PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Modelling of Crop Response to Nitrogen Fertilizer [and Discussion]

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Phil. Trans. R. Soc. Lond. B 1982 **296**, 351-362
doi: 10.1098/rstb.1982.0011

Phil. Trans. R. Soc. Lond. B **296**, 351–362 (1982)
Printed in Great Britain

Modelling of crop response to nitrogen fertilizer

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Quantitative theories have been developed for some of the principal plant processes governing crop response to N fertilizer. One shows that the same simple equation governs the dry matter increase of many U.K. crops during May to September when there are ample supplies of water and nutrients. Another defines the decline in the critical concentration of N in plant material with crop development. Others cover root development in soil and uptake of nitrate by these roots. These theories have been combined to form a dynamic model for estimating day-to-day responses to N fertilizer of crops grown in the field. Simulation studies with the model indicate that failure to take account of variations in subsoil nitrate and rooting depth is a major cause of uncertainty in forecasting fertilizer requirements in the U.K.

INTRODUCTION

Nitrogen fertilizer requirements vary greatly from site to site in a manner that is difficult to forecast. The position in the U.K. is well illustrated by measurements of the optimum N fertilizer levels of winter wheat in a comprehensive set of experiments (Batey 1976). Optimum levels varied between 0 and 195 kg N ha^{-1}, yet only 9% of the total variation in these levels could be removed by regression against the corresponding levels recommended by the Ministry of Agriculture, Fisheries and Food.

Current practical advice relies heavily on empirical interpretation of field trials by simple statistical procedures. The approach permits little input of existing principles of soil science and plant nutrition and, in consequence, it is difficult to see how it can ever take proper account of many interacting processes that influence fertilizer response and the way that they differ from one situation to another. There is a need to develop alternative approaches based on mechanistic interpretation of soil and plant processes. Expecially important are those where processes are represented by equations that are combined to form predictive models which are then tested experimentally.

Much progress has been made in developing equations for soil processes including the mineralization of organic N (Smith *et al.* 1977), the volatilization of ammonia (Parton *et al.* 1981) and the transport of water (Rowse & Barnes 1979), of nitrate (Greenwood & Burns 1979), of heat (Mahrer & Katan 1981) and of oxygen (Smith 1980) through soil. Less attention has been given to the plant aspects of response to N fertilizer.

The primary purpose of this paper is to show that simple quantitative theories do in fact govern important plant processes including the demand of crops for N, the development of roots within soil and the abilities of these roots to extract nitrate from soil. A secondary purpose is to show how these theories may facilitate the development of better means of forecasting how to adjust N fertilizer levels for differences in conditions.

POTENTIAL DEMAND OF CROPS FOR NITROGEN

The rate of crop demand for N is the product of the potential growth rate (i.e. when N supply is non-limiting) and the fraction of N in the plant needed to permit maximum growth. These two factors vary throughout growth in a way that will now be discussed.

Crop growth rate

The pattern of growth of dry matter of many crops is similar. By considering CO_2 fixation in individual leaves, transmission of light through the leaf canopy, losses of CO_2 by respiration and the increase in leaf area index in relation to plant mass, it has been deduced (Greenwood *et al.* 1977) that net photosynthesis should be asymptotically related to plant mass by

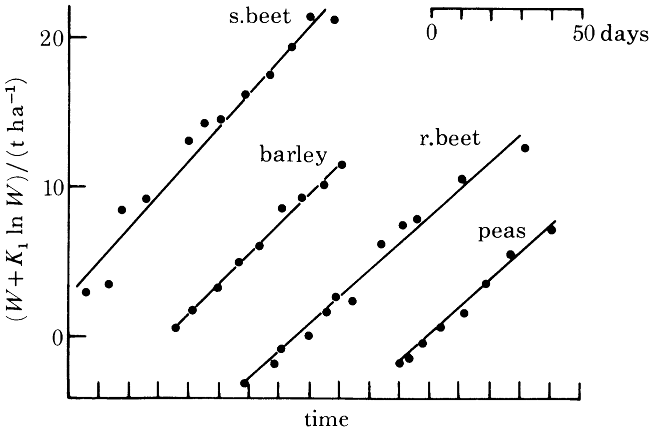

FIGURE 1. Relation between $W+K_1 \ln W$ and time during growth between May and September. Measurements on barley were discontinued at start of senescence. The timescale is a general one and the graphs have been displaced relative to one another. Source of data: Greenwood *et al.* (1977).

$$\mathrm{d}W/\mathrm{d}t = K_2 W/(K_1+W), \tag{1}$$

where W is mass of dry matter per unit area, t is time, and K_1 and K_2 are coefficients. It was also deduced that if W is in tonnes per hectare, K_1 should be about 1 t ha^{-1}. The equation would be expected to apply when growth rate is not limited by lack of water or nutrients and incoming radiation is constant.

Integration of (1) gives

$$K_2(t-t_0) = W+K_1 \ln W - W_0 - K_1 \ln W_0, \tag{2}$$

where W_0 is the mass of plant dry matter per unit area at the start time t_0, and W is the mass at a later time t.

Increases of dry matter of many crops grown with adequate water and nutrients during the main growing period from May to September fitted (2) with K_1 set at 1 t ha^{-1} very well (see figure 1). Also the values of K_2 were usually about 0.2 t ha^{-1} d^{-1} and did not vary much from year to year despite differences in weather conditions. Values of W_0, however, varied considerably from crop to crop (Greenwood *et al.* 1977), which is to be expected as seed masses and plant populations vary and W_0 for drilled crops is roughly the product of unit seed mass and plant population. It therefore appears that most of the differences between the increase in dry mass–time curves of the various temperate crops may be attributed to differences in W_0 rather than to differences in species or weather. Although the equation cannot cover all cropping situations (for example low crop densities) it can be used with $K_2 = 0.2\ \mathrm{t\ ha^{-1}\ d^{-1}}$ and $K_1 = 1\ \mathrm{t\ ha^{-1}}$ to give a reasonable estimate of the potential maximum growth of dry matter of many field crops.

Percentage nitrogen in plant material

The average percentage of organic N in the dry matter of whole plants declines as they grow larger even when they are growing well and are amply supplied with N. Such a decline occurs because as plants develop an increasing proportion of photosynthate is diverted to the synthesis of N-free material required for structural support (Greenwood & Barnes 1978). A theory for this decline in percentage organic N in plants has been developed by considering a simplification of the biochemical processes that take place within plants. It is considered that photosynthetically fixed CO_2 is first converted into glucose, which is used either (i) for the synthesis of structural and storage materials that are nitrogen-free and require no energy for their maintenance, or (ii) for the synthesis and maintenance of protein or enzyme systems that carry out the metabolic processes within the plant. It is also considered that throughout growth there is balance between the proportions of glucose metabolized for each of these two purposes and that the masses of glucose metabolized per unit mass of N-free organic material and per unit mass of protein synthesized are constants. In addition the rate at which glucose is metabolized to maintain protein is assumed to be a constant fraction of the mass of protein.

From these premises it has been deduced that when plants are adequately supplied with N, the mass of protein per plant (P) after a given time (t) is related to the mass of N-free material per plant (F) by

$$\ln P/P_0 = (\delta\beta/\alpha)\ln F/F_0 - \beta M_g(t-t_0), \tag{3}$$

where P_0 and F_0 are the corresponding values of P and F at time t_0, δ is a coefficient related to the relative rates of production of protein and N-free material, β and α are coefficients for the conversion of glucose into the two constituents (P and F), and M_g is the maintenance respiration rate in terms of mass of glucose per unit mass of protein per unit time.

The validity of the model was tested (Greenwood *et al.* 1978) by considering the total amounts of protein (calculated from percentage organic N per plant) at intervals during the growing season in different crops grown with adequate nutrients in the field. For each crop it was found that $\ln P$ of individual plants of similar age (but of different sizes) was linearly related to $\ln F$. The slopes were almost the same for each harvest date and had values that were similar to those calculated from δ, β and α (estimated from the chemical composition by the methods outlined by Greenwood & Barnes (1978). The intercepts showed an approximately linear decline with length of growing period, from which values for the maintenance respiration rate M_g were calculated. Although the direct measurement of maintenance respiration rate is difficult and there have been no direct measurements in the field, the range of calculated values of M_g for the different crops fell roughly within the same range as those expected from measurements under controlled conditions in the laboratory. All this evidence is consistent with the validity of the theory.

Total protein contents of plants grown with adequate nitrogen will therefore be critically dependent on plant size and age. They will also be related to the protein contents in the young plant, the amounts of plant material synthesized per gram of glucose metabolized and perhaps to temperature, as M_g is temperature-dependent.

Equation (3) is, however, more precise than is needed for field crops because of the large plant-to-plant variation. Greenwood *et al.* (1980) showed it could be simplified with little loss of accuracy to give

$$\ln N = A + B(t - t_0), \tag{4}$$

where N is the percentage organic N (calculated as percentage protein divided by 6.25) at time t, t_0 is time at the start and A and B are coefficients. Combination of (4) and (2) gives

$$\ln N = A' + B'(W + K_1 \ln W), \tag{5}$$

where A' and B' are coefficients characteristic of the crop and K_1 is 1 t ha^{-1}.

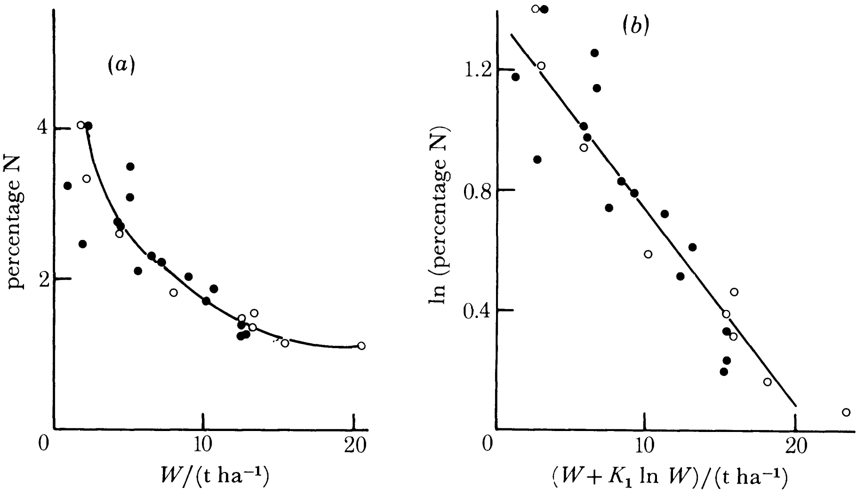

FIGURE 2. Relations between average percentage N in the entire plant (excluding fibrous roots) of 22 different species at harvest and W after being grown with adequate levels of N fertilizer. Some crops (●) were grown on plots that received the optimum levels of N fertilizer in fertilizer experiments; others (○) were crops that attained exceptionally high yields and were kindly provided by A. E. Johnston of Rothamsted Experimental Station (see also Greenwood *et al.* 1980).

The value for ln N of the total plant dry matter (excluding fibrous roots) at harvest of 22 different crop species that had been grown with adequate soil N was linearly related to $W + K_1 \ln W$ with $K_1 = 1$ t ha^{-1} (figure 2). The percentage N in the dry matter needed for the maximum growth is thus determined largely by the dry mass per unit area at harvest rather than by the species.

Parenthetically it may be noted that this finding offers an explanation for the generally higher yields of cereal than of legume grains (F.A.O. 1978). If most plant N is translocated to the grain, then yield of grain N of widely different crops will be dependent on the mass of total plant biomass. As legume grain has a much higher percentage N than cereal grain and the rates of biomass increase of both types of crop are similar (see figure 2), potential maximum yields of legume grains must be much less than those of cereals (see Sinclair & De Wit 1975).

But whether this reasoning is correct or not there can be no doubt that the total dry mass, the percentage N in the dry matter and thus the total demand of many crops for N can be estimated by (2) and (5) from readily available information.

ROOT DEVELOPMENT

Simple equations may also be useful for defining root development. Although root growth responds to water and nutrient stress in ways that are difficult to quantify, it appears that when there are ample nutrients and water there is a general relation between root and shoot growth. During early exponential growth of plants, Pearsall (1927) found that the logarithm of root mass was linearly related to the logarithm of top mass. This implies that the specific rate of use of photosynthate for root synthesis (i.e. the rate of use per gram of root already there) was proportional to the specific rate of use of photosynthate for shoot growth.

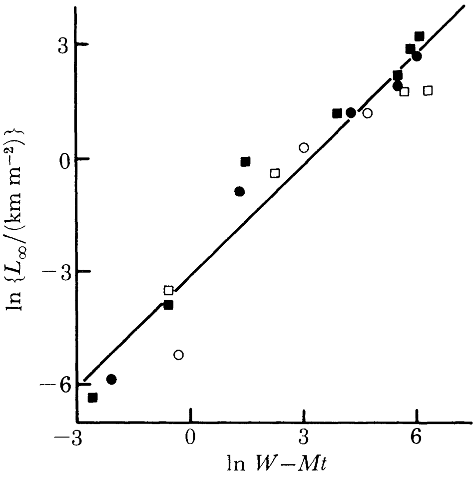

FIGURE 3. Relation between length of root (L_∞), dry mass ($W/(\mathrm{t\ ha^{-1}})$) of entire plant (excluding fibrous roots) and time (t/d) where M of equation (6) is $0.56 \times 10^{-2}\ \mathrm{d^{-1}}$, for cauliflower (●), lettuce (○), turnip (■) and parsnip (□) grown on the same soil; data kindly provided by A. Gerwitz.

If in addition it is assumed that throughout growth, root destruction (e.g. by microorganisms) proceeds at a rate that is a constant fraction of existing live root mass then it may be deduced that

$$\ln R_\infty = C \ln W - Mt + D, \tag{6}$$

where R_∞ is the mass of roots and W is the mass of above-ground plant material per unit area, t is time and C, D and M are constants, C defining the partition of assimilate between root and shoot and its conversion into these two organs, D being related to the initial state of the plant and M being the fraction of root destroyed per day. All measurements of roots and shoots, whether of crops grown in the field or in solution culture, that I have studied fitted this equation. A typical example is the information given in figure 3, which also shows that the parameter values of widely different crops grown on the same soil were similar if root length, L_∞, is assumed to be proportional to root mass.

The distribution of roots can be greatly affected by the physical conditions within the soil profile. Even so, Gerwitz & Page (1974) found that more than 70% of root distributions in their review of world literature could be accurately represented by

$$R_x = R_\infty(1 - \mathrm{e}^{-fx}), \tag{7}$$

where R_x is the total mass of roots (often assumed to be proportional to total length) per unit area within depth x from the soil surface, R_∞ is the total mass of roots throughout the entire profile, and f is a coefficient. When a given crop is harvested at a given time, R_∞ and f are constant. For a group of crops grown on the same soil but harvested at different times I found that

$$f = c - m \ln R_\infty, \tag{8}$$

where c and m are constants.

Further evidence that root distribution down the soil profile may be defined in terms of only few parameters is provided by Burns (1980). He found that 77 % of the total variation in rooting depth of 12 different crop species measured at intervals during growth was removed by a simple regression equation having terms for above-ground plant mass, population density and root radius and only four coefficients. There are therefore good prospects of obtaining simple equations for predicting root distributions in soil.

TABLE 1. MINIMUM VALUES FOR THE AVERAGE CONCENTRATIONS OF NO_3-N IN THE BULK OF SOIL NEEDED TO MAINTAIN INFLOW OF NO_3-N TO THE ROOTS AT THE INDICATED RATES UNDER DIFFERENT CONDITIONS

I / mol cm^{-2} s^{-1}	root density / cm^{-2}	θ	a	average NO_3-N in dry soil / mg kg^{-1}
10^{-12}	1	0.2	0.02	1.1
10^{-12}	20	0.2	0.02	0.6
10^{-12}	20	0.2	0.04	0.3
10^{-12}	20	0.4	0.02	0.3
10^{-11}	1	0.2	0.02	11.4
10^{-11}	20	0.2	0.02	5.6
10^{-11}	20	0.2	0.04	3.1
10^{-11}	20	0.4	0.02	2.8

UPTAKE OF NITRATE BY PLANT ROOTS

Roots of arable crops in the U.K. absorb most of their nitrogen as nitrate rather than as ammonium ions. Nitrate is transported through the bulk of soil to the root surfaces by both convective (mass) and diffusive flow, but the drop in concentration from that in the bulk of soil to that at the root surfaces is largest when convective flow is minimal. It has been deduced (Burns 1980) from steady-state solutions of the transport equations that

$$\overline{C_1} = C_a - \frac{I}{4\pi D_1 \gamma \theta}\left\{1 + \left(\frac{1}{1-\pi a^2 L_v}\right) \ln\,(\pi a^2 L_v)\right\}, \tag{9}$$

where $\overline{C_1}$ is the mean solution concentration, C_a is the concentration at the root surface, I is the rate of inflow of NO_3-N per unit area of root, a is the root radius, D_1 is the diffusion coefficient of nitrate in free solution, θ is the water content of the soil, γ is an impedance factor and L_v is root density. The validity of the equation is supported by experimental evidence (Nye & Tinker 1977).

Measurements of nitrate uptake by roots from rapidly stirred solutions indicated that the rate of nitrate uptake is hardly depressed by lowering of the nitrate concentration at the root surface (C_a) until extremely low values are reached (see, for example, Clement *et al.* 1978). An estimate of the minimum concentration $\overline{C_1}$ that needs to be maintained in the bulk of soil to permit roots to absorb nitrate at a given rate, I, can therefore be obtained from (9) by setting $C_a = 0$ and substituting values for the other parameters. Typical values for I, L_v, θ and a are given in table 1; D_1 is about 1.85×10^{-5} cm^2 s^{-1} and γ may be taken as equal to θ. Average values for C_1 calculated in this way are also given in table 1. These values for minimum concentration needed to meet crop demand for nitrate are insensitive to root density but are proportional to inflow rate and inversely proportional to the soil water content and to root radius. The average concentration for all the different conditions is very low, 3.1 mg NO_3-N kg^{-1}, which is equivalent to about 6 kg N ha^{-1} in the top 20 cm of soil, sufficient to support only one day's good growth.

Lowering of the soil water content can severely restrict movement of nitrate towards roots. In fact nitrogen deficiency within crops has been found when nitrate was confined to a dry layer of soil and the roots were able to satisfy the crops' demands for water from a wet layer that was nitrate-free (Rehatta *et al.* 1979). Distinctive layers of this kind seldom appear to occur in the field. It is more usual for drying of the soil to induce both a decrease in the mobility of nitrate towards the roots and an increase in plant water stress. Increased stress can reduce photosynthesis, the capacity of the crop to metabolize nitrate and in consequence the value for I in (9). According to this equation a decrease in I tends to reduce the minimum concentration of nitrate in soil needed to prevent the crop from being deficient in N and acts in the opposite direction to the decrease in nitrate mobility brought about by a decline in θ. If drying of the soil resulted in the two effects counterbalancing one another it would have little effect on the percentage N or on the percentage of nitrate in plant tissues. As this is generally found to be true (Mathas & Pauli 1965; Maynard *et al.* 1976; Plaut 1973; Ramig & Rhoades 1963; Younis *et al.* 1965), it may be argued that over a range of soil moisture contents, N uptake by plant roots is unlikely to be impeded until the nitrate concentration within soil falls to low values.

Plant roots adapt so as to mitigate any adverse effects of uneven distributions of nitrate within soil on crop intake. When nitrate is withheld from a large proportion of the root system and in consequence plants experience nitrogen stress, the remaining roots increase the rate at which they absorb nitrate by up to fivefold and proliferate far more rapidly than those that have been deprived of a supply of nitrate. After a short period of adaptation, the entire crop's requirement for nitrate may be satisfied by only 20% of the root system absorbing nitrate (Burns 1980).

Consideration of these arguments leads to two general conclusions that should apply to many conditions. First, all the nitrate at a concentration above a low value and in the rooting zone should be available to the crop no matter how it is distributed. Secondly, the rooting zone should extend to where the rooting density is low, which could be a considerable depth from the soil surface as root penetration often exceeds 100 cm (see Burns 1980).

These conclusions are supported by ^{15}N studies, which show that maize can recover as much NO_3-N when it is placed at a depth of 120 cm as when it is placed near the surface (Gass *et al.* 1971; Herron *et al.* 1968). They are also supported by many experiments on winter wheat. The crop can absorb about half of its nitrate from between 20 cm (plough longer) and 100 cm from the soil surface (Jungk & Wehrmann 1978), it can remove virtually all the nitrate in the soil to a depth of 100 cm whenever insufficient N is applied to permit maximum uptake (Jungk & Wehrmann 1978), and it can recover N from fertilizer at depths of 50, 100 and 150 cm from the soil surface equally well (Daigger & Sander 1976). In addition the optimum fertilizer levels determined in experiments in similar soils declined almost in proportion to the total quantity of nitrate in the top 100 cm of soil in spring (figure 4), the indication being that all the nitrate to that depth had to be taken up before N deficiency occurred.

DYNAMIC MODEL

It should therefore often be possible to obtain a good estimate of the N fertilizer requirements of a given crop on a given soil from a consideration of just four factors: the potential demand of the crop for N (i.e. the amount of N needed to permit maximum growth), the depth of the root zone, the amount of nitrate in that zone at drilling and the amount released during the growing season. In consequence the theory for nitrate uptake together with (2), (3), (6), (7) and (8) have been combined to form a dynamic model for day-to-day increases in dry mass of crops receiving different amounts of N fertilizer. The techniques adopted were similar to those described previously (Barnes *et al.* 1976; Scaife 1974). Essentially the model calculates for each day the maximum possible uptake of nitrate by the crop, the depth of rooting, the amount of nitrate released by microbial decomposition in relation to depth from the soil surface, the total amount of nitrate within the rooting depth, the actual uptake of nitrate, the percentage N in the plant, the increase in the mass of plant dry matter, and the total mass of dry matter. Input data are the level of N fertilizer, the initial plant size, the initial distributions of nitrate and soil organic matter down the soil profile, and coefficients to characterize the breakdown of soil organic matter and the growth of the crop under optimum conditions. Movement of nitrate up and down the soil profile was assumed to have no effect on uptake, a reasonable assumption for much of the growing season. For most simulations the values of the variables were set to these representing growth of a typical spring-sown U.K. crop on an average arable soil (containing 11 t organic N ha^{-1} m^{-1} and releasing 120 kg NO_3-N ha^{-1} per year).

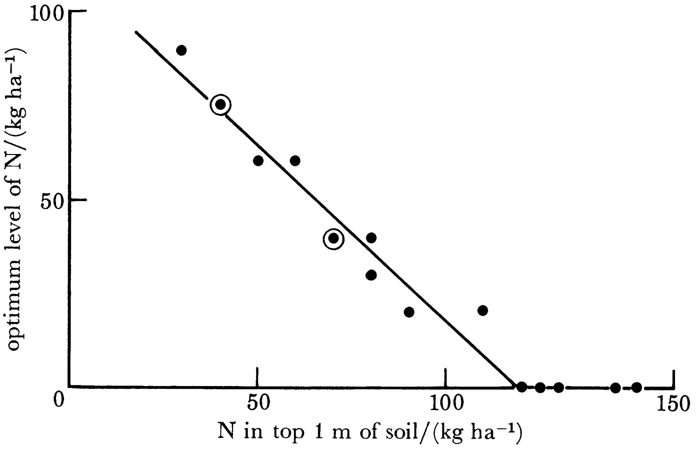

FIGURE 4. Optimum levels of N fertilizer found experimentally for winter wheat on loess soils containing different amounts of NO_3-N in the top 1 m during February–March (Jungk & Wehrmann 1978).

It was predicted that responses to N fertilizer increased with increase in mass of dry matter up to about 8 t ha^{-1} but thereafter only changed slowly. Responses were dependent on the rate of organic matter breakdown; doubling the rate from 120 to 240 kg of NO_3-N ha^{-1} per year increased yields of plant dry matter from 4.2 to 5.6 t ha^{-1} when N fertilizers were withheld and roots penetrated to 1 m depth. Simulated dry matter yields were very sensitive to depth of rooting and to the quantity of NO_3-N in the subsoil. When roots were confined to the top 42 cm and the soil contained 33 kg of NO_3-N ha^{-1} m^{-1} at sowing, yields were only 2.7 t ha^{-1} compared with 8.2 t ha^{-1} when the roots penetrated to 1 m depth and the initial quantity of nitrate was 99 kg of NO_3-N ha^{-1} m^{-1}. For a constant depth of rooting (1 m), increasing the initial quantity of nitrate in the subsoil from 33 to 99 kg NO_3-N ha^{-1} m^{-1} raised yields from 4.7 to 8.2 t ha^{-1} compared with 10 t ha^{-1} obtained when there was no deficiency of N in the crop.

The quantities of inorganic N, in spring, in the top 1 m of U.K. arable soils cover a greater span than those used in the simulation studies. They varied from 30 to 200 kg N ha^{-1} m^{-1} in a recent survey carried out by I.C.I. (J. D. Hollies, personal communication). Failure to take account of this variation and also the variation in rooting depth may well be the major cause of present unreliability of advice on the levels of N fertilizers to be used in different fields in the U.K.

Conclusions

Important processes influencing crop response to N fertilizer can thus be represented by mechanistic equations of wide applicability that can be combined to form dynamic models for estimating day-to-day responses to N fertilizer. Simulation studies with these dynamic models suggest new ways of improving the reliability of N fertilizer recommendations. Opportunities clearly exist for developing a general theory for crop response to N fertilizer, which could be of immense practical value the world over.

I am very grateful to Mr A. Gerwitz, Mr A. E. Johnson and Mr J. D. Hollies for very generously permitting me to quote unpublished data, and to Mr A. Barnes for mathematical assistance.

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Discussion

M. J. S. FLOATE (*Hill Farming Research Organization*, *Penicuik*, *Midlothian*, *U.K.*). My question concerns NH_4-N, and the role of plants in the nitrogen cycle: would Greenwood's relationship between production and subsoil NO_3-N be the same for NH_4-N, and what would be the similar and contrasting effects of NO_3-N and NH_4-N nutrition of plants upon nitrogen cycle? This question is of great interest in hill grasslands, where plants rely heavily upon NH_4-N nutrition.

D. J. GREENWOOD. Our model assumes that the crop relies entirely on the uptake of nitrate to meet its needs for nitrogen. I believe that ammonium would be absorbed strongly on the surface soil and thus would not move in appreciable quantities to the lower horizons. The model applies to arable crops but not hill grassland.

My understanding is that plants that are normally grown on cold acid soils grow better on NH_4-N than NO_3-N and that the converse is true for crops that are normally grown in warm neutral or alkaline soils. Some crops prefer a mixture of ammonium and nitrate ions to either alone. When crops adsorb ammonium ions the growth medium becomes more acid, and when nitrate is absorbed, more alkaline. The local effects around the roots can affect phosphate and trace element concentrations in soil and their uptake by roots.

The form of nitrogen absorbed profoundly affects cation uptake and the levels of organic acids within the plants. Uptake of ammonium is associated with less cation uptake and organic acid formation than is uptake of nitrate. Nevertheless the amount of metabolizable energy needed to convert both nitrate and ammonia to protein may be similar, because nitrate can be reduced to ammonia by the direct reduction in the plant by radiant energy and without the consumption of carbohydrate. Thus some crops can grow equally well with either nitrate or ammonium ions as a source of nitrogen.

J. A. Nelder (*Rothamsted Experimental Station*, *Harpenden*, *U.K.*). I should like to question the usefulness of the distinction that Dr Frissel made between models for improving scientific understanding and models for prediction; indeed I would question the value of the distinction, often made, between empirical and mechanistic models. Often the distinction between an empirical and a mechanistic relation is a matter of chronology: what was once an empirical relation is now embedded in scientific thought and has become mechanistic.

I suggest that it would be more useful to assess models in terms of two criteria, invariance and scope. By invariance I mean the establishing that something remains constant when something else varies, for example Dr Greenwood's demonstration of quantities that remain (approximately) constant when species vary. Scope means the range of conditions over which a model can be shown to apply. Clearly both scope and invariance are necessary in the making of predictions; furthermore I believe that these criteria provide a roughly quantifiable measure of success of a model. Such measures are badly needed if models are to be compared adequately.

M. J. Frissel. I agree only partly with the statement that the distinction between empirical and mechanistic relations is a matter of chronology. Indeed the first ones developed were empirical, but the mechanistic relations that came after have improved many empirical relations in many disciplines, in turn.

As far as crop production models are concerned, many of these models are still empirical, and only the photosynthetic and respiration parts are conceptual. That means that for crop production models, invariance and scope, as defined by Nelder, have to be determined by experiments. The great advantage of conceptual models is that they are applicable over a wider range of conditions; invarance and scope therefore play a less important role.

D. J. Greenwood. I think that there have been considerable changes in the ways we have been developing computer simulation models over the past 10 years.

Initially our approach was dominated by the one thought that we must try to represent individual processes by separate equations and then combine them into a simulation model. Not too much trouble was taken about whether the equations had a sound physiological background or whether they were obtained by statistical fitting. Even so, predictions with these models were in good agreement with the results of independent experiments. We became concerned, however, lest some of the individual equations were too empirical and thus of limited generality, so that we did not feel justified in testing our initial models over a wide range of conditions.

These considerations led to two main developments. First we attempted to gain a very deep understanding of key processes by reviewing the literature and to represent this understanding by the simplest equations. This enabled us to make, for example, predictions about maintenance respiration rates from such unlikely measurements as those of the N contents of individual plants. Secondly, we attempted to review quantitative relations for each of a group of processes with a view to evolving a general principle to cover the entire group. Our treatment of N uptake by roots illustrates the point. We used to calculate movement of nitrate to and absorption by each individual root and sum over the entire population. Then we developed an overall simple concept which dealt with uptake of nitrate by the root populaton as a whole to the depth of rooting. So our dynamic models have become simpler over time.

I believe therefore that the procedure in which we now develop models is very dependent on gaining a deep understanding of the key processes both in the development of individual equations and in determining their structural relation to one another. It is much less dependent on searching for empirical statistical relations than hitherto. I also believe that a criterion of success is 'Does it predict any new general principle that was unforeseen?' But whether these views are correct or not it is becoming increasingly clear that key processes governing crop response to N fertilizer are governed by widely applicable concepts that can be expressed in terms of the simplest equations.