

# **Crop Nutrients: Control and Efficiency of Use [and Discussion]**

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# Crop nutrients: control and efficiency of use

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Inputs of chemical fertilizers are essential in almost all intensive agricultures to reach maximum crop yield, but efficiency of use, expressed as the fraction recovered in the harvested crop, is often low. The more accurate control of quantity and better timing of application could improve efficiency, and new methods for achieving this are discussed, including computer simulation.

Some species and cultivars are particularly efficient in their use of soil nutrients, partly by having a low content in their tissues, but more often by special root processes and symbionts that aid uptake. Greater use of these should be possible.

More exact control of crop elemental composition can be important for quality. Plant processes which control composition via uptake rate are only now being investigated, but possible methods of modifying these are considered.

# 1. Introduction: the present situation

Plant and crop nutrition have not been seen as exciting subjects in the last four decades. This is largely because of the enormous practical success of simple nutrient salts as chemical fertilizers. These are mainly stable, cheap and simple to manufacture and large reserves of the raw materials exist. Thus superphosphate (monocalcium phosphate) was developed as a fertilizer 140 years ago, but is still very difficult to improve upon in terms of plant growth. Meanwhile, academic studies on plant nutrition have proceeded almost in isolation, having neither contact with nor effect upon the practical control of nutrition in the field, which has been largely left to soil scientists to deal with. Yet there is clearly scope for greater activity. The basic processes of plant nutrition are exceedingly complex, both at sub-cellular, cellular and organ levels, and our understanding of how a whole plant controls its nutrition is very poor. Equally, on the applied side, the control of fertilizer use is very crude in many situations, with obvious waste and inefficiency.

There have been important practical developments in the last two decades, particularly the great increase in rates of application to maintain increasing yields (figure 1) and the rise in importance of urea. Most of the developments in actual technology, such as the use of anhydrous ammonia, high-concentration liquid fertilizers, or slow-release nitrogen fertilizers, have failed to break into the market in Britain, or have found only a minor use. The great bulk of fertilizer is used in ways not very different in principle from those of 50 years ago, though it is applied more rapidly and accurately. It is indeed a great bulk; the total mass of nutrients used in Britain is now around 1.5 Mt N, 0.4 Mt P and 0.4 Mt K, at a cost of around £750 M.

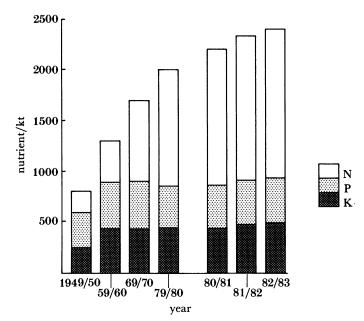


FIGURE 1. Use of N, P and K fertilizers in Britain (from Fertilizer Manufacturers Association 1984).

#### 2. The social and economic background

# (a) Importance of costs

Costs are central to the themes of this review. There is little prospect that processes will be invented to do what simply cannot be done at present, but there are possibilities of making present practice more effective or more cheap. The main thrust of fertilizer research must be towards more exact and accurate control of cropping procedures, to diminish the inaccuracy and unpredictability inherent in working in a natural and highly variable environment. The importance of such possibilities depends very much upon relative costs. The price of fertilizers relative to the retail price index has fallen on average for a number of years (Fertilizer Manufacturers Association 1984). However, there have been discontinuities such as in 1973 when nitrogen and particularly phosphate prices increased massively. A new world oil shortage would increase nitrogen prices sharply again, and any interruption of phosphate supplies would do the same for that nutrient. The future is discussed here in relation to the conditions which now seem likely; any marked change in costs could considerably change these conditions and hence my conclusions. New crops may be introduced, but it seems unlikely that they will involve any new principles in nutrition.

#### (b) Environmental problems

Over the last five years the need to take account of pollution dangers and other environmental problems that may follow fertilizer use has become much more urgent (Cooke 1984). The most important nutritional question concerns nitrate pollution in aquifers and rivers. In part this results directly from the enhanced use of nitrogen fertilizers, but the importance of this relative to other sources is still in dispute. This topic is sensitive because of suggestions that high nitrate in drinking water tends to induce stomach cancer. The most recent information (Formen et al. 1985) suggests an inverse link between nitrate ingestion and stomach cancer. Any clear

evidence of such a link would make this a highly emotive issue and this would affect nitrogen use. Phosphate is less of a problem, because very little enters watercourses from soil or fertilizer except where soil erosion occurs, which is rarely serious in Britain.

A related problem is that of heavy metals in sewage sludge, which is often applied to land as an organic manure. This is more a problem of waste disposal than of crop nutrition, but it raises many similar problems and it is particularly intractable because the metals remain in the soil almost indefinitely and appear to diminish the soil biomass (Brookes & McGrath 1984). Methods of removing such metals from primary sewage are essential in the long term.

# (c) Low input agriculture

This concept is widely debated, but its underlying ideas are by no means clear (Sanchez & Salinas 1983). Most inputs are tested at several rates and the consequences of applying lower rates of fertilizers can be predicted with reasonable certainty (Lidgate 1984). With the present structure of fixed and variable costs it is very difficult to see any economic justification for deliberately applying fertilizers at below-average optimum rates. Obviously, if a farmer can obtain the same yield with cheaper or more carefully controlled inputs, he is well advised to do so, but this has always been true. The only real justification for a reduced input appears to be if there is a large risk that the expected benefit will not be obtained (Tinker 1985a) or if social or economic constraints make it advantageous to spread a fixed amount of production over a larger area of land than is strictly necessary, as when production quotas are applied. By contrast, F.A.O. (1981) predicts that huge increases in fertilizer use (7-8% per annum) are necessary to meet world food demand in the next 20 years.

# (d) Organic farming

I find it difficult to follow some of the arguments advanced to support organic farming. Nevertheless, there is a growing demand for such produce and it will need to be met. It is a simple matter to show from nutrient balances (table 1) that organic manure could not possibly meet the whole demand for N, P and K by our agriculture, especially with the rather poor recovery of nutrients from organic manures (Cooke 1982), but so long as the organic agriculture remains a small fraction of the whole, this requirement can be met.

Table 1. Nitrogen balance of the United Kingdom<sup>a</sup>

	inputs		outputs
rain	275	crops and grass	1367
seeds	14	leaching	326
fertilizers	1150	ammonia volatilization	
sewage	26	livestock excreta	536
livestock excreta	1020	crop wastes	50
silage effluent	9	sewage	9
straw	15	balance by difference	380
feed waste	9	(mainly denitrification	
biological $N_2$ fixation	150	and immobilization)	
totals	2668		2668

<sup>&</sup>lt;sup>a</sup> From Royal Society (1983). Values in kilotonnes of N.

#### 3. NITROGEN

# (a) Efficiency of recovery

It is generally assumed that about 50% of applied nitrogen is removed in the harvested parts of the crop, varying somewhat with species (Royal Society 1983). Novoa & Loomis (1981) give a mean value of 30% and recoveries between 0 and 100% are reported in single experiments (Craswell & Godwin 1984). The percentage recovery can be measured either by using labelled 15N fertilizer or by 'difference', i.e. the difference in N uptake by crops, on plots in the same experiment with or without N fertilizer. The use of 15N appears most reliable, but in fact it is open to serious bias. The continued interchange of <sup>15</sup>N nitrate or ammonia with the <sup>14</sup>N present in the organic matter of the soil and the microbial biomass, by mineralization and immobilization, results in a steady dilution of the isotopic label. The fertilizer taken up can therefore be seriously underestimated if the normal methods of calculation are used. Detailed measurements by the difference method has shown uptakes in the  $70\,\%$  range. However, of this nitrogen in the total crop including roots, only some 75% is in the grain at harvest, so the normal recovery in grain is 50-60% under the best circumstances (Tinker 1979). It is interesting that the ratio of mean yield of grain per hectare to mean use of N per hectare has remained astonishingly constant over many years, at 24 kg grain kg<sup>-1</sup> of N (Tinker 1983). Because there is an input from rain and soil processes of some 30-50 kg ha<sup>-1</sup>, this implies that fertilizer nitrogen recovery has been increasing slightly as yields have risen. Taking a mean grain nitrogen percentage of 2.0%, it suggests that the average recovery of nitrogen in grain has always been less than 48%. The fate of the rest of the nitrogen is by no means clear, and will vary with time, soil type and weather (Royal Society 1983). Some is taken up by the crop in succeeding years, but it is a relatively small percentage of that initially added (Jenkinson 1984). The processes leading to loss are leaching into groundwater, runoff into rivers, volatilization as ammonia or denitrification to  $N_2$  or  $N_2O$ .

The attempt to consider nitrogen efficiency should clearly start from the total N balance for the country (table 1) (Royal Society 1983). The major losses are leaching of nitrate and ammonia volatilization from animal wastes and grazed grassland. Denitrification losses are included with the 'balance by difference', which also contains all of the errors in table 1. The main point is the huge loss of ammonia by volatilization from animal wastes, and attempts to reduce this must be essential in the future. It is, however, a very difficult problem to overcome in the field; the application of the zeolite clinoptilorite to the soil surface reduces this loss, but this is likely to be an expensive remedy (Ryden 1984).

The potentially most troublesome form of loss is leaching into subsoil and thence into the aquifers from which our water supplies are drawn. The present E.E.C. standard for nitrate in water is only 11.2 mg N l<sup>-1</sup>, which is considerably below the average concentration of nitrate in the soil solution and there is serious concern about the future course of nitrate accumulation (Wild & Cameron 1980). It has been accepted for some time that nitrate concentrations below arable land are high (5–25 mg N l<sup>-1</sup>) but lower under grassland (1–10 mg N l<sup>-1</sup>) (Royal Society 1983). However, recent work (Ryden et al. 1984) shows that where grazing animals are depositing nitrogen in patches, the concentration of nitrate in the deeper subsoil below grassland can also be relatively high. This is to be expected, because the offtake of nitrogen in produce is far less on a grazed than a cut field, and the surplus must be lost in one way or another. The immediate mechanism of loss is presumably that the rate of application of N

immediately around the point of application of dung or urine is so high that the grass cannot use it, and it is eventually lost by leaching or denitrification. In all, the efficiency of use of nitrogen on grazed land is only 5–15%, but on cut grass it is 85%. For the latter, the inefficiency arises at the final stage of disposal of slurry (Ryden 1984).

Nitrogen cycling under grassland is a particularly interesting topic, because of the very large flows that can take place and because it has been generally accepted that the average rate of fertilizer use will rise steadily in the future. However, this conclusion must be very much in doubt after the imposition of milk quotas in 1984. The way in which this reduction has been enforced puts a premium on low input costs per unit area, whereas a price cut, for example, might have favoured concentration of the industry in the most intensive areas. There is thus a clear indication that biological nitrogen fixation may become more desirable and the predicted increase in use of N fertilizer on grassland may not occur.

## (b) Possible improvements in nitrogen requirement prediction

Current methods of predicting nitrogen need in individual fields are based on past cropping, modified for soil type and rainfall in very general ways. Again, there is no published fully quantitative assessment of the success of this system, though it is probably inaccurate (Needham 1982; Greenwood 1982; Sylvester-Bradley et al. 1984). Farmers tend to over-fertilize for safety if they have no great confidence in the advisory method, but yields may also be lost by under-fertilizing in some cases. The improvement of this situation is a crucial problem in practical plant nutrition today in Britain.

The difficulty is due to the complexity of the nitrogen cycle (Royal Society 1983), so that many simultaneous processes have to be measured or predicted. Mineral N (nitrate and ammonium) is being produced at varying rates throughout the year, so no single measurement is adequate to determine the soil supply. In Europe various systems have been developed which measure mineral N in spring to a depth of 1 m, regarding this as the store of N before the period of rapid growth (Wehrmann 1982; Greenwood 1985). The principle underlying these 'Nmin' systems is to assess the amount of nitrogen needed by the crop, to compare it with this store of soil mineral nitrogen in spring and to make up the balance with fertilizers. There are various additions to this basic scheme, not all of which are well grounded on proper information. This basic system, with slight variants, has been tested in several north European countries, and the correlation between the best rate of N fertilizer and the N<sub>min</sub> measurement, is usually between 0.45 and 0.95 (Greenwood 1985). These methods are regarded as highly useful in northern Germany (Kuhlmann et al. 1983), but there may be practical problems in such deep soil sampling, particularly on stony soils. The final success of such methods is thus still uncertain, but they are the only ones with any significant promise for arable crops at present and with any reasonable scientific basis.

## (c) Simulation modelling

The most exciting prospect now is the use of computer simulation models. I will discuss here only those that aim at controlling plant nutrition, but the principles are of much wider scope (Greenwood 1982; France & Thorneley 1984; de Wit, this symposium). The advances in the development of whole-crop models are already considerable (Weir et al. 1985) and in the long run I expect much of the present advisory work to be based on computer simulation.

A major reason for modelling lies in cost. The N<sub>min</sub> methods, while practical to use, are

expensive. The present cost of nitrogen fertilizer, in relation to the cost of grain, is so small that even significant savings in nitrogen give only small economic benefit; e.g. 20 kg ha<sup>-1</sup> of N saved represents only about £7 ha<sup>-1</sup>, or about 1% of the value of the average wheat crop in 1984. There are significant environmental benefits in lessened use of nitrogen, but the farmer does not always take such factors into account in his planning. There is consequently a great need for cheaper methods, and computer simulation is extremely cheap if the necessary data are easily acquired. At present several such systems are being developed and I use that of Addiscott for winter wheat as an example (Tinker & Addiscott 1984). This simulates leaching, mineralization, nitrification and crop uptake, and from this predicts the nitrogen held in the crop and that in the soil profile, at any time during winter and spring. This information can be used directly in the same way as measured mineral N.

There are further advantages in such systems. Because the data required relate only to weather and soil, the programme can be run at any time. It can thus predict a need for early winter N, or a later application after the main N top dressing. This use may be greatly increased by the results of Powlson et al. (1983), which show that there is a loss of up to 30% of the applied nitrogen, probably by denitrification, in the month following application and that this is directly related to rainfall. Further extensions of modelling to cover the whole nitrogen cycle over several years are being developed (Jenkinson 1984). All the methods would be rendered far more powerful if dependable weather forecasts were available even for a month.

Simulations of this type could have an additional use in estimating the concentration and amount of nitrate in the drainage water. As the simulation is reasonably site-specific, a nitrate budget for single farms could be determined. This would be of special interest if any restriction on nitrogen fertilizer use was introduced in any area, because it might allow the control to be based on the actual concentrations in the drainage water on that site rather than on some average value, which could be very wasteful.

#### (d) Chemical control of nitrogen transformation

The hydrolysis of urea to ammonium carbonate, and the oxidation of ammonium to nitrate are particularly important, because they control the amount of loss of nitrogen by, respectively, volatilization of ammonia, anaerobic denitrification and leaching. There has been a great amount of work on nitrification inhibitors and a range of compounds are available that inhibit the oxidation markedly for different periods. At least one (Nitrapyrin) is used commercially on a fair scale, but it has been difficult to define conditions in which their use is profitable in Britain. There are a few cases where autumn nitrogen application is advantageous, but spring top-dressings normally give yields as good as systems using inhibitors and autumn nitrogen.

There are, however, still possibilities for more use of nitrification inhibitors.

- (i) Use to control nitrate levels in vegetables with high N manuring (Slangen & Kerkhoff 1984).
- (ii) Use to control losses by leaching of early applied N dressing. This could be particularly important for oilseed rape and grass, but also occasionally for cereals. Dicyandiamide (DCD) is now becoming available and appears promising when mixed with urea in a prilled form. This in effect acts on a slow-release N fertilizer, and prevents the soil nitrate level under a growing crop increasing for a period of months (figure 2).
- (iii) Rodgers (1983) has suggested that nitrification inhibition could be used to prevent the nitrification of the large flush of ammonia produced after grassland is ploughed up. This has

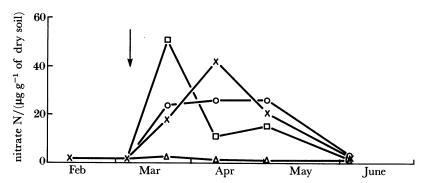


FIGURE 2. Changes in soil nitrate nitrogen under oilseed rape after application of urea with DCD (nitrification inhibitor) or hydroquinone (urease inhibitor). Arrow marks time at which fertilizer was applied; ×, urea; △, urea + DCD; ⊙, urea + hydroquinone; □, nitrochalk. After A. Rodgers (personal communication).

been implicated in high concentrations of nitrate in groundwaters. However, the nitrogen will eventually nitrify, hence the strategy will only be successful if nitrogen can be absorbed and removed from the field in a crop.

- (iv) Very large losses by leaching of nitrogen can occur from slurry, especially if applied in autumn. There is the possibility that DCD or other inhibitors could prevent this (Amberger 1983), but the cost may prove to be a problem.
- (v) Major losses of N by denitrification in spring (§ 3c) could be reduced by delaying nitrification for a very few weeks at this time, which could be done with an ammonium or urea fertilizer and a nitrification inhibitor. This is being tested now. Nitrification inhibitors are obviously of little use with ammonium nitrate, the standard nitrogen fertilizer at present. However, urea is rapidly becoming the most common nitrogen fertilizer on a world basis. The main argument against urea has been that it is prone to loss by volatilization after hydrolysis, on calcareous soils. This loss is unpredictable, because it depends upon the weather, so that it becomes difficult to achieve controlled manuring. Inhibition of the ubiquitous urease enzyme would allow the urea to remain unhydrolysed for long enough to be washed into the soil, after which losses are very small. A number of potential inhibitors have been tested in the past (Bremner & Douglas 1971) and a moderate degree of inhibition has been obtained. The inhibitor phenyl phosphorodiamidate (PPDA) is proving successful in field tests. It may also be used to prevent damage to seedlings from ammonia and high pH caused by rapid hydrolysis of urea. The largest use of such an inhibitor would, however, be in the tropics, in plantation crops such as oil palm and rubber, and in rice growing where the efficiency of use of urea can be very poor (Craswell & Godwin 1984).

#### 4. OTHER ELEMENTS

The efficiency of use of phosphorus depends on totally different mechanisms to that of nitrogen. Little if any applied phosphorus escapes from the soil profile after it has been applied, but the recovery from the profile is poor, being often less than 10% by a single crop. However, as the concentration of phosphate in the soil increases, the crop can extract a steadily larger fraction of new additions. This is because of the very curved adsorption isotherm for phosphate in most soils, leading to a rapid rise in solution concentrations and hence availability,

at the upper end of the isotherm (White 1980). Ultimately the amount extracted by the crop is almost equal to that added, so that recovery, by the difference method, can be very good

in the best cases. There are, however, still very controversial questions on the reversibility or hysteresis of sorption of phosphate, and of slow recrystallization or solid-phase diffusion, so that

100% recovery is unlikely to be attained over a period of uniform cropping and fertilizing.

The true inefficiency of phosphorus use thus lies in the need to deposit sometimes very large amounts of phosphate fertilizer in the soil profile before crops will attain their maximum growth rate. This phosphorus is not recoverable if high yields are to be maintained. However, many British soils at present contain more phosphorus than is needed for maximum production of the most usual crops, especially cereals. Some of this could be recovered by simply continuing to crop without replacement fertilizer, and an example of what would then happen is shown in figure 3 (Johnston, personal communication). A limit is reached (around 15 μg P g<sup>-1</sup> of soil for cereals), at which the growth rate of crops begins to be affected and this represents the store of labile phosphate in British soils, which under current conditions cannot be used. It is difficult to calculate how large this is, but on average it cannot be less than 200 kg P ha<sup>-1</sup> on arable soils. There are various ways in which some of this could be exploited, such as rotations including efficient extractive crops, new P-efficient cultivars, or better use of improved mycorrhizal fungi, but at present it may not be worth the investment and time needed. However, in other countries, where the ratio of yield value: fertilizer cost is very much smaller, it may be highly desirable to be able to extract this phosphorus, or not to have to deposit it there in the first place.

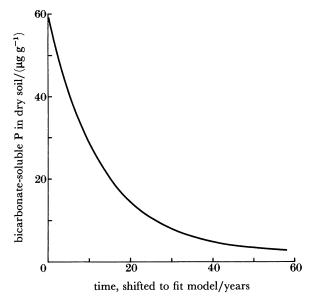


FIGURE 3. Decline of soil phosphorus in Beccles series soil continuously cropped with cereals without phosphorus fertilizer additions at Saxmundham 1969-1982. (Johnston, personal communication.)

## (a) Potassium

This element is intermediate between nitrogen and phosphorus in its behaviour. It is held as an exchangeable cation, or trapped in the lattice of 2:1 expanding clays, but there is often sufficient in solution to cause an important loss by leaching. This is, however, very dependent upon soil texture, rainfall, fertilizer policy, etc. As it is a cheaper and rather less used fertilizer than nitrogen, questions of low efficiency are not so important and many clay soils are able to release potassium to crops, from hydrous micas. A more precise method for prediction of this last process would be useful (Goulding 1984).

## (b) Calcium and magnesium

Calcium is not added as a nutrient, but for acidity control. The costs are not high and there is little possibility of making improvements and savings by more exact control. The use of magnesium as a nutrient is only moderate; there are relatively cheap forms and consequently no great pressure for improvements. Indeed, the efficiency of uptake, on the sandy-textured soil where it is normally applied, is probably quite good.

## (c) Trace elements

The cost of some trace element applications, for example Mo for legumes, is trivial. For others the cost is more serious, such as manganese, which is applied as a foliar spray; but the total material cost is small compared with the major nutrients. There may be improvements in formulations for application. At present there is little need for sulphur additions except in limited areas (Scott et al. 1983; Bristow & Garwood 1984) but any further effort to remove sulphur from flue gases could increase the demand very greatly.

## (d) Advisory methods

Current methods of advising on the use of phosphorus and potassium are probably not highly accurate, but are sufficiently good, because any surplus applied is not lost but builds up in the soil and alters the subsequent assessment of the need for fertilizers. This assessment is done by soil analysis, by routine methods developed and tested over many years (Ministry of Agriculture, Fisheries & Food 1979). Whereas these methods are probably as good as routine soil analyses can be, there is no published independent assessment of how useful they are. This would require a test of yields with fertilizer application guided by these methods, compared with a standard rate. No such assessment appears to have been done since Boyd et al. (1956) did this for sugar beet. They determined that the cash value of an analysis was quite small at the values then prevailing. A similar assessment would be very interesting at present.

Crop size may have consequences for fertilizer use. Clearly the offtakes of P, K, Mg, etc. over a number of years will be much larger with current high yield than earlier, and this will have to be made good in a larger fertilizer programme. At present the adjustment to allow for crop size is rough (Ministry of Agriculture, Fisheries & Food 1979) and requires to be expanded and improved. It appeared possible that modern large crops would demand a higher soil-nutrient status if they required a larger inflow to the roots. However comparison of results obtained at Rothamsted (Barraclough, personal communication) for a 10 t winter wheat crop with those of Gregory et al. (1979) for a 5 t crop showed that the inflows for phosphorus did not differ greatly, i.e. the increased root growth in the larger crop compensated for the greater rate of uptake. The nutritional problems are thus basically unchanged by increased yield.

Leaf and tissue analysis methods are little used in arable crops, except for quick tests for nitrate. On the other hand, many perennial crops depend upon them greatly (Atkinson et al. 1980), especially tropical plantation crops. It is possible that more detailed analyses might give a better insight into the true nutritional status of the crop, but it is not known if this will lead to any improvements on what is agreed to be an empirical and sometimes unreliable procedure.

#### 5. More nutrient-efficient crops

## (a) Plant modification

Work aimed at increasing the efficiency of crop species at absorbing or using nutrients has frequently been talked of in the past, but has rarely been brought to a practical conclusion. Recent work is more promising (Clark 1982; Saric 1983). The fact that there are genetic differences in nutrient uptake ability is never in doubt, because different species show major differences in their ability to grow and to extract nutrients from soils. A particularly good example is in the work of Graham (1984) on copper deficiency, which shows up easily in wheat. Rye shows a high ability to obtain sufficient copper from low-copper soils, and in crosses between rye and wheat this ability was linked clearly to a single gene (figure 4). However, the mechanism by which more copper is extracted from the soil is so far not clear. As in other instances, the difference does not lie in the ability of rye to grow with less copper, because all these lines required about the same copper concentration in the tissues for normal growth.

			grain yield (g/pot)	
			-Cu	+Cu
5RL/4Aβ	4 Αα		6.8	6.9
Transec	4 Αα		0	9.2
5RL/5BL	5 BS		5.5	8.6
C.S. wheat	4 Αα	4Rβ	0	7.5

FIGURE 4. Chromosomal structure of three translocation lines of Chinese Spring Wheat with rye chromosome segments shown as serrated lines, and of Chinese Spring itself. Grain yield when grown in pots of copper-deficient soil also shown. S, L α, β designate specific arms of chromosome (after Graham 1984).

Proposals are occasionally made to breed for improved uptake mechanism in plants (i.e. the uptake parameters would change, to a larger  $V_{\rm max}$  or smaller  $K_{\rm m}$ ). All present information shows that  $V_{\rm max}$  is large enough and  $K_{\rm m}$  small enough, and that both depend upon plant nutrient status (Glass & Siddiqi 1984). Thus work done with properly controlled flowing solution culture shows that crops are able to absorb adequate amounts of the major nutrients from solutions of the order of  $10^{-6}$  M (Wild et al. 1979; Loneragan & Asher 1967). The extensive work on the ATPases involved in the uptake process is thus unlikely to have much practical application. It seems much more likely that differences in uptake ability may be a result of specific mechanisms such as root surface acidification (Hedley et al. 1982; Romheld & Marschner 1981) or chelate exudation (Gardner et al. 1983). Clearly such mechanisms will only be effective for a small number of elements and until the mechanisms are understood, breeding for 'nutrient efficiency' is a rather speculative process.

There is also the possibility of modifying root structure and architecture, which are both under a considerable degree of genetic control (Zobel 1975). This includes the root length and branching pattern, and the density and length of root hairs. The efficiency of uptake of nutrients, both mobile and immobile, seems to depend far more upon root length, morphology and distribution than upon the actual values of  $V_{\text{max}}$  and  $K_{\text{m}}$  (Nye & Tinker 1977; Itoh & Barber 1983; Barber 1985). Our understanding of the effects of structure on uptake is now such that it would be possible to design root systems for specified situations. In Britain it would be mainly a question of extracting water, and particularly nitrate, from the deeper parts of the profile. In other parts of the world the most pressing problem would be the availability of phosphorus.

These possibilities are certainly worth considering now; the question is to what degree they are worth pursuing. The actual throughput of nutrients in a healthy crop will not be changed, as the nutrient composition of the crop must be maintained, so that the savings arise largely from being able to crop a field at a lower level of availability of the nutrient. The benefit is thus a function of the type of soil; if for example it is strongly phosphate-sorbing, then large savings are possible. This is clearly important in underdeveloped countries with low yield levels, and the development of such cultivars could be very important (Graham 1984). However, the acceptance of a further aim in any breeding programme usually causes at least a proportionate increase in complexity, so that any development of such cultivars means additional delay, or the less complete attainment of another aim. In view of the high nutrient status of most British soils, there seems little reason to regard this as very important at present. It may be more an aim that should be kept in mind for a time when our ability to modify plants genetically is greater and more precise than it is now.

## (b) Use of micro-organisms

An alternative to changing the uptake properties of a crop plant is to alter it by symbiosis with a beneficial micro-organism. The best known of these is Rhizobium, which fixes dinitrogen. We can probably discount the early introduction of effective microbial nitrogen-fixation genes directly into plants and indeed this may prove to be impossible because of the physical and physiological requirements of the process. The possibility of extending the ability to form useful symbioses with Rhizobium or other nitrogen fixers such as Frankia to major crop plants is more likely, but it may be near the end of the century before this can be done in ways that are of practical value. The question has been raised of whether such symbioses would direct photosynthate away from the formation of economic yield, so that the loss of crop would be greater than the savings on nitrogen fertilizer. The amount of energy required for fixation is still in some doubt (Mahan 1985; Witty et al. 1983) but appears to be around 11 kg carbohydrate kg<sup>-1</sup> of N fixed. However, there is the possibility that the plant can compensate for this, if energy is not a limiting factor in its growth. Further, if a plant receives its nitrogen as nitrate, there is an energy cost in reduction that is in theory comparable with that of N<sub>2</sub> fixation, though reduction of nitrate in the leaves may reduce the net photosynthate demand. In practice, it is very difficult to show that legumes given nitrate nitrogen must yield more than those dependent upon dinitrogen fixation, because of a demand for energy. It is not yet possible to decide on the physiological effects of nitrogen-fixation processes in, for example, cereals and grasses, but the commercial effects in the fertilizer industry could be catastrophic.

The recent advances in understanding the genetics of Rhizobium clearly offer a great

opportunity (Beringer 1980; Postgate 1982). The ability to transfer the nodulation plasmid with reasonable ease allows the host specificity to be changed, and may allow particular characteristics, such as the ratio of hydrogen produced to nitrogen fixed, to be modified in the same way. A particularly interesting avenue is the investigation of the overall carbon efficiency of fixation, i.e. the amount of fixed nitrogen the host–endophyte combination gets back for each mole of carbohydrate used by the nodules (Witty et al. 1983). Different Rhizobium–pea combinations give a wide range of values for the energy demand of the various steps in the process, and they often differ from the theoretical values (table 2). Having this new knowledge, we must ask exactly how this is likely to affect agriculture in the next 15 years. Often it may turn out to be the properties of the host, rather than that of the Rhizobium, which controls the overall performance, but there are four general areas in which advances may be looked for.

Table 2. Energy usage for the different steps in dinitrogen fixation by Rhizobium in peas<sup>a</sup>

	theoretical	experimental
e <sup>-</sup> transfer (mol C mol <sup>-1</sup> e <sup>-</sup> )	0.75	1.1-2.3
$e^-$ to $H_2$ (mol $e^-$ mol <sup>-1</sup> $N_2$ )	2	1.8 - 6.2
$e^- \operatorname{per} N_2 \pmod{e^- \operatorname{mol}^{-1} N_2}$	8	7.8 – 12.2
carbon need for N <sub>2</sub> (mol C mol <sup>-1</sup> N <sub>2</sub> )	6	8.2 - 27.6

a Theoretical values are compared with the range of values measured in experiments, for the equation

$$(6+n) e^- + (6+n) H^+ + N_2 \rightarrow 2NH_3 + \frac{1}{2}nH_2$$

(after Witty, personal communication).

- (a) Where crops are already grown without the need for fertilizer nitrogen, so that the *Rhizobium* fully satisfies the nitrogen needs of the crop. Examples are *Vicia faba* and clover. For these, there is the possibility that *Rhizobium* with a better carbon efficiency will allow more rapid growth, especially early in the season, if each 1% of photosynthate saved could give an increase of 1% in the relative growth rate. In addition, a lower carbon demand may allow fixation to continue longer, beyond the reproductive stage, when root growth and nitrogen fixation usually stop.
- (b) More effective fixation, to supply a larger fraction of the total nitrogen need of the plant when growing at an optimal rate. The question here is why some symbioses are not sufficiently effective. This may be because of properties of the *Rhizobium* itself or of the nodules produced in response to their genetically controlled stimulus, but it may also be traced to properties of the host. Improvements may be possible simply by getting earlier nodulation, so that effective fixation starts earlier in the plants life (Lie 1981). This may also be attained with better inoculum technology, with existing *Rhizobium* strains.
- (c) It may be possible to modify *Rhizobium* to be tolerant of extreme environments, such as acid, cold or saline soils. Clearly this demands that the host shall also be tolerant and this may be more difficult to achieve. The host-*Rhizobium*-environment interaction can be extremely complicated (Devine 1982).
- (d) If clover in a grass-clover mixture continued to fix nitrogen strongly even when there was enough nitrogen to keep the grass growing vigorously, the whole system would be more efficient. This could be achieved by modifying *Rhizobium* strains to be less affected by nitrogen in the plant, or modifying clover to absorb mineral nitrogen less readily.

Alternative nitrogen-fixing systems, of the associative type, do not seem likely to gain

importance in agriculture. The amount of N fixed is trivial under our intensive conditions and so far no ways of increasing it have been established. The problem does not lie solely in the characteristics of the micro-organisms – there is a shortage of carbon substrate, which is being intensively competed for by other organisms (Tinker 1984). More definitive results are needed for such systems, particularly for accurate nitrogen balances to determine if there are significant nitrogen inputs over several years.

The other major symbiosis is that of the vesicular—arbuscular mycorrhizas that supply soil phosphorus to the host. Their wide spread and major importance for many crops are well documented (Harley & Smith 1983), but their practical use in agriculture is so far very slight. The problem is one often found with Rhizobium: the naturally present micro-organism is often perfectly adequate and there is no benefit from introducing others artificially. This tends to restrict their use to special situations (Tinker 1982). Promising results are now being obtained in Britain with artificial inoculation of clover seeded into upland pastures and of onions transplanted into the field. It has often been shown that infection with both mycorrhizas and with *Rhizobium* is particularly beneficial to legumes (e.g. Bethlenfalvay et al. 1982). However, there is as yet no prospect of their use being of significant benefit to major arable crop species in the immediate future. This may change if the present almost total ignorance of the genetics of the VA mycorrhizal fungi is overcome. At present these fungi do not grow in axenic culture, or reproduce sexually, hence only selection of natural species or strains is possible. If genetic manipulation proves possible, many exciting possibilities open up (Hirsch 1984). An interesting situation would arise if a good phloem-mobile fungicide becomes available for use against root diseases such as take-all. This would probably eliminate mycorrhizas also, with serious effects on the phosphorus nutrition of the host.

An interesting topic is the possible use of root surface bacteria to enhance crop growth (Suslow & Schroth 1982). The growth increase is erratic and the mechanism causing it uncertain, but it has been suggested that it is by excretion of bacterial siderophores which complex very strongly with iron. This element is thus denied to pathogenic fungi, though apparently the host is still able to obtain its needs, possibly by excreting its own siderophores. Iron nutrition may thus interact with root surface pathogens.

#### 5. Modification of crop quality

Cost and quality are becoming as important as yield for crops, and it is important to consider how nutrition is involved in quality. Of the possibilities, some are extremely simple, some much more speculative.

#### (a) Nitrogen in grain

The range of N concentrations in grain resulting from environmental effects is commonly larger than that between cultivars, but the environmental effects are less easily predicted and managed. Broadly speaking, the percentage of N can be increased considerably by giving nitrogen fertilizer at rates above those giving maximum grain yield. However, this method of increasing the percentage of N is expensive, and highly objectionable in environmental terms. A more effective method is by late sprays of urea (Penny et al. 1983), which now can readily be included with fungicide applications on the 'tramline' system. The real question here is grain price structure. If the incentive for a high percentage of N is large enough, much could be done in this direction.

# (b) Control of nutrient uptake and internal concentration

P. B. TINKER

Plants have an efficient feedback system for controlling their internal concentration, by modifying the uptake parameters  $V_{\text{max}}$  and  $K_{\text{m}}$  of their roots (Glass & Siddiqi 1984). Any attempt to change the internal concentration in desirable ways is thus restricted by this nutritional homeostat. At present the mechanism is not understood, but when it is, there may be better ways of changing nutrient uptake rates, and especially of altering concentrations of particular elements. This could be very desirable in pastures.

# (c) Control of solute concentration

The quality of fruits, vegetables and herbage can depend greatly upon the contents of the vacuoles of the plant tissue and the ways in which ions are partitioned between vacuole and cytoplasm. The osmoticum in the vacuoles is normally potassium and malate ions, but under different conditions a number of other solutes can be used (Leigh & Wyn Jones 1984) such as sodium, magnesium and calcium ions, chloride or nitrate ions, or soluble carbohydrates. These may affect the taste, texture and nutritional quality of plants. The understanding of the factors that affect the amount and type of solute has reached the stage at which it should be possible to control them, particularly in solution culture systems, such as nutrient film technology. In this, one could alter the vacuole composition by appropriate changes in the solution for the last few days before harvest.

#### Conclusion

No great new technical breakthrough in terms of fertilizers is visualized, but there will be major improvements. Most are likely to reside in the more exact matching of nutrient need, application rate and time. The impetus for this stems from cost reduction, environmental protection and quality control rather than from any opportunity to increase crop yields greatly. However, the matching of nutrient needs and application rates more closely must require that yield levels themselves become more predictable and less variable as a result of random and unknown factors (Tinker 1985b). In addition, a number of more speculative possibilities exist, most of which depend upon either biotechnology, or upon the use of fundamental plant nutritional physiology. It will be very disappointing if at least a few of these have not found important practical uses by the end of the century.

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#### CONTROL OF CROP NUTRIENTS

189

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#### Discussion

A. Buckwell (Agricultural Economics Unit, Wye College (University of London), Ashford, Kent TN25 5AH). All three speakers thus far have made reference to the increased variability of yields. There is certainly mounting evidence that this is a general phenomenon. Hazell (1984) working at the International Food Policy Research Institute has shown large increases in variance of cereal yields since the 1960s in India and the United States. The cause of this increased instability is not yet understood. Climatic change may be part of the explanation, although it is not likely to be a major determinant. Instability in input supply markets resulting from institutional and economic factors are also likely to be partly responsible. However, it is

probable that the adoption of newer production technologies is the main explanation. Modern technology encourages specialized rather than diversified farming systems; it relies critically on non-farm inputs and it appears to operate on a narrowed genetic base. The result seems to be production systems that are fragile and susceptible to disruption by climatic, institutional and economic forces beyond the control of producers.

If the production systems we are developing are indeed inherently more sensitive and thus produce more variable results, the implications are that uptake will be slower than otherwise and that the resulting unstable market supplies may necessitate costly stabilization schemes.

Agricultural scientists do have responsibilities to address these issues. It is not sufficient to focus entirely on the level of output. Attention must also be directed to the robustness of newer technologies and to the variability of output resulting from the use of these technologies in the field.

Do our speakers acknowledge that newer technologies may have a destabilizing effect and if so, what ideas do they have for dealing with this problem?

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Hazell, P. B. R. 1984 Instability in Indian and U.S. cereal production. Am. J. agric. Econ. 66, 302-311.

- P. B. Tinker. I am rather surprised that modern intensive crops should be inherently more variable than crops with fewer inputs. The aim of these inputs is to remove constraints on yield such as deficiencies and diseases. The incidence of these is variable, hence their prevention should promote stability. Certainly, from the historical records of famine years, there must have been a good deal of variability in the past. If it is increased now, my only explanation is that with a larger number of constraints, there may be a tendency for their effects to average out over areas or years. When fewer constraints operate, perhaps their individual variation is seen more clearly. However, I should be interested to know if this increased variability is in relative (percentage) or absolute (tonnage) terms; if the latter, it may simply reflect the larger crop size now.
- J. M. Lynch (Glasshouse Crops Research Institute, Worthing Road, Littlehampton, West Sussex BN17 6LP). Rhizobial and mycorrhizal associations will potentially be a drain on the photosynthate of the plant because the microbial partners are heterotrophs. Is there a possibility that the plant will adjust its photosynthesis to accommodate the microbial partner?
- P. B. Tinker. There is no doubt that both associations form a drain on the hosts, to perhaps 6–10% of total photosynthate for vesicular–arbuscular mycorrhizas and perhaps over 10% for *Rhizobium*, depending upon the host, the state of the infection and the conditions of growth. However, it is very difficult to prove that this leads to decreased growth, because the symbiosis is simultaneously giving a nutritional benefit. In one experiment, we found that the host compensated for the loss of photosynthate by maintaining a lower percentage of dry matter in its leaves. Also, this raises the vexed question of whether a plant is 'sink-limited' or 'source-limited' in its growth; if the former, there is no reason why a symbiont should affect growth because of photosynthate demand.