Adapting and improving crops: the endless task

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Adapting and improving crops: the endless task

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SUMMARY

The Malthusian prognosis has been undermined by an exponential increase in world food supply since 1960, even in the absence of any extension of the arable area. The requisite increases in yield of the cereal staples have come partly from agronomic intensification, especially of nitrogenous fertilizer use made possible by the dwarfing of wheat and rice, in turn made feasible by herbicide development. Cereal dwarfing also contributed to a marked rise in harvest index and yield potential.

Although there is still scope for some further improvement in harvest index and environmental adaptation, it is not apparent how a doubling of yield potential can be achieved unless crop photosynthesis can be substantially enhanced by genetic engineering. Empirical selection for yield has not enhanced photosynthetic capacity to date, but nitrogenous and other fertilizers have done so, and there is still scope for agronomic increases in yield and for new synergisms between agronomy and plant breeding.

1. INTRODUCTION

The image of a Malthusian precipice presumably derives from the striking contrast between the 'natural inequality of the two powers, of population, and of production in the earth, and that great law of our nature which must constantly keep their effects equal', as Robert Malthus put it in the first edition of his *Essay on the principle of population* 200 years ago.

His assertion that increase in food production was 'evidently arithmetical' was based on his belief in diminishing returns on a limited supply of arable land, and on his opinion that 'even the most enthusiastic speculator cannot suppose a greater increase' in Britain than by the amount of its 1798 production every 25 years. I think Malthus knew he was on shaky ground, but was loathe to abandon the striking contrast he had drawn between the powers of production and of reproduction, given its polemical impact which it has retained to this day.

However, several reservations should be noted. First, world food production has increased 'geometrically' since 1960, and at a greater rate than the populations in both developed and developing countries. Secondly, in England between the 1960s and the 1980s wheat yields rose faster than even Malthus's most enthusiastic speculator could suppose. Thirdly, for maize in the USA, wheat in the Paris basin, and rice in many countries there has been no evidence of diminishing returns to total input energy (Flinn & Duff 1985; Bonny 1993; Evans 1993). Even for high yielding maize crops the total input energy is less than 1% of the solar energy intercepted by the crop, and has its large effect on yield by enhancing the efficiency with which solar radiation is captured and used by the crop.

2. SOURCES OF INCREASED FOOD PRODUCTION

Until the 1960s, the major avenue to greater world food production was increase in the arable area, although there is little firm data to document this (figure 1). Thereafter, as the growth in world population increased rapidly, so too did the rise in the world average yields of the staple cereals, wheat, rice and maize, associated with increases in nitrogenous fertilizer use and irrigated area. Further extension of the arable area more or less ceased for the world as a whole after 1960, increases in Latin America and Africa being matched by decreases in the more developed countries, and in losses of much of the best land to urbanization. The rise in cereal yields took the pressure off extension of the arable area, reinforced to some extent by the growing demands for environmental conservation and for the restoration of degraded land. Other possible sources of increased food production are the intensification of cropping, the displacement of less productive crops by the cereals, the reduction of post-harvest losses, the replacement of cash crops by food crops and the replacement of feed crops by food crops.

The intensification of cropping has a long history in both shifting and permanent field agriculture, from 20 year fallows in the former and alternate cropping in the latter to annual and, in warm climates, to multiple cropping. In such conditions, the availability of irrigation and access to fertilizer and other agronomic inputs, together with earlier maturing varieties, permits three or more crops to be harvested each year. Herbicide development and minimum tillage techniques allow faster crop turnaround, as do the use of fertilizers and transplanted seedlings e.g. of rice. Although rising labour costs may discourage it, there is still considerable scope for crop intensification. The FAO estimates that 13% of the rise in food production

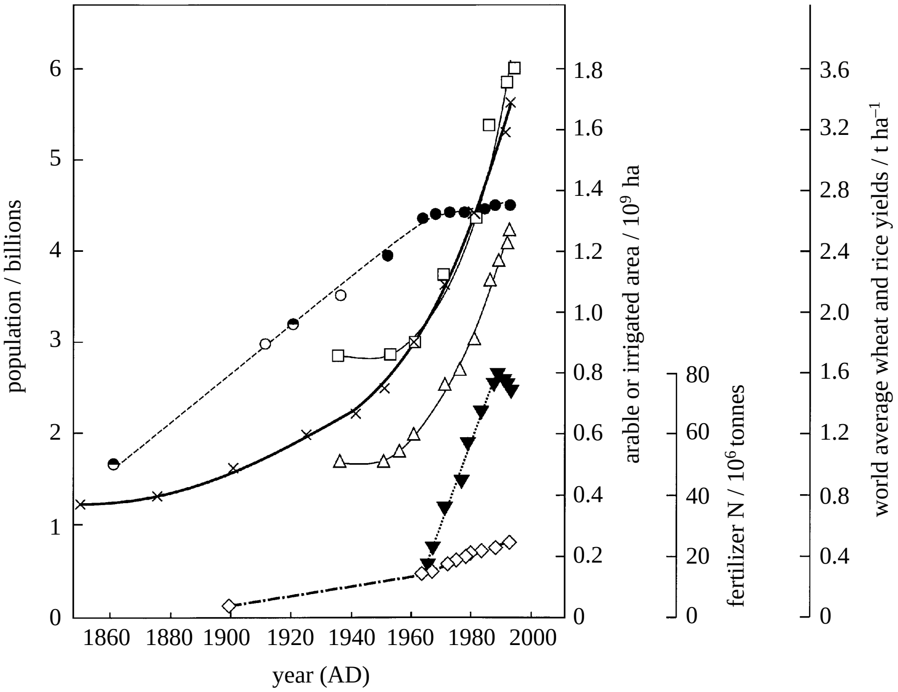

Figure 1. Increases in world population (×), arable area (○, ◓, ●), world average yields of wheat (△) and rice (□), area under irrigation (◇) and nitrogenous fertilizer use (▼). Data from the FAO production and fertilizer yearbooks, supplemented by estimates of early arable areas by Richards (1984, ◓) and Russell (1954, ○).

in developing countries by 2010 will derive from it (Alexandratos 1995), and in the long run it could contribute more than that in the warmer regions because of the strong abbreviating effect of higher temperatures on the duration of grain growth, which will tend to limit the rise in yield per crop in warm regions unless increases in grain number can compensate. With intensification, yield per day could become a more important criterion for selection than yield per crop. Four rice crops grown at Los Baños in the Philippines within a period of 335 days yielded 76.7 kg grain per hectare per day, giving a total of 25.7 t ha^{-1} for the year, 10% more than the world record maize crop.

The displacement of less productive crops by higher yielding ones also has a long history, and has led to the predominance of wheat, rice and maize in the world's food supply. The value of other crops, especially the legumes, in rotations for pest and weed control and for the maintenance of soil fertility, as well as for the variety they brought to diets, ensured their continuing importance for many years. But the advent of cheap nitrogenous fertilizers, pesticides and herbicides has reduced their role, and even in India, where they are highly cherished, they are being displaced by cereals to an increasing extent: while the wheat area has doubled, the area under chickpeas has fallen by a third and has been displaced to poorer soils. Narain (1977) estimated that about one-third of the growth in Indian food production in the 1960s was due to such locational shifts. The nutritional impact of such displacements may be counter-intuitive. Ryan & Asokan (1977) found the nutritional gains from greater wheat and rice production to outweigh the losses from reduced pulse and millet production, and to reduce the real price of protein by one-third.

3. SOURCES OF INCREASED YIELD

Although cereal yields in many countries have shown striking increases over the last 30–40 years they also exhibit substantial yearly fluctuations associated with the weather. Apparent pauses for more than a year or two are seized on eagerly by plateau spotters to conclude that crop yields are approaching their limit. However, there are many reasons besides weather for such irregularities. In recent years, for example, low cereal prices combined with environmentalist pressures have substantially reduced world consumption of nitrogen (N), phosphorus (P) and potassium (K) fertilizers, with negative impacts on average yields. More profitable crops may displace others from better growing conditions, as when sorghum again became a dryland crop in the USA in 1973. In such instances the apparently S-shaped yield curve is a sigmoid fraud; the rise in yield eventually resumes.

Between 1960 and 1986, while the world's population increased by 67% (from three to five billion), the world's average yields of wheat, rice and maize increased by 94, 56 and 82%, respectively (cf. figure 1). For both wheat and rice the rate of increase was much faster in developing countries than in the developed ones.

Direct comparison of the yields of successively released varieties of a crop indicates the overall contribution by plant breeders to rising yields, e.g. 2.7% per year for spring wheats bred at CIMMYT. However, much of this involves the maintenance of resistance to pests and diseases. When these, and other stresses such as weeds, lodging and deficiencies of water and nutrients are controlled, the rate of increase is much smaller, e.g. 0.7% per year for the CIMMYT spring wheats (CIMMYT 1993), and represents the rise in yield potential from plant breeding, together with any further improvements in adaptation.

This then allows the overall rise in yield to be partitioned between increases in genetic yield potential and advances in agronomy such as greater fertilizer use or better crop protection. In many experiments of this kind with many crops the two contributions have been roughly equal, but over different periods one or other may contribute more of the overall advance in yield (Evans 1993). However, the two components are by no means independent of one another. For example, Duvick (1984) has shown how the assessment of genetic advance in the yield potential of maize hybrids depends very much on planting density.

4. SOURCES OF INCREASED YIELD POTENTIAL

Although plant breeding contributed greatly to the increases in crop yields before 1960, through better environmental adaptation and improved resistance to pests and diseases, yield potential rose only slightly. At least for the small grain cereals such as wheat and rice, both competitiveness with weeds and the value of straw favoured tall varieties. Dwarf varieties were known, such as Piper's Thickset wheat in England and Ramai rice in the Philippines, but their yield potential could not be realized before the advent of effective herbicides, nor were cheap nitrogenous fertilizers available to drive their adoption. Among the British wheats, stem height (and weight) did not begin to fall, nor yield potential to rise markedly, until after the 1920s (Austin *et al*. 1989). With polygenic reduction in stem height until 1974 there was some rise in yield potential, but this was accelerated following the introduction of the major dwarfing genes.

The greater dwarfing conferred by these genes, introduced into both wheat and rice from Chinese and Japanese varieties in the 1960s, proved to be essential if full advantage was to be taken of the cheaper nitrogenous fertilizers then becoming available, along with more effective herbicides. Old tall varieties lodged with heavy fertilizer dressings, whereas the dwarfs did not and their yields were not reduced. Their resistance to lodging led to the rapid initial adoption of the dwarf wheats and rices, while the rise in yield potential that ensued has ensured their continuing impact.

Initially, the introduction of the dwarfing genes may have had little effect on yield potential. With further selection, however, the decline in height has been accompanied by a progressive rise in the harvest index, i.e. the proportion of crop biomass which is invested in the grains, not only in wheat and rice but also in other cereals.

In essence, as reduction in height has freed assimilates formerly needed for stem growth, empirical selection for yield has allowed these to be invested instead in the development of larger inflorescences and more grains. Although savings on other organs such as leaves, roots or tillers without ears may also have contributed, the savings on stem growth have been the dominant source of the rise in harvest index of the small grain cereals and that, in turn, the dominant component of the rise in yield potential.

Thus, the timely surge in average world yields of wheat and rice beginning in the 1960s has come largely from what may prove to be a unique conjunction of three synergistic innovations: cheap nitrogenous fertilizers, dwarf cereals and the novel herbicides which made their widespread use possible. The potential contribution of that Green Revolution, as W. S. Gaud dubbed it, is probably not yet wholly exhausted. More extreme dwarfing genes, such as *Rht3*, are available for use when agronomic advances make it feasible, and such advances might well allow other sources of higher harvest index such as earlier flowering, fewer leaves, smaller root systems or reduced reserves to be tapped.

An alternative route to higher yield potential would be through increased photosynthesis and crop growth rates. Higher CO_2 exchange rates (CER) have been found in the more advanced cultivars of many crops during grain growth. But in nearly every case these reflect a slower decline in the modern varieties from the maximum CER at flowering rather than any increase in the maximum CER itself. The latter has not yet been clearly established for any crop plant (Evans 1993). An example of the slower decline in CER in modern varieties after flowering has been provided by Wells *et al*. (1982) for soybean varieties in Groups V–VIII. Several factors may contribute to such slower decline: (i) the leaves of modern varieties, selected under conditions of more prolonged availability of soil N, may retain their photosynthetic activity for longer, as in the greater 'stay green' of modern maize hybrids; (ii) greater demand for photosynthates by the potentially larger inflorescences of the modern varieties may, through well-established feedback reactions, elicit a higher CER in the flag leaves; (iii) selection for higher yield under irrigated conditions may allow the stomata of modern varieties to remain open on hot afternoons when those of older varieties have closed, as in cotton (Radin *et al*. 1994) and wheat (R. A. Fischer *et al*., unpublished data); and (iv) in many crops there is a trade-off between CER and the area of individual leaves. This is such that photosynthesis *per leaf* is usually greater with the larger leaves of lower CER than with smaller leaves of higher CER, which is of advantage in the early, ground-covering stage of a crop. In the later stages, however, particularly in high density crops, smaller, more upright leaves with higher CER have the advantage, and may have been selected for.

Along with the absence of convincing evidence for higher maximum CER in modern varieties, there is also no clear evidence for any increase in either relative growth rate or crop growth rate in modern varieties under favourable conditions (Evans 1993). Improvements in photosynthetic rate may well prove possible in future, especially if Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) can be successfully re-engineered, but given the prolonged and intense natural selection pressures already endured by photosynthesis, we cannot be optimistic that photosynthetic efficiency will be increased significantly in the next few decades.

5. ENVIRONMENTAL ADAPTATION

Improving the adaptation of crops to their environment is as endless a task for plant breeders, as is the raising of their yield potential, even in favourable environments. In fact, some of the apparent rise in yield potential may be due to improved adaptation to local conditions. Shifts in agronomic practice may also require it. For example, anthesis in winter wheat may be delayed by 5–7 days with higher soil fertility, yet the post-anthesis period becomes more important to yield when leaves can retain their nitrogen, and indirect selection for progressively earlier flowering is apparent in the more recent British varieties (Austin *et al*. 1980). Climatic and agronomic changes in the future will likewise require continual empirical adjustments.

More profound changes are often required when crops spread to new environments. With soybeans in the USA, for example, varieties were originally classified into eight maturity groups adapted to different latitudinal belts, but pressures for extension northwards have led to the addition of maturity groups O, OO and OOO, and southwards to the addition of groups IX and X. For many crops, the first requirement for extension of their adaptation has been a change in flowering behaviour, usually accomplished by shifts in their juvenile period, vernalization, and daylength requirements. Of these we know least about juvenility, yet it is emerging as important in the adaptation of several crops where the daylength response was previously thought to be decisive.

Shifts in adaptation to more extreme temperatures have been less dramatic than those to daylength, but nevertheless important, e.g. to cooler temperatures during grain development in maize at high latitudes (Dwyer & Tollenaar 1989). Experiments with irrigated cotton crops in high irradiance environments have revealed unintentional selection for greater canopy cooling in recent varieties, which maintain more open stomata and cooler leaves through the afternoons in the hottest period of the year, enhancing prolificacy and yield (Cornish *et al*. 1991; Radin *et al*. 1994). Similar selection for afternoon canopy cooling has also been found among irrigated wheat varieties at CIMMYT, emphasizing the power of empirical selection for the subtleties of environmental adaptation. Other examples include the initially indirect selection for reduced delay between anthesis and silking in maize, found to confer greater drought avoidance, and also for more upright leaves and smaller tassels, which enhance prolificacy (Duvick 1992), possibly by improving light penetration to the leaves supplying the young inflorescence. This latter could be regarded as raising the yield potential at high planting densities in a crop in which there has been little reduction in height, and which has therefore had to follow other routes to greater yield.

An important component of improved adaptation and yield potential may be the further broadening of the genetic backgrounds of our major crops. Figure 2*a* indicates the progressive increase, in recent years, in the number of land races in the backgrounds of successive varieties of rice from IRRI, wheat from CIMMYT and maize hybrids from Pioneer. The latter is particularly interesting, given the well-known reluctance of maize breeders to use anything other than elite germplasm, and it is difficult to see how modern varieties can be accused of having too narrow a genetic base. The all-too-few data in figure 2*b* do not establish a causal relationship, but do suggest that a progressive broadening of the genetic background of cereal varieties may contribute to further improvement in adaptation and yield potential, particularly with the addition of land races from different regions.

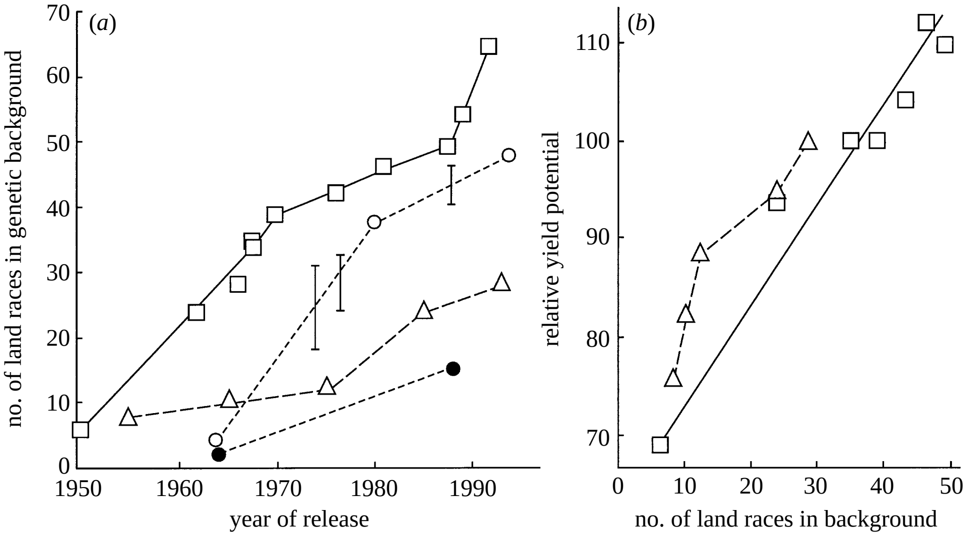

Figure 2. (*a*) The number of land races in the genetic backgrounds of 11 CIMMYT spring wheat varieties (□), 37 IRRI rice varieties (○) and 38 Pioneer maize hybrids adapted to central Iowa (△), released at various times (or decades for maize). The rise in the number of land races actually used in the IRRI breeding programmes is also indicated (●). (*b*) The relation between relative yield potential and the number of land race parents for some CIMMYT wheats (□) and Pioneer maize hybrids (△) released in successive decades. Based on data provided by Dr D. N. Duvick (maize), Dr G. S. Khush (rice) and Dr B. Skovmand (wheat). Relative yield potentials of the wheat varieties from Bell *et al*. (1995).

Another important component of adaptation over the coming decades will be to global climate changes. These will be slow but progressive, and complex in that the rise in CO_2 concentration and the rise in temperature which it induces will have some similar and some opposite effects. For example, the rise in CO_2 will increase water use efficiency by tending to close stomata in the short run and reduce stomatal density in the long run, whereas the rise in temperature will reduce water use efficiency. Short- and long-term effects may also differ. Although photosynthetic rate rises with CO_2 concentration in the short-term, it may subsequently fall as reserves accumulate in the leaves; but such feedback inhibition could be modified by selection. Genetic engineering, e.g. for enzymes governing the partitioning of assimilates in leaves, will undoubtedly contribute to adaptation to global warming, but empirical selection will be needed to optimize the varied and conflicting responses to the continuing changes in CO_2 concentration, temperature, water availability and even radiation as cloud patterns alter.

6. AGRONOMIC INCREASES IN YIELD

Across all crops, increases in yield in recent years have owed as much to innovations and improvements in agronomy as to plant breeding, more with some crops and less with others, more at some stages and less at others. It is doubtful whether the major advances made since the 1960s with the use of nitrogenous fertilizers and herbicides will be matched, but there has nevertheless been an impressive range and variety of agronomic innovations in recent years; some, like the plant growth regulants, are still to have their day.

To illustrate the variety of ways in which a given agronomic input can influence yield, often interactively with plant breeding, I shall focus only on nitrogenous fertilizers. They get the crop (even legume crops) off to a faster start, buying time that may be valuable in allowing the crop to avoid an early or late period of stress. In this sense they can be a surrogate for faster development. They enhance leaf area growth, increasing light interception in the early stages, and being a surrogate for greater radiation. They raise the N content of the leaves, and with it the photosynthetic rate, thereby acting as a surrogate for selection for higher CER. What is more, they break the trade-off between leaf area and CER by increasing both, but with their effect on leaf area extending to higher N doses. They reduce the need to mobilize N out of the leaves and into the grain, thereby extending the duration of photosynthetic activity and breaking the trade-off between duration of photosynthesis and of protein storage.

Like many other agronomic inputs they also have disadvantages. They encourage pests and diseases, contaminate ground water, etc., but these are challenges to develop better management techniques. Although the rate of increase in world population rules out any extensive return to low input agriculture, we have too few long-term experiments with high input cropping to be sure of its long-term sustainability, especially at the lower latitudes where most of the population growth will take place. I find it ironic that the widespread protestations of concern for the sustainability of our agricultural systems are coinciding with mounting threats to long-term experiments, for which computer modelling is not an adequate substitute, especially in a period of changing climatic conditions. Research on sustainability requires sustainability of the research.

Analysis of the results of long-term experiments has revealed a long-term decline in rice yields under intensive cropping at the International Rice Research Institute (IRRI) and also in India. Several factors appear to have contributed to the decline at IRRI, particularly a decrease in the effective N-supplying capacity of the soil, (Cassman *et al.* 1994), which presumably has been contributing to the decline in partial factor productivity from nitrogenous fertilizer applied by Filipino farmers in the last decade. This latter is particularly significant given the central role of N supply in sustaining high yields.

7. CONCLUSION

In a letter to The Royal Society 317 years ago, Leeuwenhoek estimated that the world could feed about 14 billion people. Cohen (1995) has recently summarized more than 60 subsequent estimates of the world's human carrying capacity, which range from one to one thousand billion. Given that range, I am not tempted to add another because, as Cohen concludes, the absolute upper limit is probably beyond the bounds that we would tolerate. Carrying capacity is also a matter of social choice. Although the limits to world food production set by the more pessimistic early estimators have been overtaken by innovations, we should recognize that the surge in cereal yields over the last 30 years, which still has some way to run, has come from what may prove to have been a unique conjunction of agronomic and plant breeding advances which may not be repeated. Further increase in the harvest index will be limited and, so far, the maximum rates of photosynthesis and crop growth have not been improved genetically.

Nevertheless, crop yields could continue to rise due to agronomic innovation and improvement on the one hand and to breeding for improved stress resistance on the other, especially as the global environment changes. Although climate change scenarios, e.g. those of Rosenzweig & Parry (1994), usually project an adverse impact on world food production, especially in the developing countries, the rise in atmospheric CO_2 concentration and water use efficiency by crops should offer scope for selection for closer adaptation and greater yield, particularly if the rise in temperature is on the low side of the predictions.

I began with Malthus and his elegant contrast between the two powers, of production and of reproduction, which I questioned. However, Malthus then went on to say: 'This implies a strong and constantly operating check on population from the difficulty of subsistence. This difficulty (of providing enough food) must fall somewhere and must necessarily be severely felt by a large portion of mankind'. The estimated 800 million people suffering from chronic malnutrition and hunger today in a world which produces enough food for all supports his conclusion. While there will be problems in raising world food production enough to feed the ten billion, the far greater problem is to ensure that all are sufficiently fed in developing countries, and even in developed ones.

I am grateful to Dr D. N. Duvick, Dr G. S. Khush and Dr B. Skovmand for unpublished data on the land race backgrounds of Pioneer maize hybrids, IRRI rice varieties and CIMMYT wheats, respectively, used in figure 2, and to Dr Duvick and Dr R. A. Fischer for other unpublished data.

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Discussion

J. S. Wallace (*Institute of Hydrology, Wallingford, UK*). Does the observation that crop varieties with more open stomata in the afternoon and higher yields conflict with earlier research showing that the amount of carbon fixed by plants per unit of water transpired is lower when the air humidity is low, as in the afternoon?

L. T. Evans. Not necessarily. First, I should emphasize that the findings I referred to were confined to well-irrigated environments, in which humidities *within* the crop canopies may be quite high. Secondly, the additional yield may come more from greater boll and grain setting than from greater plant growth.

F. Beavington (*Ryarsh, Kent, UK*). The speaker stressed the role of inorganic fertilizers, especially nitrogen, and of pesticides in achieving high yields of cereals. Is there any prospect of sustaining the world population of the future solely by organic farming systems?

L. T. Evans. The amount of atmospheric N fixed in nitrogenous fertilizers now approaches the total amount of biological terrestrial N fixation, almost doubling the amount of N available for plant growth and increasing the amount available for crops far beyond that in farmyard manure. Much of the N in farmyard manure is lost to crops before its application, which has been shown by Pimentel and his colleagues to have a considerable energy cost. Maximizing the use of farmyard manure is an important component of maintaining soil fertility, but I don't think it would be either possible or efficient to support a world population of ten billion solely on organic farming systems.