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Phil. Trans. R. Soc. Lond. B 1981 **292**, 431-440
doi: 10.1098/rstb.1981.0038

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Phil. Trans. R. Soc. Lond. B **292**, 431–440 (1981)
Printed in Great Britain

Physiological constraints to varietal improvement

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Crop production consists essentially of the conversion of environmental inputs into economic end-products, including human or animal foodstuffs or industrial raw materials. The basic climatic limitation to production is the seasonal input of solar energy, but the use of this energy by the crop can be limited by other climatic factors such as temperature or water supply, or by the supply of soil nutrients.

Both experimental results and predictive models indicate a potential fixation by a complete photosynthetic cover of 2–3% of incoming energy into total biomass, corresponding to an annual dry matter production of up to 80 t/ha for tropical and 30 t/ha for temperate environments. Many crops, however, occupy the ground for only part of the year, and their production is influenced greatly by the duration of the photosynthetic canopy. Economic yield is further determined by the harvest index, i.e. the relative partition of assimilates to the economic end product.

Appreciable genetic variation has been revealed for many of the physiological components of crop photosynthesis and of the distribution and use of assimilates, including their response to temperature and water stress. Its effective use in a breeding programme depends on the identification of those components that are most important in determining yield or quality, and the development of rapid and reliable screening procedures that correlate well with the performance of the crop in the field.

1. Introduction

Crop production consists essentially of the conversion of environmental inputs such as light energy, CO_2, water and soil nutrients into economic end-products, which may be human or animal foodstuffs or industrial raw materials. The plant breeder is concerned to improve the efficiency of this process, i.e. to maximize the output from the available inputs in biological or economic terms (Wallace *et al.* 1972; Cooper 1975; Evans 1975). He therefore needs to ask (1) what the input limitations are, (2) what the current efficiency of the crop is in dealing with them, and (3) what characteristics of the crop contribute to this efficiency and how far they can be manipulated by the plant breeder.

The basic climatic limitation to crop production is the seasonal input of light energy, but the use of this energy can be limited by other climatic factors, particularly low temperature and shortage of water, by the availability of soil nutrients or by pest and disease attack. The energy input varies with latitude and with cloud cover, being comparatively uniform through the year in equatorial regions but showing increasing seasonal amplitude with increasing latitude. The highest inputs, over 700 kJ cm^{-2} per year are found in subtropical regions with little cloud cover, while most north temperate regions have comparatively low inputs, about 400 kJ cm^{-2}. per year, but with a large seasonal amplitude.

Even for a complete photosynthetic cover, however, the proportion of incoming radiation fixed into total biomass is comparatively small (Monteith 1972; 1977). Only some 50% of the total radiation is photosynthetically active, while the quantum requirement for photosynthesis allows a maximum potential fixation of only about 10% of the total input. In crops with the usual C_3 photosynthetic pathway (though not in C_4 plants), photorespiration results in a further

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loss of some 30–40 %. Furthermore, at moderate to high light intensities, leaf and crop photosynthesis become CO_2-limited, with further reduction in energy fixation, while dark respiration usually reduces the *gross* photosynthesis by some 40–50 %. Both experimental records (Cooper 1975; Loomis & Gerakis 1975) and crop models (de Wit 1965; Duncan *et al.* 1967; Monteith 1977) indicate that closed crop canopies can usually fix only some 2–3 % of the total incoming energy, corresponding to maximum crop growth rates of 20–30 g m^{-2} day^{-1} for temperate C_3 species and over 40 g m^{-2} per day for C_4 species in the subtropics. If maintained over the year, such fixation could provide a total biomass of up to 80 t ha^{-1} per year in the subtropics and some 25–30 t ha^{-1} per year in more temperate regions, and such values have in fact been reported for perennial crops (Cooper 1975; Loomis & Gerakis 1975).

Most crops, however, do not provide a complete crop cover through the year, nor does the economic end-product usually consist of the total biomass. In the small grain cereals, for instance, the crop occupies the ground for only part of the year, and the dry matter in the grain is derived largely from current photosynthesis during or just before the period of grain filling.

The plant breeder, therefore, needs not only to provide an efficient photosynthetic cover but to maintain it for the optimum duration and to ensure the optimum partition of assimilates to the economic end-product, i.e. to maximize the harvest index.

2. Physiological components of production

In attempting to improve the physiological efficiency of his crop, the breeder needs to identify those features of the plant that contribute to such efficiency, to determine how much variation exists for them and to consider how far this variation can be used in a breeding programme.

(*a*) *Crop photosynthesis*

The photosynthetic activity of the crop will be influenced both by the photosynthetic rate of the individual leaves and by their arrangement in the crop canopy in relation to light interception.

(i) *Individual leaf photosynthesis*

The responses of the individual leaf to changes in light intensity, temperature and CO_2 supply are well documented (Wilson 1973; Troughton 1975; Cooper 1976). At low light intensities, photochemical processes are limiting and up to 10 % of the total radiation may be fixed. As light intensity increases however, CO_2 transport or utilization become more important, and eventually at light saturation, photosynthesis becomes CO_2-limited and the maximum photosynthetic rate (P_{max}) is reached.

A major distinction in photosynthetic response is between species with the C_3 pathway (most temperate crops and such tropical crops as oil palm, rice and cassava) and those with the C_4 pathway (maize, sugar cane and most tropical forage grasses). Most C_3 species reach light saturation at about 100–150 J m^{-2} s^{-1} photosynthetically active radiation, less than half of full sunlight, with a P_{max} of about 50–100 ng CO_2 cm^{-2} s^{-1}. In C_4 species, on the other hand, the photosynthetic rate usually continues to increase up to inputs of over 300 J m^{-2} s^{-1}, i.e. approaching full sunlight, providing a P_{max} up to about 220 ng CO_2 cm^{-2} s^{-1}. This higher P_{max} in C_4 species is based in part on the greater affinity for CO_2 of the initial carboxylating enzyme (PEP carboxylase in C_4 plants and RuDP carboxylase in C_3), and in part on the

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absence of photorespiration, which in C_3 plants can amount to 30–40% of the *gross* photosynthesis (Hatch *et al.* (eds) 1971; Troughton 1975).

Marked varietal or genotypic differences in maximum photosynthetic rate per unit leaf area have been reported in many C_3 crops including soybean, rice, barley, *Phaseolus*, lucerne and ryegrass, as well as in such C_4 crops as maize, sugar cane and *Cenchrus ciliaris* (Wallace *et al.* 1972; Shibles *et al.* 1975; Wilson 1981). In few cases, however, was there any regular correlation with total or economic yield, suggesting that a lower photosynthetic rate per unit leaf area was compensated for by larger but thinner leaves (Evans & Dunstone 1970; Hart *et al.* 1978), or indeed that in these comparisons at least, dry matter production was not source-limited (Evans 1975).

Since much of the greater efficiency of the C_4 over the C_3 photosynthetic pathway can be atrributed to its lack of photorespiration, it has been suggested that a decrease in the photorespiratory activity of C_3 species, possibly by uncoupling the carboxylase and oxygenase activity of RuDP carboxylase, could greatly increase their maximum photosynthetic rate (Zelitch 1976). In spite of extensive surveys, however, no individuals with C_4 characteristics have yet been found within the C_3 crop species, soybean, wheat and beet (Moss & Musgrave 1971), and crosses between C_3 and C_4 species of *Atriplex* indicate independent though complex genetic control of the various aspects of the C_4 syndrome (Björkman 1976). Quantitative variation in photorespiratory activities has, however, been recorded within a number of C_3 species, with in some cases favourable effects on net photosynthesis (Wilson 1972; Zelitch 1976).

(ii) *Leaf arrangement and canopy photosynthesis*

Most crops consist of a more or less closed canopy of leaves in which incoming light is distributed over a considerable leaf area, with a consequent increase in photosynthetic activity per unit area of ground compared with unit area of the individual leaf. In temperate C_3 crops, for instance, crop growth rates of about 20 g m^{-2} per day during May–September corresponding to a fixation of about 3–4% of the incoming photosynthetically active radiation are commonly attained, while similar crop growth rates and energy fixations have been reported for tropical C_3 species. For C_4 species, however, growing under conditions of high insolation, higher values of about 50 g m^{-2} per day, corresponding to over 6% fixation of photosynthetically active radiation have been recorded for such crops as maize, sudan grass and bulrush millet (Cooper 1975; Loomis & Gerakis 1975).

The penetration of light down the crop, the area of leaf that can be illuminated, and hence the potential crop photosynthesis, will be influenced by the arrangement of leaves in the canopy. An erect leaf arrangement, as in the cereals, for instance, allows the incoming light energy to be distributed over a greater leaf area than in a crop such as white clover or cotton with broad flat leaves (Saeki 1975; Monteith 1969).

Variation in leaf arrangement and canopy structure has been reported within many crops including maize, rice, soybean and forage grasses (Wallace *et al.* 1972), and in some cases varieties with more erect leaves have been found to possess higher crop growth rates or photosynthetic rates (Sheehy & Cooper 1973; Rhodes 1975; Austin *et al.* 1976). The optimum leaf arrangement will, however, depend on the stage of growth of the crop. During early establishment, a more prostrate habit of growth is advantageous to enable the interception of the maximum amount of light, but once complete interception has been achieved, an erect canopy, which spreads the incoming light energy over a larger leaf area, is likely to be more valuable.

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It must not be forgotten, however, that variation in canopy structure may also have important effects on the distribution of CO_2, temperature and water vapour through the crop.

(iii) *Respiratory losses*

A large part of the assimilates produced by photosynthesis, in many crops up to some 50%, are utilized in respiration (Robson 1973; Biscoe *et al.* 1975). Much respiration is likely to be coupled to active growth processes, but its separation into a 'biosynthetic' component, used for growth, and a 'maintenance' component has recently been posulated (McCree 1970; Penning de Vries 1974; Thornley 1977), raising the possibility of reducing the requirements for maintenance respiration. In the early stages of crop growth, much of the energy expenditure is concerned with active cell division and expansion, but as the crop develops the proportion of non-growing tissue increases, and 'maintenance' respiration becomes proportionately greater. Reduction in 'maintenance' respiration should therefore have its greatest influence at later states of crop growth, when there is a larger standing biomass. In fact, a negative relation between dark respiration of mature tissues and crop growth has been reported in a number of species including sorghum, ryegrass and barley (Heichel 1971; Wilson 1975*b*). Ryegrass, for instance, showed a significant response to selection for slow dark respiration of mature leaves with little effect on the growth of young seedlings, but considerably increased dry matter production in older plants (Wilson 1975*b*, 1976).

Even so, although appreciable genetic variation in many of the components of crop photosynthesis has been reported, in only a few cases has a consistent relation with total or economic yield been recorded. In practice, the duration of the photosynthetic canopy and the relative partition of assimilates to the economic yield, i.e. the harvest index, appear to be more important.

(*b*) *Leaf area duration*

The importance of leaf area duration in determining both total and economic yield was early demonstrated by Watson (1947) and, more recently, Monteith (1977) has shown a close relationship for a range of crops in the U.K. between total dry matter production and radiation intercepted by the canopy.

The possible duration of the growing season is often limited by local climatic factors, particularly temperature or water limitations and/or by the requirements of particular farming systems. Where sowing or planting are limited by low temperature, selection for a lower temperature threshold for germination or leaf growth may be an important breeding objective. In temperate crops such as potatoes it should allow of earlier planting and hence more effective use of increasing light energy in the spring (Moorby & Milthorpe 1975; Wareing & Allen 1977), while in subtropical crops such as maize or *Phaseolus* it may make possible their adaptation to a wider climatic range. Again, in temperate regions, selection for improved cold tolerance may make possible autumn rather than spring sowing, thereby providing a closed photosynthetic cover to take advantage of the increasing energy inputs in the spring. As mentioned later, considerable genetic variation exists in most crops for those temperature responses that influence germination, leaf growth and plant survival, and so determine sowing or planting dates.

Increasing leaf area duration by a later harvest date, when this does not conflict with other farming requirements, may also be advantageous, particularly in crops such as sugar beet and potato (Moorby & Milthorpe 1975), which can continue to transfer assimilates into the re-

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quired vegetative sinks. In determinate crops such as the cereals, on the other hand, the timing of flowering and seed production, and hence the termination of the active growing season, is usually based on responses to photoperiod and low-temperature vernalization (Evans *et al.* 1975). These responses can often be manipulated by the breeder, as in the adaptation of such short-day species as maize (Duncan 1975) and soybean (Shibles *et al.* 1975) to higher latitudes, or the wider regional adaptation of the day-neutral CIMMYT wheats (Evans 1975).

(*c*) *Partition of assimilates* (*harvest index*)

The most important determinant of economic yield is often not crop photosynthesis, i.e. the supply of assimilates, but the way in which they are distributed within the plant either for continued vegetative growth or for accumulation in particular sinks such as storage organs, seeds or fruits. It is often not clear how far economic yield is limited by the supply of assimilates i.e. source strength, by the ability of the sinks to make use of them, or by the rate of translocation, nor indeed how far sink strength can itself influence photosynthetic rates (Evans 1975; Wareing & Patrick 1975).

Apart from those crops in which the leaf canopy itself forms the economic yield, as in green vegetables and forage grasses, an important distinction is between crops with a strictly determinate habit, as in the cereals, which show a clear separation of vegetative and reproductive allocation of assimilates, and those such as potatoes, sugar beet and sugar cane, which can continue indefinite growth and allocation of assimilates to a vegetative sink. In yet other crops such as cotton and field beans, with an indeterminate habit, allocation to vegetative growth and to flowering and seed production can continue simultaneously (Evans 1975).

In crops with vegetative sinks, a major objective is the prolongation of the growing season together with a maximum partition of assimilates to the required end-product, since both total and economic yield are likely to be proportional to the total energy intercepted. In the potato, for example, marked varietal differences exist in both the onset and rate of bulking (Moorby & Milthorpe 1975). In determinate crops, on the other hand, the appropriate balance of source and sink is more complex. In wheat and barley, the content of the grain results largely from current assimilation by the ear and flag leaf, with some transfer from the stem, but the potential sink size, i.e. the number of grain initials, is determined during ear differentiation (Evans *et al.* 1975; Austin & Jones 1976; Biscoe *et al.* 1975). Maize, on the other hand, shows a considerable transfer of assimilates from stem to grain, and crop photosynthesis can contribute directly to grain yield over a longer period (Adelana & Milbourne 1972; Duncan 1975). In the indeterminate group of crops, such as cotton, soybean and field bean, competition between continued vegetative growth and reproductive sinks often results in a rather unpredictable yield from year to year; the introduction of the determinate habit, as is now possible in field beans, should improve harvest index and reliability of yield (Shibles *et al.* 1975).

Considerable variation in harvest index is apparent in most crops, and selection for such features as onset and rate of tuberization in potatoes (Moorby & Milthorpe 1975), high root or sugar yield in beet, and short straw or restricted tillering in cereals (Donald & Hamblin 1976) continue to be important breeding objectives. Even so, comparatively little is known of the physiological basis of those processes that determine harvest index, including the translocation of assimilates, their partition to different morphological sinks in the plant, or, in certain crops, to particular biochemical end-products.

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(*d*) *Response to climatic stress*

Both the duration of the growing season and the rate of photosynthesis and growth during that season can be limited by temperature or water shortage. Furthermore, the breeder is often presented with two conflicting requirements, continued active growth at moderate stress, and/or survival of more extreme conditions, often involving a degree of dormancy.

(i) *Temperature*

The temperature responses for both photosynthesis and leaf growth are usually related to the climatic origin of the crop, most temperate species having a broad temperature optimum between 15 and 25 °C though some photosynthesis and extension growth can occur at temperatures as low as 5 °C. Net photosynthesis and active extension growth are usually greatly reduced at temperatures above 30–35 °C. Most tropical and subtropical species (whether C_3 or C_4), on the other hand, have higher temperature optima, up to 35 °C or more, and both photosynthesis and leaf extension growth are usually limited at temperatures below 15 °C (Bauer *et al.* 1975; Cooper 1976).

Even within the same species, however, populations from different climatic regions may differ in their temperature response, offering scope for the plant breeder. In temperate forage grasses, for instance, populations from the Mediterranean region, where winter is the active growing season, can expand leaves actively at moderately low temperatures (0–5 °C), while collections from northern or central Europe show a degree of winter dormancy, associated with increased winter hardiness (Cooper 1964; Østgård & Eagles 1971). In annual temperate crops, more active leaf growth at lower temperatures can be valuable in improving light interception in the spring, while in such subtropical crops as maize and *Phaseolus*, variation in temperature response is important in increasing the climatic range of these crops.

The survival of more extreme cold can be achieved by two contrasting strategies. First, the life cycle may be timed to avoid the period of extreme stress, as in many annual crops in north temperate or continental climates. The spring cereals, for instance, are spring-sown and harvested in late summer or early autumn, while potatoes or sugar beet, though potentially biennial or perennial, are grown as spring-planted annuals. Secondly, the crop may develop sufficient cold hardiness, often associated with dormancy to survive the unfavourable season. Many temperate tree crops cease extension growth in the winter, and similar seasonal dormancy patterns are shown by forage crops or winter cereals adapted to higher latitudes. The timing of such dormancy in locally adapted varieties is usually related to the length and severity of the winter, and is often influenced by response to other climatic factors such as photoperiod, thus enabling the plant to become dormant before conditions become too severe (Wareing 1969; Østgård & Eagles 1971; Bauer *et al.* 1975).

(ii) *Water stress*

Water stress can be induced by shortage of water supply to the roots and/or by excessive water demand from the leaves, and often coincides with periods of high insolation and hence high potential crop photosynthesis. In environments with moderate or intermittent water shortage, continued growth may involve the ability to tap greater reserves of soil water by increase in root range, as in bulrush millet compared with sorghum (Wetselaar & Norman 1960), and/or the conservation of water by the control of transpiration. An important advantage of the

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C_4 photosynthetic pathway, for instance, is increased efficiency in water use, based both on a higher photosynthetic rate and a greater stomatal resistance to water vapour transfer (Downton 1971), while a more extreme conservation strategy is shown by species with the Crassulacean acid metabolism photosynthetic system, such as pineapple, in which the stomata can close during the high evaporative demand of the day (Troughton 1975).

Even within a single species, however, variation has been reported for certain leaf characteristics that influence transpiration and water use efficiency. In barley (Misken *et al.* 1972; Yoshida 1978) and *Panicum antidotale* (Dobrenz *et al.* 1969), a lower stomatal frequency can lead to reduced transpiration without any corresponding reduction in photosynthesis, while in perennial ryegrass lines selected for smaller stomata or fewer stomata per unit surface area can continue active leaf growth for a longer period when exposed to moderate water stress (Wilson 1975*a*, 1981).

In more extreme environments with long and regular periods of drought, the two contrasting strategies of avoidance and/or resistance have been developed. In a Mediterranean environment, for instance, many grain and forage crops germinate with the autumn rains, grow actively through the winter, and flower and produce seed in the spring before the summer drought stops further growth. In these crops, the temperature and photoperiod requirements for flowering and seed production of locally adapted varieties are closely tailored to the length of the potential growing season (Cooper & McWilliam 1966; Finlay & Wilkinson 1963). On the other hand, perennial grasses such as *Phalaris tuberosa* and *Hordeum bulbosum* become dormant during the Mediterranean summer while maintaining a deep rooting system (McWilliam 1968; Koller 1969). Even so, in spite of its great agricultural significance, comparatively little is known of the physiological basis of variation in response to water stress.

In conclusion, appreciable genetic variation appears to exist for many of the physiological features that affect crop photosynthesis, leaf area duration, harvest index and response of the plant to climatic stresses. How far can this variation be consciously used in a breeding programme?

3. USE OF PHYSIOLOGICAL VARIATION IN A BREEDING PROGRAMME

In practice, the plant breeder is concerned with the performance of his crop in the field, and any physiological screening procedures must not only provide more effective assessment than can be obtained in the field, but also show a good correlation with yield or quality. He therefore needs to consider not only which particular physiological features are important in determining crop yield but how far they can be screened rapidly and reliably, and what advantages such screening has over conventional field or glasshouse assessment (Wallace *et al.* 1972; Cooper 1974).

The relative importance of any physiological feature can be assessed in three complementary ways.

1. The analysis of contrasting climatic or agronomic varieties or collections. Much of our knowledge of the physiological basis of response to climatic stress, of developmental responses to temperature and photoperiod, of leaf area duration and of the distribution of assimilates, i.e. harvest index, has been gained from such comparative studies.

2. Selection from within a variety or segregating population for high and low expression of a particular physiological feature. The direct effect of such selection on performance in the field

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can then be assessed, while any correlated responses, either favourable or unfavourable, will become apparent. Furthermore, those selection lines that show promise can be readily incorporated into a breeding programme.

3. The use of models of crop photosynthesis and growth to predict the effects on yield of changes in such features such as individual leaf photosynthesis, canopy structure and the distribution of assimilates. Such models are rapidly being developed, though as yet they have hardly attained the degree of precision required for use in a breeding programme (de Wit 1965; Monteith 1972, 1977).

Even where the importance of a particular physiological feature has been demonstrated, however, any operational screening tests must be able to handle large numbers of individuals rapidly and reliably, preferably early in the life cycle and at any time of the year, and, of course, show a good correlation with subsequent performance in the field. A reasonable heritability with no unfavourable correlated responses is also important.

At present, early screening tests are likely to be particularly valuable for stress response, where field assessment is restricted to one season of the year and can be influenced by unpredictable environmental fluctuations. In many crops, particularly the cereals and forage grasses, seedling tests under controlled conditions have been developed to assess either cold hardiness or leaf growth at moderately low temperatures, which relate well to subsequent performance in the field. Direct methods of screening for response to water stress are less well developed, but indirect techniques such as selection for smaller stomata or fewer stomata per unit area in the forage grasses have led to improved water use efficiency and a marked increase in summer production (Wilson 1975*a*, 1981).

Similarly, those developmental responses to low-temperature vernalization or photoperiod that control the onset of flowering or tuberization can often be measured reliably under controlled conditions, though since the seasonal cycle of photoperiod varies regularly in the field, any advantage over field assessment for a single location is more doubtful. Even so, such screening may be of value in predicting the flowering behaviour of the material in other environments, and can lead to the development of controlled techniques for the acceleration of flowering and hence a more rapid turnover of generations.

The potential value of screening for components of crop photosynthesis is rather less clear (Wallace *et al.* 1972). Although variation in the maximum photosynthetic rate of the individual leaf has been recorded in many crops, in few cases has it been possible to relate this to differences in total dry matter or in economic yield. The effect of variation in photorespiration in C_3 crop species is also not clear, though on theoretical grounds a possible reduction of photorespiration could greatly increase dry matter production and crop yield. Furthermore, rapid and reliable laboratory techniques for the routine screening of large numbers of individuals for photosynthesis or photorespiration still remain to be developed.

More information, however, is accumulating on the possible effects of reducing maintenance respiration. In the forage grasses, for instance, selection for reduced dark respiration of mature leaves has resulted in an increase of some 12% in annual dry matter production, the increase being particularly marked in the higher temperatures of summer (Wilson 1975*b*, 1976).

Similarly, considerable variation has been recorded within crop species for such canopy characters as leaf angle, leaf length and leaf rigidity, which determine the distribution of light down the canopy, but, as discussed earlier, the effects of such differences vary with the crop and the stage of growth. Even so, in the forage grasses, selection for such characters in the early

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seedling stage has resulted in marked changes in light distribution and in maximum crop growth rate (Rhodes 1975).

In general, however, the extent to which variation in total biomass, and certainly in economic yield, is determined by variation in net photosynthesis of the crop canopy is far from clear. In practice, differences in the distribution and use of assimilates either to provide more effective light interception, i.e. a greater leaf area duration, or more effective partition to economic yield, i.e. a greater harvest index, would appear to be more important (Evans 1975). It is in these two areas that comparative physiological studies are likely to lead to greater understanding and improvement of crop yield.

Furthermore, the present discussions have been concerned primarily with the limitations to crop improvement set by the main climatic variables of energy input, temperature and water supply. Looking ahead, the cost and availability of other inputs, including the major nutrients nitrogen and phosphorus, may become important limitations, and the physiological efficiency of the crop in dealing with these inputs also requires serious study.

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