

Cereal breeding and its future trends

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This paper seeks to show that cereal breeders have been successful when their objectives have been clear. It is suggested that the end of cereal improvement is not in sight and that breeders will continue to make significant advances in many directions. In order to look at future trends it is necessary to examine what has been achieved and to consider the principles on which cereal breeding is based.

As crop improvement is a consciously directed form of evolution, it is worth remembering that all plant species, whether cultivated or not, have evolved from species and genera quite different from themselves. The capacity for change is enormous. Cereal crops have had the course of their evolution modified by man's activities since before recorded history, but only during this century have deliberate attempts been made to improve the performance of cereals based on a knowledge of inheritance. Indeed the scale of cereal breeding remained quite small throughout the first half of this century. The considerable advances achieved should, therefore, be measured against the comparatively short history of scientific breeding.

Observations of varieties in cultivation in the first half of this century show that their straw heights and life spans have both been reduced compared with more recent varieties. Furthermore, varieties released in the last decade have shown a continuing height reduction, but not at the expense of yield.

Increases in grain yield are often attributed to better husbandry, more fertilizer and easier harvests, but frequently it is the improvement in the varieties, for example stiffer straw and earlier ripening, which allows the increased yields to be secured. The effect of large seasonal fluctuations can be reduced by plotting the 5-year national means (Agricultural Statistics, H.M. Stationery Office). These are shown separately in Fig. 1 for wheat, oats and barley in Scotland and in England and Wales for the periods 1945-49 until 1972-76. With few exceptions the trends for all the curves have been continuously upwards, with the Scottish figures higher than the southern ones for barley and wheat but not for oats. There is no evidence that a limit to yield has been reached.

Improvements in quality characters have often preceded an understanding of their biology and genetics. Long before much was known about the biochemistry of these attributes breeders were successfully selecting for them in an empirical way using correlated visual characters. It is still true that the biochemistry of good malting quality is being analysed and as each new component is described it becomes possible to define the objectives in more precise terms. When the barley

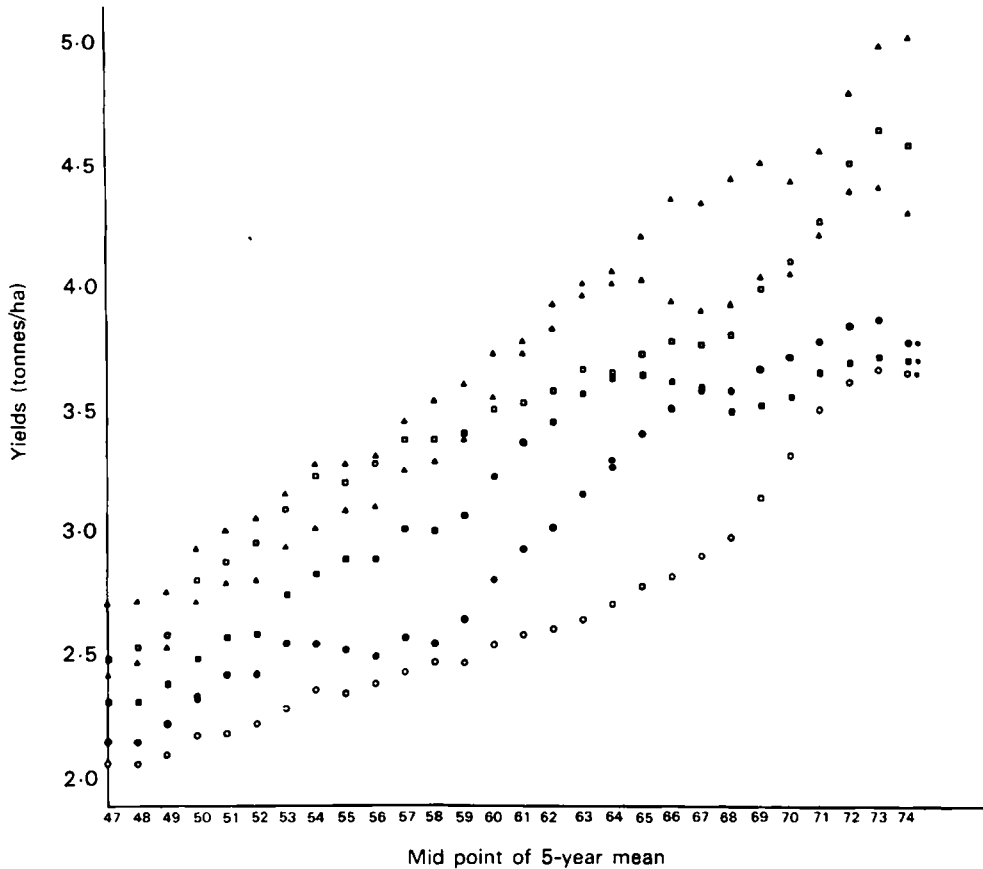


Fig. 1. Five-year mean yields of wheat, barley and oats for Scotland and for England and Wales in tonnes/hectare for the periods 1945-49 to 1972-76. Wheat: Δ Scotland, \blacktriangle England and Wales; Barley: \square Scotland, \blacksquare England and Wales; Oats: \circ Scotland, \bullet England and Wales; \bullet provisional.

variety Proctor, which set a standard for good malting quality, was being selected nearly 40 years ago, the small scale tests available to the breeder were largely confined to an estimation of nitrogen content and an inspection of the grain. Breeders now are faced with a range of enzyme and substrate components, which may add to our understanding of malting quality, but certainly increase the complexity of the model for a high quality barley.

The cereals wheat, barley and oats are largely self-pollinating and can, therefore, be maintained in a more or less homozygous condition. In this country before this century (and still in many areas elsewhere) the crops usually consisted of mixtures of inbred lines. The 'old land races' were the source of variation from which the early 'selectors' derived new varieties. By this process the demand for homogeneity increased until now the sale of seed with even minor deviations from uniformity is proscribed. This has the advantage that the quality and performance of a crop variety can be described and are, to a large extent, predictable. Interest in varietal mixtures and multiline varieties consisting of a number of components is

increasing, partly because there is some evidence that they can exploit their environment better than can pure lines, but also because, if they include a diversity of disease-resistant genes, they provide a barrier to the development of pathogens. The breeding of varieties of this kind with controlled diversity for some characters but retaining uniformity for most morphological and nutritional ones would provide a considerable extra burden. It is pertinent then to ask how important is genetic uniformity for quality characters, bearing in mind that millers' and maltsters' grists are almost always mixed and that compounders are, by definition, mixing materials.

Cereal breeding procedures

The production of a new cereal variety involves at least six distinct steps. A recognition of these is essential if discussion of future trends is to be related to practical possibilities.

(a) An objective must be defined in terms of the needs of the grower and processor (whether human or animal). Gross terms, describing yield, disease resistance and quality, are inadequate and have to be replaced, as our knowledge improves, by physiological, biochemical and ultimately genetic models. There is little information concerning the genetics of any but a few of the important physiological and biochemical characters.

(b) A model is useless unless the characteristics described in it can also be recognized. A test is required for every character which, at best, will measure the level at which it is expressed and, at worst, detect its presence or absence. Such tests may range from a simple field observation to a complex assay involving large amounts of material.

(c) Plant breeding is a procedure for assembling collections of genes and can proceed only when sources of genetic variability have been located. These may be found ready assembled amongst the constituents of an old land race or be created by either mutagenesis or hybridization. As breeding objectives become more precise, the search for genes affecting particular molecular constituents has been intensified, with, at least, some success.

(d) Selection of potentially useful genotypes must proceed by employing recognition tests for all the important characters segregating in the population. Such tests may differ from those employed in establishing the model, since the latter might have required large amounts of crop material, as, for example, in a feeding trial involving livestock. It may be possible to select for an easily estimated related character or to devise a screening method which needs only small quantities of plant material. The ultimate in this respect has been achieved with assays of enzyme activity using only half a grain, leaving the other half, containing the embryo, to grow.

(e) At each stage the choice of genotypes to be retained in the next generation is rarely simple. It may be easy to eliminate those in which the expression of some character falls below an acceptable level. A group usually remains, however, the members of which show various combinations of desirable characters. In later

generations, tests over sites and years will indicate the consistency of performance, but ultimately a breeder must resort to some kind of multivariate test to discriminate between his selections. This is frequently a matter of subjective judgement in which the merits of rival selections are weighed against each other. Statistical techniques are available and can be used but are often precluded by the time and effort involved.

(f) Finally, when a decision has been taken to proceed with marketing a particular genotype it is necessary to produce enough seed of the right quality to satisfy, firstly, the demands of legislation and, secondly, the needs of the growers. Five years are likely to be needed to complete this final stage, to which must be added between five and ten years for the earlier stages.

The addition of each new character complicates the procedure and may involve including a new parent and many unwanted characters in the programme. It will involve establishing new tests and may require the use of larger plots and more grain. It will certainly make the choice of selections more difficult. For these reasons breeders tend to work with a limited number of characters and, having established a range of varieties adapted to the locality and to the general farming system, they can then proceed to breed varieties of a more specialized kind adapted to particular farm procedures or processing methods.

Advances in nutritional quality have been slow, principally because the model has not been clearly written. In contrast the maltster, miller, brewer and baker have defined their requirements either in empirical terms (such as, that a dough ball thrown at a wall should stick) or, more recently, with regard to enzyme activities and chemical constituents. These blueprints have often been backed by the offers of premium prices or ready markets which have helped to offset the often lower yields of quality grain. There is, of course, no one definition of feeding quality but a series of models, if endorsed by nutritionists, compounders and agricultural advisers, would stimulate interest in the breeding of suitable varieties. If nutritional characters have any significance, farmers should be aware of them when choosing seed to sow.

Barley

Amongst grain characters in barley, most progress has been made with those related to the technology of alcohol production rather than nutrition. Malting quality has been progressively analysed into a series of components which suggest that any departure from a theoretical optimum quality may be due to limiting factors in the array of enzymes, or in their substrates, or to some imbalance between them. Breeders have most of the essential requirements to set up their programme: the model can be defined according to the needs of maltsters; a micro-malting test (Whitmore & Sparrow, 1957) provides a means of estimating the whole character; a number of rapid tests have recently become available which assay limiting factors. The substrates may be examined by measuring milling energy (Allison, Cowe & McHale, 1976) or sedimentation rate (Palmer, 1975) or extract viscosity (Greenberg & Whitmore, 1974; Morgan & Gothard, 1977).

Enzyme activities, particularly α -amylase and β -amylase, can also be estimated using quick tests (Briggs, 1962; Hayter & Allison, 1972; Allison & Swanston, 1974).

Both α -amylase and β -amylase exist as a number of isoenzymes which can be detected in malt using horizontal gel electrophoresis. The alleles initiating the formation of these enzymes can be handled by genetic means and studies are in progress at the Scottish Plant Breeding Station to determine their effectiveness for starch breakdown. Large numbers of varieties have been screened for their enzyme type and can be used for hybridization if need be. Malting quality is a complex character involving the structure of cell walls, the envelope of starch granules, the composition of starch and the activation, at the right moment, of the many related enzyme systems. Considerable progress has already been made and all the indications are that more will follow.

The alleles determining amylase isoenzymes can be found in existing cultivars. Increased diastatic power can also be induced and selected by a procedure which has significance for the breeding of nutritional characters. After a mutagen treatment of barley grain, Allison screened M_2 grains for their ability to germinate in the presence of abscisic acid at a concentration which restricted growth of untreated material (Hayter & Allison, 1976a). The logic of this method is that abscisic acid inhibits the effects of gibberellic acid which, itself, stimulates the enzyme activation necessary for germination. Thus only those grains with excess gibberellic acid might be expected to grow. The technique was successful and led to the production of genotypes with increased diastatic power.

Biochemical variants of nutritional importance are less well documented, apart from those affecting the lysine content of barley grains. Once the need for improved lysine levels was clearly indicated, a search of existing cultivars (Munck, Karlsson & Hagberg, 1969) isolated the Ethiopian variety, subsequently named Hiproly, and a mutation and a screening programme (Doll, K  ie & Eggum, 1974) isolated a number of mutants the best known of which is Ris   1508. The method of screening a population with an inhibitor of a natural process or an analogue of a constituent in short supply offers a valuable means of locating useful genotypes. These provide the raw material for a breeding programme and are not the end point.

The high-lysine genes function by reducing the amount of storage protein, hordein, which is low in lysine. The use of these genes, especially that in Hiproly, has given rise to difficulties in the breeding of high-yielding cultivars with satisfactory grain characters. Nevertheless, there can be little doubt that such cultivars will be produced. Care is needed in the use of chemical assays which may overestimate available lysine if the lysine-rich proteins have low digestibility (Eggum & Jacobsen, 1976). This may be the reason for the comparatively poor performance of germinated barley in animal feeding experiments, despite its increased lysine content.

Rather than search for lysine variants low in hordein it would be better to screen for mutants with higher levels of lysine-rich proteins, since these may break the

strong negative correlation which exists between the lysine content of protein and the protein content of the grain. The production of barley varieties with high diastatic power (Hayter & Allison, 1976*b*) is one way in which this might be achieved if the increase in β -amylase is sufficient. In addition to an improved amino acid balance such varieties may give higher protein yields than would conventional varieties grown under the same conditions. There have been many claims for the production of varieties giving increased protein contents, often as a result of mutation work, but few have been backed by statistical evidence that dry matter yields have not fallen proportionally. At present, the evidence for increased protein production as a varietal character is scanty in barley. It is often true that because of the negative correlation between grain yield and protein content, the highest yields of protein are given by the varieties with the highest yields and the lowest protein contents. Bansal, Srivastava, Eggum & Mehta (1977) recommend selecting for lysine or protein yields and quote figures for two barley varieties with improved protein quantity or quality, showing that they yielded about 50% more lysine per square metre than the mean of two controls.

A successful search for a particular biochemical variant was reported by Walker & Merritt (1969) who located a barley variety with increased levels of amylose in the starch. By back-crossing, this character was transferred to adapted varieties so that its effect could be studied. Unfortunately, it was then found to have little or no merit for either distilling or feeding (Ellis, 1976). Its unsuitability for malting probably results from the lack of the appropriate starch-degrading enzyme system.

Wheat

Most progress has been made with characters related to the technology of bread and biscuit making rather than to nutrition. As with malting quality in barley, components of milling and baking quality have been identified and correlated with endosperm structure and with biochemical composition. Some of these, such as milling texture, flour extraction, protein type and α -amylase activity in non-sprouted grain, are sufficiently heritable to make them straightforward to handle in a breeding programme using simple visual or mechanical screening tests. Other characters, such as the proportion of protein in the grain, are strongly affected by environment but do have a genetic component. In many seasons the protein content of British wheat is too low for making good bread and, since there is a negative correlation between grain yield and protein content, the highest yielding varieties are likely to be the worst. Wheats for biscuit making, however, are readily grown in the UK, especially in Scotland, since for this purpose lower levels of protein are preferred.

Progress towards improved nutritional quality is very limited but there are varieties which have higher protein contents than would be expected from their yields. The variety Atlas 66 is reported (Johnson, Mattern & Schmidt, 1972) to give slightly higher yields of protein and has been used in breeding programmes. Austin, Ford, Edrich & Blackwell (1977) have shown that plants of Atlas 66 and its derivative, Lancota, continue to take up N during grain filling and that this

characteristic was correlated with the maintenance of stem and leaf dry weight during the same period. This is presumably associated with the maintenance of an effective photosynthetic system. Unfortunately for the breeders of dwarf wheats with high protein content, it was also shown that height and protein uptake were positively correlated.

Oats

Relatively little attention has been given by breeders to the physical and biochemical characters of oat grains, but those related to the technology of milling have fared better than nutritional characters. Amongst temperate cereals oats are perhaps the most interesting and challenging. The grain, although slightly lower than barley in metabolizable energy, 12.0 compared with 12.9 MJ/kg (Wainman, 1976) is nutritionally slightly superior and is often regarded as a safer farm feed for livestock, particularly if animal husbandry skills are limiting.

Information on the Osborne fractions of oat protein is conflicting but the prolamin fraction appears to be low compared with wheat and barley: 4% (Ewart, 1968), 12% (Draper, 1973), 9–13% (Peterson & Smith, 1976). The major components are described by Peterson & Smith (1976) as globulin (55%) and by Draper (1973) as glutelin (69%). The differences from other cereals have significance for plant breeding since oat proteins are less deficient in lysine and their biological value is little affected by raising the N content of the grain (Eppendorfer, 1976). Improvements in either the content or yield of protein would be worthwhile.

Like wheat, oats can be crossed with a number of related species; this offers the possibility of transferring useful characters into cultivated oats. Varieties claimed to have improved protein contents have been bred using either *Avena strigosa* (Burrows, 1974) or *A. sterilis* (Lyrene & Shands, 1975), but carry a yield penalty. Despite rather low digestibility, oat proteins are of high nutritional value, especially when supplemented with other protein products such as soya flour (Graham, Baertl & Placko, 1972). If kernel protein contents reach 20% of the dry weight, fractionation into starch, gum, oil and protein becomes an economic proposition. The protein fraction would find a ready market, but research is needed into the industrial uses of the other components. This may be one situation in which protein content is more important than protein yield.

The decline in the oat acreage during the last few decades has been a world phenomenon. It is generally true that less effort has been given to the improvement of oats than of barley or wheat and that progress has been less. Breeders are confronted with a range of problems, the first of which is to keep oats competitive with the other cereals which have some advantages in straw height, grain yield, resistance to lodging, ease of harvesting and length of growing period. Some inherited characters, such as oil and kernel contents, have been neglected and the nutritional problems involved in breeding varieties with enhanced contents of the limiting amino acids, lysine, threonine and methionine, have yet to be tackled. There would seem to be good reasons to endeavour to locate genes affecting the

biochemical composition of oats and to breed varieties with enhanced food value especially for human consumption.

Physiological and biochemical characters

Morphological and other 'field' characters are also being analysed into more precise components of a physiological nature. In a recent review of physiological attributes for a wheat model, Austin & Jones (1975) list 21 characters many of which are still fairly crude and of most of which very little is known concerning their genetic control. From ever-expanding lists of this kind breeders must select characters which have a major effect on crop performance and which are amenable to large-scale screening tests. Attributes such as height and days from sowing to maturity are relatively simple although they need to be quantified in relation to environmental conditions. They can be observed or quickly measured. Factors which are basic to the plants growth, such as mitochondrial activity, photosynthetic efficiency, apical development and cytokinin production, must come to figure in the breeders' models but will be difficult to use in practice.

Of all characters grain yield is the most important and most complex because it involves so many aspects of crop growth and because it is strongly dependent on environment. It is an integrated expression of the development of the crop throughout its life and must be determined by many biochemical activities. These are rarely of sufficient magnitude to be correlated with grain yield. Lorenz (1975) found a negative correlation between yield of maize and the proportions of some amino acids. Deckard, Lambert & Hageman (1973) reported that grain yield is associated with nitrate reductase activity in leaves. These are tentative associations and will certainly be followed by more as the precision of analytical methods improves.

The future of cereal breeding must move away from the methods which, despite their achievements, have been rather crude, into a realm where the characters of model plants are written in biochemical and physiological terms. Breeders will become far more dependent on laboratory analytical methods to point the way ahead, but still need to remember that the ultimate test lies in field performance and it is in the fields that successful breeders will continue to spend the bulk of their time.

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