassium ions. Higher rates of application lead to longer residence times of these ions in the soil and hence to a proportionally greater share for the soil colloids.

In a first approximation we can assume a constant recovery of fertilizer, the actual value of the proportionality factor being determined mainly by soil and weather conditions.

4 Conclusions

The analysis presented in this paper shows again (c.f. de Wit, 1953) that the results of fertilizer experiments can only be meaningfully interpreted when not only the relation between application rate and yield is determined, but also the 'intermediate' value of uptake of the element concerned. Only then can causal relationships be detected, which may form a basis for improvement in the local situation and for extrapolation of the results to other sites and conditions. This calls for chemical analysis of plant material from fertilizer experiments. Especially in developing countries we believe that a large proportion of the effort and money invested in fertilizer experiments would be used much more efficiently if plant analysis would be carried out on a routine basis.

If uptake of an element and crop yield are determined one can evaluate whether yield is really limited by the element under consideration or whether some other growth factor is in short supply. If the nutrient is limiting the data points are arranged along a straight line whose slope is dictated by the minimum contents of the element in the various plant parts, taking into account possible variations in the harvest index, which may be the result of special conditions during the growing season, either intended (long vegetative period of rice in monsoonal climates) or by chance (emergency ripening as a result of water shortage). In the situation where another growth factor is limiting, the content of the element under study is well above minimum and the uptake-yield curve has a tendency to level off, indicating that higher uptake does not result in higher yields. It is realized of course that there is a transition zone, where yield does not increase proportionally to the amount of the element taken up, but where a yield-increasing effect is still present. Higher contents in the tissue during the growing season improve its photosynthetic performance, leading to higher production because of a higher rate of production and a longer production period (Sinclair & de Wit, 1976). Schematically this transition can, however, be neglected and the 'law of the minimum' (Liebig, 1855) may be applied.

The same relation between uptake and yield may also provide a tool for the estimation of the yield potential on the basis of the total amount of a particular element available during the growing season for a particular crop. The main drawback of this procedure is that no standardized methods are available to determine the absolute amounts of the various elements that will be available for uptake by the plants from a given soil under well-defined environmental conditions. This may not be too serious if the situation on a regional level has to be defined, but is so for the purpose of understanding and extrapolation.

The relation between fertilizer application rate and uptake by the crop is in general a straight line for nitrogen and potassium, suggesting that the processes involved in uptake and in losses are of first-order kinetics, that is proportional to the concentration of the element in the soil solution. Especially for nitrogen, however, large variations in recovery do occur. It is not always obvious whether the complementary fraction of

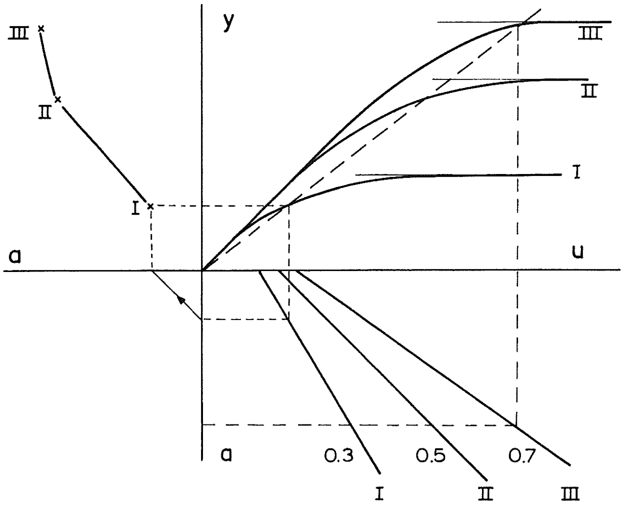


Figure 17. Relation between uptake (u) and yield (y), that between application (a) and uptake and that between application and yield, at three reclamation levels (I, II and III).

the fertilizer is lost from the system or is only temporarily rendered unavailable because the system is not in equilibrium. In many situations, however, the method of application is such that large proportions of the applied fertilizer are lost from the system (volatilization, denitrification, leaching). Recognition of these phenomena may lead to the exploration and application of different management techniques, which will limit such losses and hence result in a much more efficient fertilizer use. The consequences of such improved techniques, when combined with changes in the reclamation level (land improvement, water control) are schematically worked out in Fig. 17. Land improvement generally leads to higher plateau levels, since water shortage or waterlogging during part of the season can be prevented. Such measures lead at the same time to higher zero-N levels and to higher recovery, if one assumes that the same processes act on both fertilizer nitrogen and nitrogen released from the soil organic matter (Fig. 14I). In Quadrant 1 of Fig. 17, the dotted line represents the uptake at which adverse effects may just be avoided (e.g. lodging), which is the point always aimed at. The result of this analysis (Quadrant 3 of Fig. 17), shows that the efficiency of fertilizer application increases with increasing rates of application, thus illustrating the 'law of increasing return'. The same basic reasoning holds when only the level of the plateau is changed for instance by removing constraints imposed by other nutrient elements. Then the situation changes from diminishing returns to one of constant returns in terms of fertilizer application.

Especially if, as now, more emphasis is put on the efficient use of resources, such management practices are of crucial importance. Moreover they can change the economics of fertilizer application drastically and hence have a major impact on the economically feasible production potential under given price ratios of inputs and outputs.

Summary

In many parts of the world, crop production is limited by the availability of plant nutrients. To estimate the scope for improvements in the present situation and the requirements to achieve that improvement, a quantitative description of the relation between production and nutrient supply is necessary.

In this paper a method is described, based on two relations: on the one hand the relation between the total uptake of a nutrient element and yield, on the other hand the relation between application of the element and uptake by the crop.

It is shown, that for small grains (rice, wheat, barley), potatoes and sugar beet growing under limiting nutrient conditions, the concentration of the limiting element in the tissue reaches a characteristic minimum value. The relation between uptake and yield is therefore characteristic for each combination of crop and nutrient in the low range of nutrient availabilities. The values obtained, were: 70 kg of grain, 100 kg of dry tubers and 80 kg of sugar per kg of nitrogen taken up, for small grains, potatoes and sugar beet, respectively; 600 kg of grain, 600 kg of dry tubers and 430 kg of sugar per kg phosphorus absorbed and 65 kg of grains, 80 kg of dry tubers and 60 kg of sugar per kg potassium taken up.

The wide variability in fertilizer response curves found between sites and seasons resulted thus mainly from the widely varying relations between fertilizer application and nutrient uptake by the crop. It is shown that for nitrogen that relation is practically always a straight line, suggesting a constant recovery fraction, irrespective of the rate of application. The recovery fractions varied however from 0.10 under unfavourable conditions to 0.80 under very favourable management.

For phosporus the shape of the application uptake curve differed for different experiments, mainly as a result of soil conditions. These different shapes reflect the non-linearity of the dynamics of phosphorus in the soil. Recovery fractions were generally low, seldom exceeding 0.3.

For potassium the application-uptake curve again was a straight line, except in soils having potassium fixing properties. Recovery fractions were generally high, varying between 0.5 and 0.8.

The concept developed in this paper may be used to predict crop yield under nutrient limiting conditions and estimates can be made of the fertilizer requirements for removal of nutrient constraints.

Samenvatting

Op veel plaatsen in de wereld wordt de gewasproduktie bepaald door de beschikbaarheid van voedingsstoffen. Om inzicht te verkrijgen in de mogelijkheden tot verhoging van de produktie en de daarvoor benodigde inputs, is een kwantitative beschrijving nodig van het verband tussen de opbrengst en het aanbod aan voedingsstoffen.

In deze publikatie wordt een methode beschreven om tot zo'n verband te komen, gebaseerd op twee deelverbanden: enerzijds die tussen de totale opname van een element en de opbrengst van het gewas, anderzijds die tussen de toegediende hoeveelheid van een element en z'n opname door het gewas.

Voor de korrelgewassen rijst, tarwe, gerst en haver en voor aardappelen en suikerbieten, die groeien onder omstandigheden waar het aanbod van voedingsstoffen limiterend is, bereikt de concentratie van het limiterende element in het weefsel een karakteristieke minimumwaarde. Het verband tussen opname en opbrengst is derhalve voor iedere combinatie van gewas en voedingselement constant in het lage opnamegebied en onafhankelijk van de omstandigheden. De gevonden waarden zijn: 70 kg korrels, 100 kg knollen en 80 kg suiker per kg opgenomen stikstof; 600 kg korrels, 600 kg knollen en 430 kg suiker per kg opgenomen fosfor en 65 kg korrels, 80 kg knollen en 60 kg suiker per kg opgenomen kali voor de drie gewassen.

De grote verscheidenheid in responscurven die wordt gevonden in bemestingsproeven moet volledig worden toegeschreven aan de variabiliteit in het verband tussen de toegediende hoeveelheid kunstmest en de opname door het gewas.

Bij stikstof is het verband tussen opname en toegediende hoeveelheid bijna altijd rechtlijnig. Dit wijst op een constante uitbatingsfractie, onafhankelijk van de hoogte van de gift, tenzij zeer grote hoeveelheden worden toegediend. De gevonden uitbatingsfracties variëren van 0.10 bij onoordeelkundig toedienen op slechte gronden, tot 0.80 bij optimaal beheer op goede gronden.

Voor fosfor worden grote verschillen gevonden in de vorm van de opname-gift curven, voornamelijk als gevolg van verschillen in bodemeigenschappen, zoals fosfaatfixatie en/of neerslag van onoplosbare fosfaten. De uitbatingsfracties liggen veel lager dan voor stikstof en overschrijden zelden de waarde 0.3.

Voor kali is het verband tussen opname en gift in de meeste gevallen rechtlijnig, behalve wanneer de grond kalifixerende eigenschappen heeft. De gevonden uitbatingsfracties liggen tussen 0.5 en 0.8.

De in deze publikatie ontwikkelde concepten kunnen worden gebruikt voor opbrengstschattingen onder omstandigheden waar voedingsstoffen limiterend zijn en voor het schatten van de meststofhoeveelheden die nodig zijn om de beperkingen op te heffen.

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