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The Achievements of Conventional Plant Breeding [and Discussion]

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The achievements of conventional plant breeding

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Varietal improvements in yield are often strongly associated with increases in the ratio of the harvested organ or product to total biomass, which itself has shown relatively little change. Thus the greatest opportunities for increasing yield have been for the cereal species, with root crops intermediate and forages the most difficult to improve. In favourable climates the yields of cereals are frequently double those obtained in 1950, improvements in varieties accounting for about half this increase. The work has been much less effective where growth is dominated by environmental stresses, especially water supply, and in these situations yields are inconsistent, with little average improvement.

Breeding for resistance to the hazards of pests and disease, storms, temperature extremes and mineral deficiencies has had numerous successes. There remain considerable problems in the durability of resistance to pathogens, and in a number of cases there are no known sources of resistance that can be utilized by conventional breeding methods.

Improvements in the quality of food crops are most notable for meeting technological requirements and consumer preferences; there are few examples of improvement in nutritional value other than in the elimination of nutritionally deleterious substances. In cereals and many other crops there are considerable limitations in protein content due to an inverse relation with yielding ability.

INTRODUCTION

Plant breeding has contributed significantly to all the major crops of agriculture and horticulture, in many cases enabling the grower to obtain higher yields, adopt more efficient methods of production and meet the demands of the processor or consumer for increasingly close specifications in the harvested product. In the context of this meeting, little would be gained by attempting to catalogue these achievements. It is more appropriate to consider them with the particular purpose of identifying areas of plant breeding in which the present work may be considered wanting.

First, there are many examples of characters in which varietal improvements have made a major contribution and may be expected to continue to do so. In such cases new methods must have a cost effective advantage in rate of progress or in more efficient use of the breeder's time and facilities. The new methods will have to compete with well established practices, which often amount to massive experiments in genetics, though the application of the work may owe little to detailed genetic information. For example, in cereals it is now common for a breeding group to handle all stages of a programme based on about 1000000 plants in F_2 and 40000 single plant progenies in F_3 (Bingham 1979).

Secondly, it may be possible to delineate some objectives with serious limitations in prospect for improvement by conventional methods, either in the rate of progress or in the ultimate level of expression of a desirable character. Breeding problems in this area may be due to a lack of genetic resources, to cytogenetic barriers in their use or to the lack of effective selection methods. Characters where the rate of progress is now decelerating after a period of rapid advance should be included in this group.

In following this general theme, examples will be drawn mostly from those agricultural and horticultural crops grown as food for man and animals. The objectives will be considered in the interrelated classes of yield potential, resistance to environmental hazards, and quality of the product.

Varietal improvement in yield potential

The average yields obtained by growers of many agricultural and horticultural crops have doubled over the last 30 years. For wheat (figure 1), yields in the United Kingdom increased slowly over the first 50 years of this century from about 2.1 to 3.0 t/ha; they have since advanced more rapidly to an estimated 5.7 t/ha (at 15% moisture) in 1980, with below-average years due to bad harvest weather in 1968 and to drought in 1976.

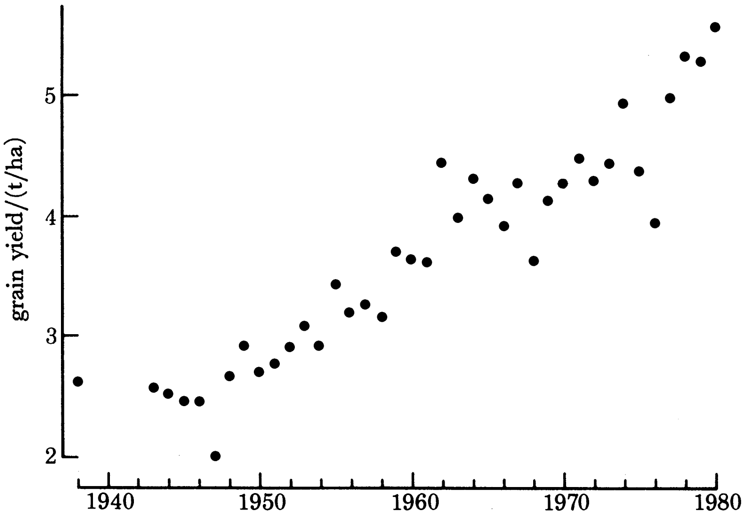

Figure 1. National average yields (15% moisture content) for wheat in the United Kingdom.

The highest recorded farm yields in the United Kingdom have increased correspondingly. For example, in 1980, R. Harvey at Braiseworth Hall Farms, Tannington, Suffolk, obtained 11.5 t/ha (15% moisture) for a 83 ha field of the winter wheat variety Hustler, on a deep, moisture retentive soil of the Beccles Series, with an average of 10.9 t/ha over 420 ha. J. Muirhead, on a deep alluvial soil at Eastlands Farm, Bradwell on Sea, Essex, also recorded 11.5 t/ha for 10.4 ha of the variety Virtue. These yields are close to the theoretical maximum for present-day varieties in this country of 11.4–12.9 t/ha, calculated by Austin (1978) on the basis of measurements of photosynthesis and the proportion of assimilates used in grain filling.

The increases in yield have been obtained over a period of rapidly changing husbandry practices, with greatly increased inputs of fertilizers, herbicides and fungicides. For the self-fertilized cereal species, the proportion of the increase in yield due to improvements in varieties may be assessed by direct comparison of varieties. For the period 1947–75, Silvey (1978) estimated, from the yields of controls in National Institute of Agricultural Botany (N.I.A.B.)

trials, that varietal improvement accounted for increases of 50 % in national average yields for wheat and 30 % for barley. These calculations compound the effects of potential yielding ability with resistance to lodging and disease resistance, and may be an overestimate because standards of comparison change owing to increases in the virulence of pathogens on varieties used as controls.

To isolate the effects of varietal improvement in yield potential from resistance to hazards, Austin *et al.* (1980) compared winter wheat varieties, representing a chronological series, in yield trials protected by fungicides and supported by nets to prevent lodging. The trials were grown with high and low levels of nitrogen fertilizer application. Apart from one line, Benoist 10483, the yields for the two levels of soil fertility were strongly correlated (figure 2), indicating that percentage advantage in yield of the newer varieties was independent of nitrogen application, Hobbit and Norman outyielding the average of Little Joss and Holdfast by 45–49 % in each treatment. The higher yielding varieties were, however, more responsive and efficient users of nitrogen in the sense that they gave a greater return in grain yield per kilogram N applied. This effect on yield potential is additional to the practicality of using higher rates of nitrogen fertilizer on varieties with improved standing ability.

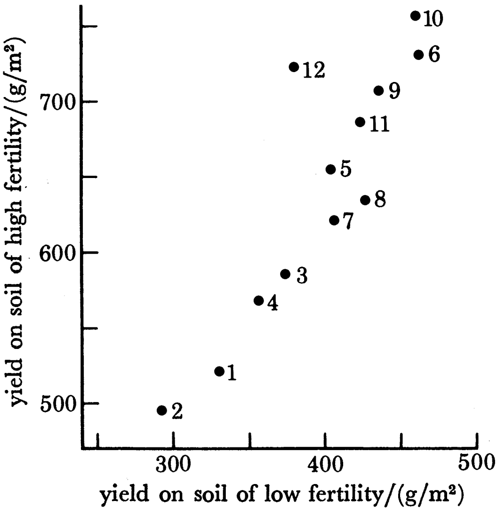

FIGURE 2. Grain yield (dry mass) of a series of winter wheat varieties when grown on soil of high fertility, receiving 104 kg N/ha, and low fertility, receiving 38 kg N/ha (Austin *et al.* 1980). Varieties and year of introduction: 1, Little Joss (1908); 2, Holdfast (1935); 3, Cappelle-Desprez (1953); 4, Maris Widgeon (1964); 5, Maris Huntsman (1972); 6, Hobbit (1977); 7, Mardler (1978); 8, 370/500(†); 9, Galahad(†); 10, Norman (1981); 11, Armada (1978); 12, Benoist 10483(†). †, Breeder's lines or varieties not grown commercially.

The varietal improvement in grain yield in this series of varieties was associated predominantly with increases in harvest index (ratio of grain yield to that of straw and grain combined). There were only small differences between varieties in total dry matter production, but these were not related to grain yield, so that there was a strong tendency for higher yielding varieties to have lower straw masses per square metre. The varieties were similar in maximum leaf area index, and yielding ability was not associated with any particular combination of the harvest components of ear number, ear size or 1000 grain mass. T. J. Riggs (personal communication) obtained similar results with a series of spring barley varieties in experiments carried out in

1979 and 1980. Other investigations have also indicated that change in dry matter distribution is the most important difference between old and modern varieties.

In recent years, increases in the harvest index of wheat varieties have depended mainly on the major semi-dwarfing genes *Rht*1 and *Rht*2 derived from Norin 10, and on other factors from Italian varieties. Such factors can be combined to give further reductions in height, but there remains only limited scope for increasing yield by substituting grain for straw. This approach is likely to become counter-productive if much shorter lines are developed, owing to adverse effects on the spatial arrangement of the leaves, and in taller lines because diversion of structural materials from the straw would reduce resistance to lodging.

More attention should therefore be given to increasing total biomass. It is probable that some increase in biomass can be achieved by selecting within the available variation in *Triticum aestivum* for morphological characters, such as erectness of leaves, which improve the uniformity of light distribution in the canopy and thus increase crop photosynthesis. The greatest remaining challenge in breeding for yield potential is, however, to increase the light-saturated rate of photosynthesis of individual leaves. It has been found by Evans & Dunstone (1970), and confirmed by R. B. Austin in field experiments (personal communication), that some primitive species of *Aegilops* and of *Triticum*, notably the diploids *T. thaoudar* and *T. urartu*, have rates of photosynthesis per unit area of flag leaf up to double those of *T. aestivum* varieties. There is, however, a strong negative correlation between leaf size and photosynthetic rate. Evans & Dunstone therefore concluded that photosynthetic rate had not yet limited the evolution of yield in wheat but might well do so in the future. For the very dense crops now grown on fertile soils it is unlikely that reductions in leaf size would seriously reduce light interception. As such crops become more common it is probable that selection for photosynthetic rate will become of increasing importance. It has yet to be shown whether the high photosynthetic rate of the diploid species can be maintained at the hexaploid level, and this may not be so if it is dependent on small cell size. However, even at the hexaploid level it should be possible to make some progress by deliberate selection for photosynthetic rate.

Taking these physiological considerations into account, there is no reason to suppose that a ceiling has been reached in yielding ability with present-day varieties of wheat and barley. This view is supported by genetical studies; for example, Laabassi (1979), using a recessive nuclear gene to produce F_1 wheat hybrids, found that heterosis for yield was commonly 15–20 % above the higher-yielding parent, indicating that it should be possible to obtain increases of at least this order by pure line breeding. Nevertheless, as genetic variation at the varietal level is exploited, a diminishing return in potential yield is inevitable and it is significant that maintenance of the present rate of progress is involving larger breeding teams and intensification of selection methods.

Increases in the on-farm yields of other crops in many cases equal those for cereals, but it is often more difficult to estimate the contribution of varietal improvement. Varieties of outbreeding species sown from seed may have been reselected or reconstituted during their period of use, and even comparatively recent varieties may no longer exist in their original form. In maize, many of the inbred lines used in the production of double and single cross hybrids have been maintained in collections, so it is possible to remake varieties grown since hybrids were first widely grown in the late 1920s. Russell (1974), working in Iowa, found that optimum seeding rates were higher for new than for old varieties of maize because they produced fewer barren stems. When sets of varieties representing different periods of cultivation were grown at a range of seed rates, those of the 1970s outyielded those of the 1930s by 38 % at the optimum seed rate for each group and by 57 % when averaged over all sowing rates. Thus the genetic gain in yield for maize in Iowa has been similar to that for wheat and barley in the United Kingdom.

When other crop species are compared with cereals, it is evident that those already giving the highest yields of harvested product are the most difficult to improve further, especially when the high yields are associated with high harvest index. Rating of crops grown in the United Kingdom on this basis indicates that the breeder's task has been easiest for cereals, with potatoes and sugar beet considerably more difficult and herbage crops the most intransigent (tables 1 and 2). Thus the potato varieties Home Guard and King Edward are still recommended by the N.I.A.B., though they are not now grown on such large areas as varieties of higher yielding ability, notably the maincrop varieties Maris Piper and Pentland Crown and the early potato Maris Bard. In the Netherlands, Bintje, bred in 1910, is still the most widely grown variety despite large breeding programmes in which about one million seedlings are assessed each year.

Table 1. National average yields (dry mass) and typical harvest indices of crops grown in the United Kingdom

	average yield, 1979 t/ha	harvest index†
wheat	4.4	44–48
barley	3.5	48–52
potatoes	6.6	75–85
sugar beet		
tap root	7.6	73
sugar	5.7	55
perennial ryegrass	no data	85–90

† Ratio of harvested dry matter to total dry matter, excluding fibrous roots.

Table 2. Varietal improvement in yield of crops grown in England and Wales

	baseline variety	yield of best current varieties (percentage of baseline)	source of data
wheat	Bersee 1947	156	Silvey (1978)
barley	Plumage Archer 1947	132	
potatoes			
early	Home Guard 1943	120	Plant Breeding Institute trials (1980)
main crop	King Edward 1902	114	
perennial ryegrass	S24 1937	106	National Institute of Agricultural Botany (1980), *Recommended varieties of grasses*
	S23 1933	108	
sugar beet	no reliable data		

There are no reliable estimates of genetic gain in yielding ability for sugar beet because the old varieties are no longer available. It is relevant that the rate of increase in national average yield for this crop kept pace with that of the cereals until the late 1960s, and it is now more difficult to obtain further advances in yield by selection within the genetic variability at present available to the breeder. Introduction of the monogerm character was an essential step in mechanization, and selection for greater vernalization requirement, to improve resistance to bolting, was a major contributor to yield increases from 1950 to 1970, enabling growers to bring sowing dates forward and thereby to extend the growing season by 4–6 weeks.

PROTECTION FROM HAZARDS

Alleviation of adverse climatic factors, and improvements in resistance to pests and diseases, are often of greater importance in the quest for higher and more stable production than are the genetic gains in yield potential that have been demonstrated for many crops.

Adaptation to soils and climate

For the small-grain cereal species, improved standing ability is probably the most significant achievement in overcoming limitations of the physical environment, even though it is of major value only where the soils and climate allow high yields to be obtained. Throughout the first half of this century, resistance to lodging in wheat was sought most strongly in west Europe, where considerable progress was made by exploiting polygenic variation for shorter, stronger straw. This improvement was, however, obtained at the expense of discarding very high proportions of breeding lines that did not meet the required standards, and may have retarded the rate of progress in yield potential. In this breeding situation one of the main attractions of major semi-dwarfing genes is in allowing breeders to give more attention to other characters.

Major semi-dwarfing genes were used by Japanese wheat breeders for many years before Salmon took seed of Norin 10 and related Japanese varieties to the U.S.A. in 1946 (Dalrymple 1980). This material was used by Vogel in breeding of Gaines and other semi-dwarf winter wheat varieties for the high-yielding areas of the Pacific Northwest. It enabled Borlaug to make rapid progress in breeding spring wheats for areas of Mexico and other low-latitude countries where irrigation was available or rainfall was adequate. In these countries comparatively little attention had previously been given to reducing height, because the soils were so infertile that lodging was rarely an important limiting factor. Against this background, the new semi-dwarf varieties provided the stimulus for rapid advances in agronomy of the crop, especially in the greater use of nitrogenous fertilizers and in the development of irrigation systems (Arnold 1980).

The distribution of the two major semi-dwarfing genes from Norin 10, *Rht*1 and *Rht*2, has since been determined for a wide range of varieties based on this material. These genes have also been shown to have advantageous pleiotropic effects on harvest index, grain number per spikelet and grain yield (Gale 1978). In west Europe, *Rht*1 and *Rht*2 have been used most intensively by the Plant Breeding Institute and by the Miln Marsters Group. Similar work in central and east Europe is based on other factors derived from Japanese varieties by the Italian breeder Strampelli. These factors have not been fully characterized, but it has been shown that they differ in their mode of action from *Rht*1 and *Rht*2 in being sensitive to gibberellic acid. They were also involved in the breeding of Talent, at present the most widely grown variety of wheat in France, and in some new lines recently entered into National List Trials by the Plant Breeding Institute.

In India the introduction of semi-dwarf varieties of wheat in the mid-1960s, combined with increases in agronomic inputs and a greater area sown to wheat, has led to increases in production comparable to those in west Europe, from 10–12 Mt in the years 1961–5 to 35 Mt in 1979.

This achievement has been criticized by some because the increase in area of wheat has been obtained partly at the expense of less productive crops, including legumes, but it is now more generally held that the considerable increase in overall production is nutritionally of much greater significance (Arnold 1980). Moreover, improvements in soil fertility, increases in the irrigated area and the introduction of earlier-maturing varieties have made it possible to extend the practice of multiple cropping. There are, however, wide disparities in yields of wheat between the States of India. Average yields in the Punjab, where irrigation is widely available, are now about three times those in States where the crop is rainfed (Swaminathan 1977). The yields from demonstration plots on trial grounds with irrigation and optimum fertilizer use confirm that water supply is the overriding factor. It is also clear that the prospects for advances in yield, at least in the short term, are greatest in those areas that have already benefited.

Plant breeding has had little success in increasing the yields of wheat in other ecologically difficult areas, especially where the effects of drought are accentuated by the temperature extremes of continental climates. For example, on the high plateau of Turkey and Iran the effective growing season is very short owing to low winter temperatures, and in North Africa the sudden onset of very high temperatures when the grain is filling frequently causes premature death of the plant. In such areas the crop is unreliable and average yields often show virtually no advance. The increases in production that have been obtained owe more to improvements in agronomy, especially in the management of fallows to conserve moisture, than to plant breeding.

There is a comparable situation with rice, where semi-dwarf varieties have led to greatly increased production in regions with well controlled irrigation systems, most notably in Thailand, North India and Sri Lanka. In these areas, where advantage can be taken of their ability to respond effectively to fertilizers, the potential for further increase in production has been estimated at 46 % (Anon. 1978). About 70 % of the world's rice is, however, rainfed and even in some monsoon regions the crop may suffer from drought in the later stages of development. For these areas, and on the plains of east India and Bangladesh, which do not have adequate flood water control, there has been little increase in average yields; the corresponding estimate for further improvement is only 3–8 %.

Although there are many cases of genetic improvement in tolerance of low or high temperature, the most productive achievements in minimizing losses due to exigencies of the climate are probably those that have involved changes in the timing of developmental and growth stages to match periods of favourable weather. Extension of the environmental range of a crop species to new regions has often depended in the first instance on adaptation in this respect, followed by improvements in the distribution of assimilates as a second phase of the work. Water supply remains the principal limitation to yield in many situations, and even at the high levels of yield for arable crops common in west Europe, it is often the most important factor. In dryland areas the yields of some perennial crops have been increased by an ability to survive and resume growth after a period of drought. With annual crops, especially cereals, the predominant trend has been in avoidance of drought by earlier ear emergence and maturity. Further changes in this direction are, however, likely to be counter-productive owing to reductions in biomass that can be offset only partly by increases in harvest index (Fischer 1979).

Within species, there is little evidence of genetic gain in the efficiency of water use, as measured by the ratio of biomass to water transpired, and the resolution of this problem is of the highest priority. Reducing transpiration by increasing stomatal resistance to diffusion generally has a similar effect on uptake of CO_2, so mechanisms are needed that increase the diffusion gradient for CO_2 within the leaf. By analogy with drought-resistant species, these may have an anatomical basis in smaller mesophyll cells, or a biochemical one in CO_2 fixation, and identify closely with those proposed for higher photosynthetic rate. Thus, selection for greater biomass under conditions of water stress may also provide useful parental material for higher photosynthetic rate when water supply is not limiting (Austin 1980).

Disease resistance

A large proportion of the work in most breeding programmes is concerned with resistance to pests and disease, and may be overruling when alternative methods of chemical or husbandry control are too costly, or not sufficiently effective. A broad division may be made between problems in circumventing the ability of pathogens to evolve new virulences and work aimed at increasing the level of resistance. The former if typically associated with the obligate foliar pathogens of cereals, which tend to show host-specificity especially to species and to varieties, and the latter with facultative pathogens, which show specificity towards different species much more than towards different varieties (Scott *et al.* 1980).

The strategy of breeding for resistance to obligate pathogens and the progress obtained may be illustrated with yellow rust (*Puccinia striiformis*) of wheat. Very high levels of resistance are common, but there is no certain method of selecting breeding lines for durable resistance, defined as resistance that remains effective while a cultivar is widely grown (Johnson 1981). More than 10 new races of yellow rust with additional virulences on varieties or breeders' lines have been discovered in the United Kingdom over the last 15 years. Many of the varieties affected had major genes for race-specific resistance, usually seen as a hypersensitive reaction to infection in seedling tests. The genes concerned include *Yr1* to *Yr7* from *T. aestivum* varieties (Lupton & Macer 1962; Macer 1966), *Yr8* from *Aegilops comosa* as a chromosome 2M/2D translocation (Riley *et al.* 1968) and *Yr9* as a 1R/1B substitution from rye. Moreover, the deliberate assembly of combinations of such genes has not given a useful increase in durability. For this reason it is now common practice to avoid lines that have seedling-resistance to all known races.

There is indisputable evidence that durable resistance to yellow rust does exist, in that the resistance of some old varieties, notably Browick, Little Joss, Yeoman, Vilmorin 27, Atle, Hybride de Bersee, Cappelle-Desprez and Maris Widgeon, remained effective over long periods of cultivation. It also seems likely that Maris Huntsman has a residual level of durable resistance equivalent to Cappelle-Desprez. These varieties are all susceptible to one or more races in seedling tests but develop sufficient resistance in the adult plant to restrict the development of epidemics; this is sometimes referred to as 'slow-rusting'. However, selection for a combination of seedling susceptibility and adult plant resistance does not in itself guarantee durability, as is evident from the discovery of adult plant adapted variants of yellow rust on Joss Cambier in 1971, and on Maris Bilbo and Hobbit in 1973.

Although it is not possible to test for the durability of resistance to yellow rust, the probability of obtaining such resistance should be increased by the procedures described by Johnson (1978) and applied to the breeding of the winter variety Bounty (Bingham *et al.* 1980; Bingham 1981). Bounty was selected from a cross of an adult plant susceptible variety, Durin, with Ploughman; the latter was derived from a partial backcross of Hybrid 46 to Maris Widgeon as recurrent parent, and was therefore assumed to carry durable adult plant resistance. From the parents it would have been possible to combine race-specific genes giving complete resistance to all races known at the time, i.e. *Yr1*, *Yr3b* and *Yr4b* (table 3). This was avoided by selection for the same pattern of seedling resistance as Durin, so that adult plant resistance from Plougham could be detected.

Similar considerations apply to other obligate pathogens of the cereals, especially brown rust (*Puccinia recondita*), stem rust (*Puccinia graminis*) and powdery mildew (*Erysiphe graminis*). The work is hampered by a lack of information on the resistance mechanisms that determine durability and their genetic control. Durability is not necessarily dependent on polygenic control (Eenink 1977), although it has been shown that some particular cases of durability are associated with a combination of more than one resistance mechanism (Russell 1978). No distinction has yet been made, however, between forms of adult resistance that have proved to be durable and those that give similar reactions in field tests, for example 'slow rusting', but are not durable.

Table 3. Pedigree of the winter wheat variety Bounty, showing the genes for seedling reaction to yellow rust, and the reaction of Bounty and its parents to two races of yellow rust in the seedling and adult plant stages

(Key: r, resistant; s, susceptible.)

Ploughman ——×—— Durin

race	*Yr 3b 4b* seedling	adult	*Yr 1 3a 4* seedling	adult
41 E 136	r	r	s	s
104 E 137	s	r	r	r

Bounty

race	*Yr 1 3a 4a* seedling	adult
41 E 136	s	r
104 E 137	r	r

Despite these limitations, many obligate pathogens have been kept under good control by breeding for resistance, one of the best known examples being resistant to stem rust of wheat in Australia, and also in North America where there have been no major epidemics since 1954. Such achievements have, however, been made at the expense of progress in other characters, owing to the high breeding input needed to maintain equilibrium with increasing virulence, and the obligation to discard many lines when new races appear. Many schemes have been proposed for a more orderly exploitation of resistance factors. Of these, the *Varietal diversification schemes* published by the National Institute of Agricultural Botany (Anon. 1981) are widely followed by growers, and have made a major contribution to the control of wheat yellow rust and barley mildew in the United Kingdom. Multilines and varietal mixtures are also complementary to pure line breeding, mixtures having the benefit of greater flexibility in composition, so that limitations in the range and combination of virulences possessed by pathogen populations can be continually exploited. This method is applicable to the control of many diseases where the durability of resistance is elusive, and its effectiveness has been clearly demonstrated in field trials with mixtures of spring barley varieties differing in genes for resistance to powdery mildew

(Wolfe *et al.* (1981). Mixtures could also be used to improve the stability of wheat yields in low-latitude countries, where it is most difficult to obtain durable resistance to brown rust.

In these ways some progress has been made in the strategy of using race-specific resistance and in methods of breeding for durability. There is no certainty that resistance introduced from alien sources will be more durable; this possibility should be investigated, but the main objective of new methods of genetic manipulation should be to improve the level of resistance to those pests and diseases where the sources of resistance available by conventional methods are inadequate (table 4). Some of these objectives can be attained by established cytological methods (Law 1981); for example, resistance of wheat to eyespot (*Pseudocercosporella herpotrichoides*) has already been increased by transfer of additional factors from *Aegilops ventricosa* (Doussinault *et al.* 1974).

TABLE 4. EXAMPLES OF PESTS AND DISEASES OF ARABLE CROPS WITH SERIOUS LIMITATIONS IN THE LEVEL OF RESISTANCE ATTAINED BY CONVENTIONAL BREEDING METHODS

wheat	take-all	*Gaeumannomyces graminis*
	shoot fly	*Opomyza florum*
	bulb fly	*Leptohylemyia coarctata*
	† grain aphid	*Sitobion avenae*
barley	take-all	*Gaeumannomyces graminis*
	† barley yellow dwarf virus	
	‡ mildew	*Erysiphe graminis*
	aphids	*Sitobion avenae* and *Metopolophium dirhodum*
potato	gangrene	*Phoma exigua* var. *foveata*
	‡ late blight	*Phytophthora infestans*
	leaf roll virus	
	cream cyst nematode	*Globodera pallida*
sugar beet	† virus yellows	
oilseed rape	stem canker	*Phoma lingam*
field bean	chocolate spot	*Botrytis fabae*
	leaf and pod spot	*Ascochyta fabae*
	blackfly	*Aphis fabae*

† Moderate levels of resistance available but higher levels would be beneficial.
‡ Level of durable resistance not adequate.

Technological properties and nutritional value

As the yields of many crops have increased, often to the point of surpluses in production, breeders have given increasing attention to the quality of the harvested product in terms of cooking quality, palatability and nutritional value, or suitability for manufacturing processes. In wheat the main objectives have been related to the technological requirements for the manufacture of bread, biscuits and other foods; little attention has been given to the possible effects of variety on the nutritional value of the grain, though there are many regulations governing the use of additives in manufacturing processes and the nutritional value of the foods produced.

The maritime climate of the United Kingdom is very well suited to the production of biscuit-making wheats, but difficult for bread-making quality, as has been well appreciated since the beginning of this century when all the varieties grown, such as Browick and Squarehead, were derivatives of land races of biscuit-making type. R. H. Biffen was the first to demonstrate that bread-making quality was heritable, by the breeding of Yeoman, marketed in 1916, from a cross of Browick with the Canadian spring wheat Red Fife. Bread-making quality was further improved by F. L. Engledow, using another Canadian variety, White Fife, in the parentage of Holdfast (1935), and these varieties figure in the lineage of Maris Widgeon (1964), Maris Freeman (1974), Bounty (1979) and Avalon (1980).

The United Kingdom has been self-sufficient in production of wheat for all uses other than bread-making since 1978. Increases in the area sown to varieties suitable for bread-making, in conjunction with improvements in baking technology, have enabled millers to reduce to 40–45 % the proportion of imported wheats of Manitoba type required in grists for white bread. However, imports of wheat in this class still amount to 1.8–2.0 Mt annually, so it is important to define the objectives for further varietal improvement. The best of present varieties meet all the requirements for the purely mechanical operation of milling, giving high flour-extraction rates. They also have the essential biochemical attributes of a low α-amylase activity in the grain, provided germination in the ear has not commenced, and good protein quality as shown by measurements of dough strength and elasticity. There are also excellent prospects for obtaining further improvements in protein quality by the deliberate recombination of glutenin subunits associated with good bread-making quality (Payne *et al.* 1981). The main breeding problems are concerned with liability to sprouting during wet harvest weather and with low grain protein content. It should be possible to obtain a sufficient improvement in harvest dormancy by the exploitation of recently discovered variation in *T. aestivum* but there are major physiological limitations to breeding for higher grain protein content.

There is a very strong tendency for varietal differences in grain protein content to be inversely related to yielding ability (Pushman & Bingham 1976). This is a general situation for many other crop plants, and arises largely because the opportunities for breeding varieties able to scavenge more nitrogen from the soil and increase harvest index for proteins are much less than those for transferring more carbohydrate products to the grain. Some genotypes indicate that it may be possible to offset in part the decline in protein content of higher-yielding varieties, but there is no prospect that a major improvement in this respect can be achieved by conventional breeding methods.

Nutritional value

Thus, for many crop plants, quality is defined by technological characters, and by consumer preferences in appearance, cooking properties and taste, which bear little relation to nutritional value. In fruit and vegetable crops especially, these objectives can be of greater importance than any other breeding character. The concept that nutritional value can be improved by breeding is of relatively recent origin, largely stemming from the discovery of the high lysine maize mutants *opaque 2* and *floury 2* (Mertz *et al.* 1964). No varieties of maize with this character are being grown on a substantial scale owing to associations with lower yielding ability, poorer cooking quality and greater susceptibility to storage pests and diseases, though some breeders are confident that these problems are surmountable.

Breeding for higher protein content involves a penalty in yielding ability partly because the energy requirement for the production of storage proteins, from a nitrate substrate, is practically double that needed for a similar mass of starch. There are only small differences between amino acids in this respect, so it should be possible to increase the proportion of limiting amino acids with no loss in yield. In practice, this objective has proved difficult to attain; many breeders have discontinued work with the high lysine barley mutant Risø 1508, owing to an association with shrunken grain, but other sources, especially from Ethiopian material, are considered more promising.

The elimination of toxic substances in rapeseed oil and meal is one of the most effective achievements in breeding for improved nutritional value. After the discovery of lines with low erucic acid content in Canada in 1961 (Downey 1974) and the implication in 1970 that this long-chain fatty acid was a possible cause of myocardial lesions, breeders were able to respond so rapidly that by 1980 an almost complete change to varieties with low erucic acid content had occurred. Feeding experiments have confirmed the improved nutritional value of such varieties, though it is now considered that the association of erucic acid content with myocardial lesions was originally exaggerated. Good progress is now being made in reduction of glucosinolates, which give breakdown products of bitter taste in rapeseed meal and reduce its consumption by animals.

Conclusion

Despite the wide differences between crop species in the environments where they are grown, in the pests and diseases that confront them, and in the plant organ that composes the harvested product, it is possible to identify some general limitations in objectives that can be attained by conventional breeding methods.

It is inevitable that genetic advances in yield potential will become increasingly difficult to obtain, and for many crops, especially those where harvest index is already high, the main limitations will be in biomass. There is probably little scope or advantage for increasing the leaf areas of high yielding crops grown in favourable environments. There may be some possibility for small advances in biomass by changes in leaf arrangement and in leaf longevity, but the greatest challenge is to increase photosynthetic rate per unit area of leaf. An increase in this respect would, however, be of limited value unless achieved by an anatomical or biochemical mechanism that also resulted in an equivalent increase in the efficiency of water use, thus giving improved resistance to drought.

There are two outstanding requirements in breeding for resistance to pests and diseases. One is for combined studies of the mechanisms and genetics of durable resistance, with the objective of devising selection methods applicable to large numbers of progenies. Some progress is, however, being made in strategies for handling available sources of resistance; the main limitation is often in the level of resistance that can be attained. New methods of genetic manipulation should therefore be directed primarily to increasing the level of resistance, by introduction of genetic factors from alien material not available by conventional methods.

Most consumer preferences, and the technological requirements for processing, can be met by breeding methods currently employed. There are also opportunities for improving nutritional value by changes in biochemical composition that are compatible with yield, but in many crops other than leguminous species there are serious restrictions in protein content.

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Discussion

P. S. WELLINGTON (*National Institute of Agricultural Botany, Cambridge, U.K.*). Skill in farm management could be a limiting factor that is now contributing to the increasing gap between the national average yield of cereals in the U.K. and the highest yields obtained by certain individual farmers. Reference was made in the paper to the estimates made by Mrs Silvey in 1978, that new varieties of wheat had contributed 50%, and new varieties of barley 30%, to the increases in national yields over the last three decades. Estimates were made at the same time of the contributions of other factors such as improved husbandry. It is significant that these made an additional contribution to national yields at least equal to that of new varieties in the period 1947–57, whereas improved techniques for cultivation and drilling and greater use of fertilizers, growth regulators, herbicides and fungicides did not appear to make any additional contribution between 1967 and 1977. It therefore seems that a high level of crop management is now required to obtain the higher yields from new varieties. This demands of the farmer detailed knowledge of local constraints, production planned to maximize profit and skilful use of the increasingly expensive inputs.

Reference was also made to the need for a more comprehensive system of variety trials to assess interactions with environmental conditions before new varieties are recommended to farmers. In practice the two main factors are sites and seasons, and the aim of the present N.I.A.B. trial system is to provide adequate samples of both for the main commercial production areas for the crop concerned. The recommendations are based on the statistical analysis of past trial results, but the farmer needs to predict the probable performance of the varieties, under his particular conditions, in a future season for which the weather conditions, in spite of long range forecasting, are not yet known. The present numbers of sites and seasons for variety trials are based on past experience, and calculation of the actual variations that have occurred. The objective is to use the resources available to obtain the best estimate of differences in the characteristics that make up commercial performance between all the varieties under consideration for inclusion on the Recommended Lists. The achievement of this objective requires complex methods of statistical analysis, but so far as seasonal variations are concerned, experience has shown that in practice the average over all sites for at least three, and if possible five, seasons provides a good prediction of behaviour under all except extreme conditions.

M. S. WOLFE (*Plant Breeding Institute, Cambridge, U.K.*). I should like to comment on the question of breeding for specific rather than general adaptation, and on the problem of defining, or predicting, the environmental variation that necessitates adaptability in the crop. In recent years, Dr J. A. Barrett and I have been investigating mixtures of cereal varieties, particularly barley, for disease control. Appropriately designed mixtures of three varieties have been highly effective in this respect, but we have become increasingly aware of the more general advantages of using mixtures over a wide range of environmental conditions. It is clear that they provide considerable buffering against both unpredictable and predictable environmental variation, so that stable high yields can be more easily attained, with fewer management problems for the farmer. Plants of different varieties grown side by side can compensate for each other under different environmental conditions; when they are grown in pure stands they cannot.

D. R. Johnston (*Forestry Commission, Forest Research Station, Farnham, Surrey, U.K.*). Dr Wolfe has discussed buffering against biological factors. I should like to refer to buffering against economic trends. Plant breeders in forestry are beginning to question whether it is prudent to bequeath to posterity genetically improved tree crops that will take 50 years or so to mature and which have been selected and developed under high-input régimes. It is likely that the price of fertilizers and chemicals will increase in real terms, and it may be wise to devote some research effort to the breeding of genetic material that will be relatively successful under low-input régimes. I should be interested to know if this aspect of plant breeding has been considered by the agriculturists.

J. Bingham. In extensive areas of the world where the yields of cereals and other crops are severely restricted by limitations of soil or climate (especially water supply), fertilizers and other chemical inputs can be used economically only at relatively low levels. Much of the work of the international centres is now aimed at improving yields for such situations, including a major part of the programme at CIMMYT, International Centre for Maize and Wheat Improvement.

In the favourable climate of the U.K. it is more appropriate to select for efficiency of fertilizer use, as measured by the return in yield per unit of fertilizer applied. The increases in potential yield of varieties so far obtained are in the main related to improvements in this respect and are effective over a wide range in rate of N fertilizer use. There is a danger that such varietal differences may no longer be detected as the use of N fertilizer increases to very high rates. It is therefore desirable to reintroduce the practice of testing for yielding ability at more than one rate of N fertilizer application in national trials.