ANALYSIS OF THE CONTROL OF CROP GROWTH BY NUTRIENT SUPPLY

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ABSTRACT

Despite much research, the determination of fertiliser requirements for optimum crop yields may be unreliable. This paper reviews critically the general procedures used to identify where crop yield is limited by nutrient supply and to define the likely response to applied fertiliser.

Routine soil and plant analyses, often with empirical calibrations, have been used widely to define crop nutrient status but have limited reliability. Procedures for plant analysis which are based on the physiological function of nutrients in plant tissue are attracting increased interest.

Descriptions of crop response to applied fertiliser, using various empirical functions, can be useful for determining applications required for optimum yields. The uncertainties involved will be reduced if the mechanisms of control of crop growth by nutrient supply are defined clearly. Mechanistic mathematical models are useful tools for relating plant growth responses to nutrient inputs but they must be accompanied by fundamental studies of the physiological role of nutrients in crop growth.

Additional Key Words: crop yield, mathematical modelling, plant analysis, plant nutrition, soil analysis.

INTRODUCTION

It has long been known that crops require inorganic nutrients for growth and that nutrients removed from the soil by crops must be returned in some other form if production levels are to be maintained (Mengel and Kirby, 1978). Since this early research, much effort has been aimed at determining the nutrient requirements in crop production. However, it is often unclear whether crop growth and yields, in given conditions, will respond positively to fertiliser applications.

Nitrogen, phosphorus and potassium are the three nutrients most commonly limiting yields and feature in much of the literature on the control of crop growth by nutrient supply. In the present paper I review major procedures used today for estimating the requirements of these three nutrients for optimum crop yields. This appraisal of our present ability to determine fertiliser requirements highlights the weakness in our knowledge of the control of crop growth by nutrient supply and suggests areas where future research is worthwhile.

SOIL ANALYSIS

Soil analysis is used as a predictive tool for determining fertiliser requirements. Samples can be taken before crops are sown or prior to the period of most rapid growth. Most soil analysis methods involve chemical extraction of that fraction of total nutrients which may be considered accessible to plant roots.

Nitrogen

A reliable estimate of available nitrogen (N) in the soil has yet to be developed for routine use over a wide variety of situations. A reliable test should consider the mineral N available for plant growth at sowing as well as losses (e.g. leaching) and additions (e.g. mineralisation) to this pool during crop growth (e.g. Addiscott, 1981; Quin *et al.*, 1982; Steele *et al.*, 1982).

The crop N requirement may be related to growth rate. Crop yields are influenced strongly by early growth rates so may be related to estimates of plant-available N most reliably during periods of rapid growth. For short-season crops this is likely to be soon after emergence but for perennial crops and winter-sown crops, spring is likely to be a more appropriate time. Effects of N supply on yield quality should be considered also. For example, N taken up by cereals during the vegetative stage is likely to be used mainly for vegetative growth, whereas N taken up after flowering is directed mainly towards the synthesis of grain products (Michael and Blume, 1960).

Phosphorus

The plant-available fraction of total soil phosphorus (P), at least on calcareous soils, is considered to be represented by the quantity extracted by $NaHCO_3$ (Cornforth, 1980). However, this soil test accounts for only 50% to 60% of the between-site variance in yield response (Draycott *et al.*, 1971). This limited reliability may be attributed to the factors such as soil moisture, pH, structure and depth, vesicular-arbuscular mycorrhiza and phosphate buffer capacity.

Crop growth responses to the level of plant-available P persist through to relatively late stages of growth (e.g. Mohammed and Marshall, 1980; Sutton *et al.*, 1983). However, the $NaHCO_3$ soluble P content of most soils to which fertiliser has not been recently applied changes only slowly so, for short season crops at least, estimates made at sowing represent indices of the P status of the soil throughout growth.

Potassium

The plant available fraction of total potassium (K) in soils is generally measured by the exchangeable K fraction, extracted with ammonium acetate. However, poor correlations between exchangeable K levels and plant response to applied K may occur in soils of different clay content and degrees of K saturation (e.g. During and Duganzich, 1979) and on some soils which contain significant quantities of non-exchangeable but plant-available K (Cornforth, 1980). The K buffer capacity must also be important in determining plant-available K in soils (Barrow, 1966).

The exchangeable K content of the soil can decline considerably during crop growth following crop uptake and leaching. For short-season crops, there is evidence that a large proportion of the total K uptake occurs during early stages of growth and that it is the K available at this time that determines final yield (Chapman and Keay, 1971; Mengel and Kirkby, 1978; Costigan and McBurney, 1983).

PLANT ANALYSIS

Plant analysis is used frequently for determining whether crop nutrient status is limiting growth. Nutrient concentration in plant tissue is an index of actual nutrient uptake (compared with soil analysis which can indicate only the potential nutrient uptake). Thus plant analysis reflects conditions of nutrient uptake such as soil aeration and moisture, in addition to soil nutrient content.

Ideally, plant analysis should be conducted at a sufficiently early stage of crop growth to allow corrective additions of fertiliser. If nutrient abnormalities develop during later stages of growth, the value may be limited to determining fertiliser practices for subsequent years.

Plant analysis can be particularly useful for assessing the adequacy of nutrient supply at sensitive growth stages. Presently the procedure is based largely on the concentration of a nutrient in plant tissue, and related to "critical" levels required for optimum crop growth or yield (Fig. 1). Plant analysis has been used widely for predicting the likelihood of a response to fertiliser application (see Ulrich and Hills, 1967; Geraldson *et al.,* 1973; Cooke, 1982) and for assessing crop quality (Cummings and Wilcox, 1968). The procedure must be calibrated carefully for a specific combination of crop species and mineral nutrient. Nutrient content of a plant reflects factors such as organ sampled, age of organ or plant sampled, type of analysis, soil water status, supply of the plant with other nutrients.

Sampling plant tissue of a defined "physiological age" may improve the reliability of plant analysis for describing crop nutrient status. The youngest mature leaf has been used widely in this context (e.g. Geraldson *et al.,* 1973). This actively growing tissue has a high nutrient demand and is of approximately similar physiological age regardless of sampling time. However, for N and K at least, deficiency results in the translocation of nutrient from older to younger tissue, so that analysis of older tissues may demonstrate more clearly the nutrient status of the plant (Humbert, 1973; Mengel and Kirkby, 1978).

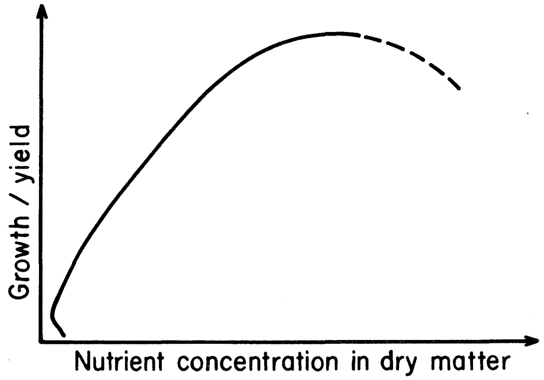

Figure 1: Generalised relationship between nutrient concentration in plant dry matter and growth or yield.

For many crops, "critical" nutrient concentrations have not been defined and a "common nutrient range" only is available. For such crops, predictions of the likelihood of response to fertiliser based on plant analysis can be unreliable.

There is increasing interest in the analysis of a physiologically active fraction, rather than the total level, of the nutrient in plant tissue, particularly for N. Ulrich and Hills (1973) reported that optimum growth of sugar beet required a petiole NO_3-N concentration of at least 0.1%. Mason and Wilcox (1982) claimed that, in tomato, NO_3-N content of petioles was more indicative of the plant N status than total N analysis of whole leaves. The concentration in plant tissue of the enzyme nitrate reductase, which depends on the presence of NO_3-N, has also been used as an index of plant N-status (Bar-Akiva and Sternbaum, 1965). Indeed, Johnson *et al.,* (1976) claimed that nitrate reductase activity during early stages of crop growth was a sensitive predictive index of wheat yields. The N-status of plant tissue may also be reflected in the concentration of soluble amino compounds (Greenwood *et al.,* 1965; Goswami and Wilcox, 1969), particularly glutamic acid (Mengel and Helal, 1970) which is one of the first amino acids synthesised during ammonia assimilation.

Potassium deficiencies appear to be related very closely to the accumulation of the diamine putrescine (Richards and Coleman, 1952; Smith, 1971; Smith *et al.,* 1982), and the crop K status may be defined more consistently using putrescine analysis than using the empirically-derived "critical" concentration (Smith *et al.,* 1982). Biochemical indicators of crop nutrient status, such as those discussed here, often involve complex analytical procedures for their determination and so are unlikely to be used routinely. However, their use may be important for calibrating routinely-used tests of crop nutrient status.

The usefulness of expressing plant nutrient status as the nutrient content in the dry matter has been questioned recently by Leigh and Johnston (1983a,b). They demonstrated that the K concentration in the dry matter of spring barley declined during growth concomitantly with tissue hydration (Fig. 2). The K concentration in tissue water remained approximately constant until near harvest but at a much higher level for crops grown with sufficient K (200 mM/kg) than in those grown with insufficient K (50-70 mM/kg). Thus K deficiency in barley could be defined clearly and simply regardless of growth stage. There is a sound physiological basis for expressing K concentrations in tissue water. Potassium has an important role as an osmoticum in plant tissue (e.g. Wyn Jones *et al.*, 1979) and is not metabolised so different forms of the nutrient in the plant do not need to be considered.

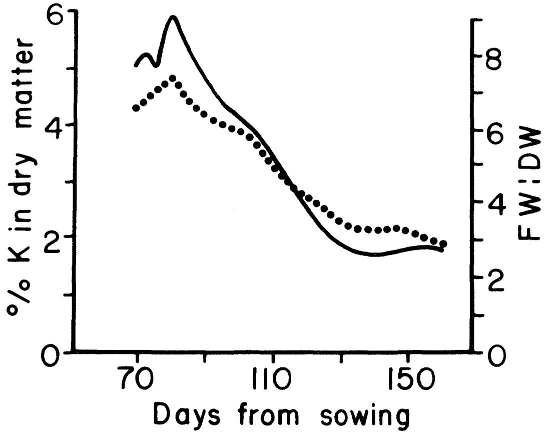

Figure 2: Concentration of potassium in the dry matter (% K, ———) and ratio of fresh weight to dry weight (FW:DW, -------) of spring barley during growth (After Leigh and Johnston, 1983a).

Thus K nutrition strongly affects tissue hydration and the ratio of fresh weight to dry weight of plant tissue increases with the K status of the crop (Mengel and Arneke, 1982; Costigan and McBurney, 1983). Potassium deficiency therefore restricts the specific leaf area and hence the relative growth rate and yield (Hunt, 1978). This may explain the good correlation between the ratio of fresh weight to dry weight of plant tissue and the grain yield of spring barley crops (Leigh and Johnston, 1983a).

It is not known whether such principles might be applied to the study of nutrients other than K. Leigh and Johnston (1982) reported that N concentrations in tissue water were insensitive to the N status of the crops, possibly because they were maintained at the expense of the growth. Nevertheless, effects of N on the growth rate may still be related clearly to the ratio of fresh weight to dry weight of plant tissue (Fig. 3).

The use of plant analysis for diagnosing nutrient deficiencies so that corrective fertiliser additions can be made is impaired by the delay involved in laboratory analysis of plant tissue. Hence, there is growing interest in procedures for diagnosing nutritional disorders rapidly and reliably in the field. In this context, a sensitive index of crop N status may be the concentration of NO_3-N in plant sap, which varies from zero to as much as 5000 ppm so can be measured using relatively crude tests. "Merckoquant" test-strips react colorimetrically to the concentration of NO_3 in plant sap expressed onto them (Prasad and Spiers, 1982; Scaife and Stevens, 1983), and can indicate the sap NO_3-N concentration within two minutes, allowing rapid and frequent assessment of the crop N status. Interpretation of the results requires that they be compared with calibrations based on data from experiments conducted under closely controlled conditions.

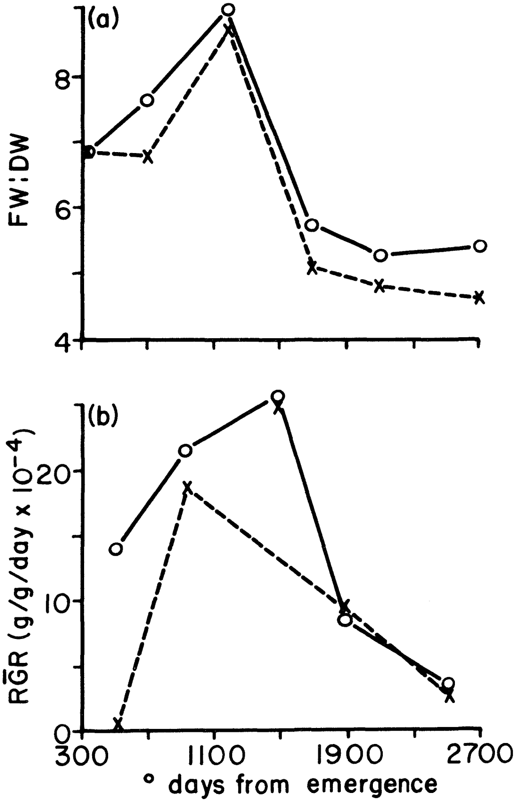

Figure 3: (a) Ratio of fresh weight to dry weight, and (b) relative growth rate of garlic supplied with 0 (x) or 120 (o) kg N/ha.

Rapid assessment of crop N status in the field may also be possible using a portable photometer which, following calibration, is capable of fast, accurate and non-destructive estimates of chlorophyll in intact leaves (Hardacre *et al.*, 1984). Plant chlorophyll is closely related to N-status (O'Neill *et al.*, 1983), because of the increased demand with N supply for photosynthetic reduction of NO_3-N and incorporation of ammonia into cell material (Mader *et al.*, 1982).

Crop nutrient status may also be defined on the basis of rates of crop growth and development (Batey, 1977). The concept of crop N stress, defined as the proportion by which crop growth rate falls short of the maximum obtained with a non-limiting N supply, may be used to predict current or potential response to applied N (Greenwood, 1976; O'Neill *et al.,* 1983). Leaf appearance rate may be a useful non-destructive index of crop N status during early stages of growth (Table 1). Leaf number is affected by N supply (e.g. Lee *et al.,* 1981) and, when N and water are non-limiting, linear relationships exist between accumulated temperature (growing degree-days) and leaf appearance of various crops (Hay and Tunnicliffe-Wilson, 1982; Warrington and Kanemasu, 1983).

TABLE 1: Rate of leaf appearance (per degree day) of garlic with 0 or 240 kg N/ha, and sown at 15 June or 11 August 1983.

N applied (kg/ha)	Sowing date 15 June	11 August
0	6.40×10^{-3}	8.13×10^{-3}
240	7.35×10^{-3}	9.10×10^{-3}

CROP RESPONSE TO FERTILISER APPLICATIONS

A fundamental question following the diagnosis of a nutrient deficiency is that of the fertiliser addition required to achieve optimum or maximum yield. The optimal fertiliser application varies considerably with many factors influencing the growth of a crop at a particular site. Consequently field experiments have been carried out to investigate crop response in particular localities but it would be impracticable to cover every combination of crop and locality. Clearly generalisations must be made.

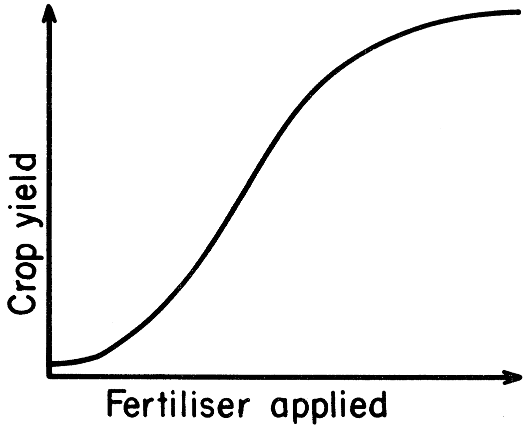

Figure 4: Generalised relationship between level of applied fertiliser and crop yield.

Yield responses to applied fertilisers are generally asymptotic; that is, the yield increment with each additional unit of fertiliser decreases as the maximum yield is approached. This yield response pattern may be more correctly part of a "sigmoidal" response (Fig. 4) in which increasing nutrient supply initially increases growth by increasing amounts for successive increments of the nutrient, but subsequently, growth is increased by decreasing amounts as the asymptote of yield is approached (Steenbjerg and Jakobsen, 1963).

Exceptions to the generally asymptotic yield response to applied nutrients include the yield depressions that often occur when excessive or imbalanced levels of some nutrients are applied. Such depressions may result for example, from increased susceptibility of the crop to fungal disease or from toxic accumulations of plant metabolites which cannot be used for growth processes because of a shortage of other plant nutrients. Excessive additions of fertiliser, particularly N, can also depress yield quality. High N supply during the late stages of sugar beet growth for example may reduce sugar yields substantially even though total yield is enhanced (Mengel and Kirkby, 1978). The proportion of the total bulb yield of garlic that is marketable is reduced where high N supply increases the incidence of "daughter" bulbs (Table 2).

TABLE 2: Effect of nitrogen level on marketable proportion of total bulb yield of garlic sown on 15 June and 11 August 1983.

N applied (kg/ha)	Sowing date 15 June	11 August
0	0.79	0.98
30	0.79	0.98
60	0.73	0.97
120	0.63	0.90
240	0.65	0.93

The results of fertiliser x yield experiments may be applied to commercial situations in various ways. Experimental work indicating the level of plant-available nutrient required for optimum yield of a particular crop may be applied to soils for which the increase in plant-available nutrient following fertiliser addition has been defined. Such a procedure is advocated for fertiliser recommendations for vegetable crops in New Zealand (M. Prasad and R.J. Wood, pers. comm.). However, there is generally still much uncertainty in predicting the level of fertiliser addition required to achieve optimum yield, even where much research has been conducted.

The analysis of yield responses to fertiliser additions may be simplified by fitting empirical mathematical functions to experimental data and using the parameters of these functions to express the overall effects of the fertilisers on yield. Mitscherlich (1954) described yield increments as proportional to the quantity of yield required to attain the maximum, i.e.

$$\frac{dy}{dx} = k(A - y)$$

where y is yield, x is the mineral nutrient applied, A is maximum yield, and k is a constant. The Mitscherlich function however is unable to describe fertiliser responses that are not asymptotic, such as yield depressions with excessive nutrient supplies. In such situations, quadratic equations, which allow for a point of inversion, may be used.

Greenwood *et al.* (1980 a, b, c) have used an inverse polynomial function, with a modification to allow for the depressive effects on yield of high N levels, to describe yield response to N, P and K fertilisers:

$$\frac{1}{Y} = [\frac{1}{A} + \frac{1}{B_N(N_S+N_F)} + \frac{1}{B_P(P_S+P_F)} + \frac{1}{B_K(K_S+K_F)} \times [\frac{1}{1-(N_S+N_F)/\alpha N}]$$

where, N_S, P_S and K_S are the amounts of nutrients in plant-available form in the soil; N_F, P_F and K_F are the amounts of nutrients added in fertilisers. B_N, B_P and B_K are terms for the responsiveness of the crop to N, P and K; $1/\alpha N$ is proportional to the adverse component of the effect of N fertiliser on yield; and A is the maximum possible yield if $\alpha N = \infty$. The validity of the equation was supported by a survey of the literature which showed that yield responses to N, P and K were additive on the reciprocal of yield more frequently than on the logarithm of yield (as in the Mitscherlich equation) or on yield itself (as used in polynomial models (Wood *et al.*, 1972). Greenwood *et al.* (1974) claimed that differences between soils or sites affected the response to fertiliser additions of all crops similarly. Hence, a "short-cut" approach, in which the responses of many crops were examined on one site and the response of one of these crops was examined on many sites, has been used as the basis of MAFF fertiliser recommendations for vegetable crops in the United Kingdom.

Our inability to predict accurately the fertiliser requirements for optimum crop yields is a consequence of the paucity in our knowledge of the control of crop growth by nutrient status. This may be overcome, at least partly, by a greater understanding of the physiological role of plant nutrients and hence the control of crop growth by nutrient supply. Plant growth analysis may be used to describe effects of nutrient supply on crop growth rates. This technique involves fitting mathematical functions to time-series plant growth data obtained over a range of nutrient levels. The effects of nutrient supply on growth are described by effects on the parameters of such functions. The exponential, polynomial, logistic, Gompertz and Richards have been the most popular functions used in this way (Hunt, 1981). However, the fitting of empirical functions to sets of data has as a primary aim the accuracy of the fit; the definition of mechanisms involved is not possible. Nevertheless, this technique can describe clearly the effects of nutrient supply on instantaneous rates of relative growth, relative accumulation (of a particular nutrient), and specific absorption (see Hunt, 1978).

Mechanistic models, using several fitted mathematical functions as components, might describe the control of crop growth by nutrient supply more fully than a single empirical function. Fig. 5 shows schematically a possible mechanistic control of crop growth by nutrient supply.

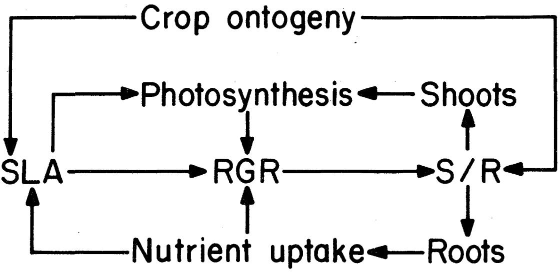

Figure 5: Schematic representationship of possible mechanisms of control of crop growth by nutrient supply; SLA = specific leaf area, RGR = relative growth rate, S/R = shoot:root ratio.

Central to the model is the crop's relative growth rate which is affected by nutrient deficiency directly through effects on the provision of mineral nutrients for growth and indirectly through effects on the specific leaf area, the ratio of shoots to roots and on the ontogenetic development of the crop (which affects much of the subsequent crop growth pattern). Such a model may be tested by fitting mathematical functions to its various components, using experimental data, and so simulating crop growth as a function of nutrient supply. Any consistent deviations of the simulation from observed experimental data should suggest alterations to the mechanisms implied in the model. Such a modelling approach represents a vehicle for thought which can help immensely in understanding physiological processes and has been used successfully to describe the control of mycorrhizal infection by the host plant (Buwalda *et al.*, 1984).

A problem inherent to analysing effects of nutrient supply on crop growth is that, subsequent to an initial effect on the pattern of growth, growth rates can differ by virtue of the differences in plant size, quite independently of the effect of the initial nutrient supply. A recent experiment with squash showed this clearly (Table 3). The large effects of nutrient supply on growth increments reflect earlier effects on the crop relative growth rate, as this latter parameter was little affected by nutrient supply during later growth. The mechanisms of control of crop growth by nutrient supply can be elucidated only if parameters of plant growth are measured both before and after differences in plant growth rates occur. Scaife *et al.* (1983) suggest that a possible solution to this problem is to run simulation models based on various assumptions about the control of crop growth and see which describes best the overall pattern of results. Fundamental studies of the mechanism of control of plant growth by nutrient supply are required for the efficient definition and successful use of such simulation models. These studies should examine the relationship between nutrient supply and physiological responses within the plant which can subsequently be seen to affect growth. There have been some interesting developments recently in this direction. Radin (1983) reported that leaf area growth was affected by N supply more strongly in dicotyledons than in monocotyledons

TABLE 3: Yield increment (g/day) and relative growth rate (g/g/day) of hybrid squash, between 2.11.83 — 18.11.83 and 18.11.83 — 5.12.83, grown with deficient or sufficient supplies of N, P or K.

Interval	Nutrient	Yield increment	Relative growth rate
2.11.83 to 18.11.83	N deficient	0.70	0.16
	N sufficient	1.03	0.17
	P deficient	0.38	0.13
	P sufficient	1.51	0.16
	K deficient	0.50	0.16
	K sufficient	1.17	0.17
18.11.83 to 5.12.83	N deficient	5.30	0.13
	N sufficent	7.66	0.13
	P deficient	3.11	0.13
	P sufficient	17.48	0.15
	K deficient	4.73	0.14
	K sufficient	8.42	0.13

while dry matter production when N was limiting was more efficient in monocotyledons than in dicotyledons. Costigan and McBurney (1983) identified that a major effect of K supply on the yield of cabbage and lettuce resulted from a pronounced effect on lateral root initiation prior to crop emergence.

Studies such as these will be important for improving our knowledge of the control of crop growth by nutrient supply.

Clearly there is still much to be learnt of the physiological role of plant nutrients. However, research into this area is likely to intensify as the popularity of simulation modelling of the control of crop growth by nutrient supply increases.

CONCLUSIONS

1. Soil and plant analyses can be used to predict the likelihood of a response of crop yield to fertiliser additions but their reliability for this purpose is limited where the crop nutrient status is not severely deficient or excessive for optimum yield.
2. Some new rapid and reliable procedures for assessing the crop nutrient status in the field are being developed.
3. Fundamental analyses of the physiological role of nutrients and the control of crop growth by nutrient status are necessary for the validation and calibration of routine soil and plant analyses as indices of crop nutrient status.
4. Mathematical modelling of the control of crop growth by nutrient status is useful for clarifying the concepts and mechanisms involved.

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