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Recent advances in cereal breeding

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Summary

National yields of wheat and barley have approximately doubled during the past 35 years, and comparisons of old and modern varieties of both crops, grown under conditions in which disease attack and lodging were prevented, shows that about half this yield increase is due to the work of the plant breeders. But the increase in yield has been mainly due to increases in harvest index, with little change in biomass, and there are obvious limits to the extent to which this process can continue. It is therefore necessary for breeders to select varieties with increased biomass; this may be achieved by breeding for increased rate of photosynthesis or for longer duration of photosynthetic organs. It is suggested that progress may be made by further use of the gibberellic acid insensitive *Rht* genes or by exploiting the high biomass production of triticale.

New varieties must have durable resistance to disease, but breeding for such resistance is difficult because its expression is often concealed by major genes the effectiveness of which may be short lived. A procedure for avoiding these problems is illustrated by reference to the breeding of the winter wheat Bounty.

Because of the negative correlation of protein content and grain yield in wheat, it is necessary to select varieties with grain of improved protein quality. This has been greatly helped by the development of the sodium dodecyl sulphate (SDS) precipitation test and by the use of electrophoretic analysis to identify varieties whose good grain quality is determined by different proteins, which might be combined by breeding to give transgression for improved grain quality.

Physiological analysis of winter barley varieties has shown the importance of grain size in obtaining vigorous plant establishment, and that varieties should be able to tiller adequately, even when sown late. But the further expansion of winter barley is likely to be limited by pathological considerations, largely arising because of contamination of early sown crops by ground keepers from the previous year's spring barley. Breeders should give special attention to resistance to net blotch (*Pyrenophora teres*) and the soil-borne Barley Yellow Mosaic Virus.

Refined selection techniques must be developed if the breeder is to maintain his present rate of progress. There has been little change in the basic selection techniques for many years, but there has been much improvement in breeders'

small-scale farm and laboratory equipment and in the development of computerised systems for recording and analysis of data. Use of the dihaploid techniques should ensure that new varieties of barley, and hopefully wheat, achieve the standards of uniformity and stability now required.

Techniques for transferring DNA between widely differing species will probably play a significant part in breeding technology during the next ten or twenty years. But it is difficult to identify the characters which could most usefully be transferred between species. The most suitable may be simply inherited physiological characters or those concerned with the synthesis of high-quality grain protein.

Progress in recent years has been largely dependent on collaboration with workers in other scientific disciplines, and in particular with plant pathologists and plant physiologists.

Introduction

It seems to me very appropriate that a meeting planned in memory of Dr. Feekes should start with an analysis of advances in cereal yields which have taken place during the years that Feekes was working on the crop. Since 1946, average yields of wheat in Britain have increased by approximately 2.5 % per annum, from 2.4 tonnes/ha in 1946 to 5.7 tonnes/ha in 1980. During the same period, average yields of barley have increased rather more slowly, at approximately 2.0 % per annum, that is from 2.3 tonnes/ha in 1946 to 4.4 tonnes/ha in 1980.

This period has of course seen many profounds changes in farm practice. The horse-drawn reaper and binder has been replaced by the combine harvester; and application rates of nitrogenous fertilisers have increased from a nominal 20-30 kg/ha to 150 kg/ha or more. At the same time, weed competition has been largely eliminated by the use of selective herbicides and, more recently, fungal diseases have been controlled by systemic fungicides.

But these increased yields would not have been possible if these changes had not been accompanied by new varieties, which in Britain started with the introduction, in 1953, of the winter wheat Cappelle Desprez and the spring barley Proctor, both of which occupied between 85 and 90 % of their crop areas by 1960.

Comparison of old and modern varieties

In order to obtain information on the contribution of new varieties to crop yields, and at the same time to identify directions in which new advances might be made, we have recently conducted at Cambridge two series of trials in which old and new varieties were compared. In both trials modern fertiliser rates and agronomic regimes were used; the effects of diseases were eliminated by prophylactic sprays and lodging was prevented by allowing the crop to grow through a supporting net.

The first trials compared a range of winter wheat varieties released between 1908 and 1980 (Austin et al., 1980). Yields ranged from 5.7 to 8.7 tonnes/ha (Table 1), suggesting that in the absence of diseases and lodging, modern varieties are about 50 % higher yielding than those they have replaced and that about half the increase in yield has been due to the work of the plant breeder. At the same time, straw height has been reduced from 142 to 80 cm and harvest index increased from 0.36 to 0.51 so that the total biomass of the more recent varieties is only about 10 % more than that of the older ones.

Analysis of yield components shows that the high yields of modern varieties are not due to improvement in any single yield component. Thus Norman and Maris Huntsman have greatly increased 1000-grain weight; Hobbit and Norman have increased grain number per spikelet; and Hobbit, Armada and the Talent sib have more ears per square metre. It may also be noted that the protein yield of the more recent varieties is 10 to 15 % greater than that of the older ones. This is mostly due to more efficient nitrogen uptake as there is little variation in nitrogen harvest index. This inevitably means that, when grown under the same circumstances, the nitrogen percentage in the grain of modern varieties is lower than that in the older varieties. The high protein yield of the Talent sib suggests, however, that there may be some scope for genetic improvement.

The second series of trials (Riggs et al., 1981) compared 37 spring barleys ranging from old land varieties cultivated in the nineteenth century to those most recently introduced. This showed that the genetic gain in yield was 0.39 % per year during the 100-year period considered, but this rate increased to 0.84 % per year during the last 30 years. As in the case of the wheat varieties, the yield improvement was associated with reduction in straw height, increase in harvest index, but only a small increase in total biomass (Table 2). It was again impossible to attribute yield improvement to any single yield component, though ear number per square metre was much increased in several varieties. In the case of Egmont, however, the increase in yield was due to increases in 1000-grain weight and number of grains per ear.

Requirements for further improvement in yield

It has frequently been suggested that the yield increases in recent years are unlikely to continue, though there is no evidence of any flattening off of the curves of national average yield against time. But there is clearly a limit to the extent to which grain yield can be increased by further increases in harvest index. It is unlikely that much further progress can be gained by breeding shorter strawed varieties in either wheat or barley, and I therefore suggest that breeders should first select for varieties with greater total biomass, and then amongst them for those with high harvest index.

The small increases in total biomass shown by modern varieties of wheat and barley indicate the possibility of selecting for this character. This implies selection of varieties with a higher photosynthetic rate per unit leaf area; or which allow light to penetrate more uniformly through the crop, so that the lower

Table 1. Genetic improvement in winter wheat (from Austin et al., 1980)

	Year of intro duction	Height (cm)	1000-grain weight (g)	Ears/m^2	Grains/ spikelet	Grain yield (t/ha)	Total biomass (t/ha)	Harvest index	Protein yield (t/ha)
Little Joss	1908	142	39	366	2.8	6.0	16.5	0.36	0.71
Holdfast	1935	126	33	468	2.6	5.7	15.9	0.36	0.82
Cappelle Desprez	1953	110	45	435	2.5	6.7	15.9	0.42	0.78
Maris Huntsman	1972	106	48	379	3.0	7.5	16.3	0.46	0.81
Talent sib	–	87	36	715	2.7	8.3	17.3	0.48	0.98
Armada	1978	97	39	535	2.7	7.9	18.3	0.43	0.86
Hobbit	1977	80	37	429	3.6	8.4	17.5	0.48	0.89
Norman	1980	84	48	366	3.5	8.7	17.1	0.51	0.91

Table 2. Genetic improvement in spring barley (from Riggs et al., 1981)

	Year of introduction	Height (cm)	1000-grain weight (g)	Ears/m^2	Grains/ ear	Grain yield (t/ha)	Total biomass (t/ha)	Harvest index
Chevallier	c.1880	98	38.3	585	17.8	4.6	13.9	0.33
Plumage	1900	112	40.4	481	21.4	4.5	12.2	0.37
Kenia	1932	95	38.1	524	21.1	5.1	12.6	0.40
Spratt Archer	1933	96	39.4	583	20.8	5.2	12.8	0.41
Proctor	1953	83	35.5	733	19.0	5.6	13.6	0.41
Zephyr	1966	79	38.5	703	19.4	5.9	12.8	0.46
Maris Mink	1973	65	35.2	796	18.9	5.9	12.5	0.47
Georgie	1976	72	40.8	717	18.7	6.3	12.7	0.49
Ark Royal	1976	82	34.9	774	19.6	6.3	14.2	0.44
Egmont	1980	83	43.6	566	22.8	6.9	14.4	0.47
Triumph	1980	70	37.9	800	19.2	6.7	13.3	0.49

leaves can make a greater contribution to photosynthesis; or in which the photosynthetic period is extended.

A number of workers have reported differences in rate of photosynthesis per unit of leaf area. Dantuma (1973) demonstrated a 22 % varietal variation in the maximum rate of photosynthesis of flag leaves of wheat and found a similar variation amongst barley varieties, and Aslam & Hunt (1978) demonstrated varietal differences in the rate at which photosynthesis of spring wheats declined after full leaf expansion. It was also shown by Evans & Dunstone (1970) that the rate of photosynthesis of primitive wheats and *Aegilops* spp. is greater than that of hexaploids. All these results were obtained in controlled environments with pot-grown plants, but Austin et al. (1981) measured photosynthesis of single leaves on field-grown plants, and confirmed that the rate of photosynthesis of diploid wheats was 36 % higher than that of hexaploids. They also showed that there was considerable variation amongst the diploids, the varieties with higher photosynthetic rates having thicker leaves with greater mesophyll cell surface, thus providing a marker which could be used by the breeder in making his selections.

But the performance of single leaves may differ from that of a crop canopy, because of differences in crop geometry, and especially in leaf angle, as was shown by Austin et al. (1976), who compared two closely related selections, one with erect and the other with horizontal flag leaves. They showed that the selection with erect flag leaves had a higher photosynthetic rate than that with the horizontal leaves, because the light was able to penetrate more effectively to the lower leaves, but that both gave similar grain yields, because the horizontal leaved selection translocated more carbohydrate from the stems to the developing grain.

The comparison of old and new varieties shows, however, that although most of the yield improvement of the past thirty years has been due to increasing harvest index associated with reduced straw length, there has at the same time been a slow increase in total biomass. Gale & Law (1977) showed that if random selections from the F_2 population of a cross between varieties of contrasting height are considered, there was a significant regression of grain yield on straw height, although many selections deviated widely from this regression. However, the parents in the cross they examined differed in respect of the dwarfing gene Rht_2, as well as in numerous background genes, and they were able to classify the phenotypes of the F_2 population in respect of this gene, because it is pleiotropically associated with non-sensitivity to exogenously applied gibberellic acid (Gale & Gregory, 1977). When this was done, they found that the former regression line of grain yield on straw height was replaced by two lines, for genotypes with or without the gene Rht_2, and that at any given height, plants with the gene Rht_2 outyielded those which lacked it. This, they suggested, was because gibberellic acid insensitivity of Rht_2 plants resulted in a disturbance of apical dominance, causing increased production of ear-bearing tillers and/or increased grain production per spikelet. They therefore advocated a policy of selection for 'tall dwarfs' – that is for tall plants carrying the dwarfing gene Rht_2, and I suggest that such a policy may enable the breeder to increase yield and dry matter production at the same time.

This has in fact been achieved in triticale selections recently developed at Cambridge (Gregory & Hampson, 1981). In this crop, they selected for short strawed lines, for use on fertile land, and for taller lines, for use on dry sandy soil poorly adapted to wheat. Both programmes show considerable promise, despite initial problems of poor grain filling, and have given selections which significantly outyielded the wheat control. It has also been found that the total dry matter yield, particularly of the taller selections, is very much greater than that of the wheat controls, in one case exceeding 22 tonnes/ha, when the wheat biomass was only 16 tonnes/ha (R.S. Gregory, personal communication). I suggest that breeders should select for improved harvest index in material of this type.

Breeding for durable disease resistance

A study of changes in the popularity of wheat and barley varieties between 1950 and 1970 is dominated by the expansion and decline of varieties carrying a succession of major genes for resistance to yellow rust and powdery mildew, and of the development of strains of the pathogens virulent on varieties carrying each of these genes in turn. Since the mid 1960's, breeders have appreciated the futility of exploiting major genes for resistance in this way, and have attempted instead to select for other forms of resistance. They have, for example, attempted to select varieties which are susceptible as seedlings but acquire resistance as they mature. But experiences with such varieties as Joss Cambier and Maris Bilbo have demonstrated the dangers of this procedure, and have led breeders to search for varieties which have continued to show a reasonable level of resistance after many years of widespread cultivation (Johnson, 1978; Bingham, 1981). Outstanding amongst such varieties are the winter wheat Cappelle Desprez and the spring barley Proctor, both of which have been very widely used in breeding programmes throughout Western Europe. A selection of varieties which appear to show durable resistance is given in Table 3, together with seedling and mature plant reactions of these varieties to four major races of yellow rust. The table also gives reactions of three high-yielding varieties which lack adequate resistance, and of two recently introduced varieties which it is hoped may have an adequate level of durable resistance.

The handling of durable resistance in a breeding programme presents considerable difficulty, because the possible durable resistance of many varieties may be complicated if they also carry simply inherited major genes the effectiveness of which is likely to be short lived. Much of the breeding material at the Plant Breeding Institute, for example, is 'contaminated' by the presence of the genes Yr_7 and Yr_9, derived from Clement and Talent, respectively, so that special precautions must be taken to ensure that these, and similar genes, do not interfere when selecting for durable disease resistance.

The situation is well illustrated by reference to the breeding of the winter wheat Bounty, derived form the cross Ploughman × Durin (Fig. 1). Ploughman,

Table 3. Seedling and adult plant reactions of wheat varieties to *P. striiformis*.

	Race 108 E 141 (2)		Race 45 E 140		Race 41 E 136 (3)		Race 41 E 136 (4)	
	seedling	adult	seedling	adult	seedling	adult	seedling	adult
Varieties with possible durable resistance								
Cappelle Desprez	S	R	S	R	S	R	S	R
Bersee	S	R	S	R	S	R	S	R
Maris Widgeon	S	R	S	R	R	R	S	R
Maris Huntsman	S	MR	S	R	S	MR	S	R
Flanders	S	R	S	R	S	R	S	R
Bounty	R	R	S	R	S	MR	S	R
Avalon	S	R	R	R	R	R	R	R
Varieties lacking adequate resistance								
Hobbit	S	MR	S	MR	S	MR	S	S
Hustler	S	MS	S	R	S	MS	S	R
Norman	S	MS	S	MS	S	MR	S	MR
Newly released varieties								
Fenman	R	R	R	R	R	R	R	R
Longbow	R	R	S	R	R	R	R	R

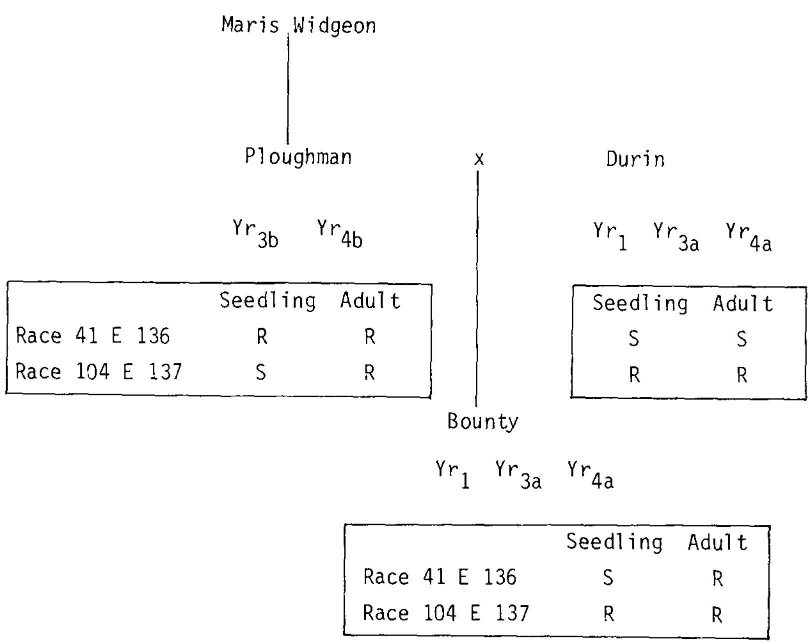

Fig. 1. Pedigree of Bounty showing genes for seedling resistance to yellow rust and reactions to two races of yellow rust (after Bingham, 1981).

which is a backcross derivative of Maris Widgeon and appears to carry its durable resistance to yellow rust, carries also the genes Yr_{3b} and Yr_{4b}, giving it seedling resistance to race 41 E 136. Durin lacks durable resistance but carries the genes Yr_1, Yr_{3a} and Yr_{4a} conferring seedling resistance to race 104 E 137. In order to obtain progeny with known durable resistance, it was necessary to select F_2 progeny showing seedling susceptibility to race 41 E 136, and to select amongst them those showing adult plant resistance to this race. Because of their seedling susceptibility these plants lack the genes Yr_{3b} and Yr_{4b}, but their mature plant resistance indicates that they are likely to have inherited the durable resistance of Ploughman. Proof that this has in fact been achieved will only be obtained after the derived variety, Bounty, has been grown for a number of years.

Combination of increased yield with good grain quality

A wheat variety which is acceptable for bread making must have grain in which the endosperm can readily be separated by milling from the pericarp and aleurone, giving flour with a high content of good quality protein. The grain must also have a low endogenous alpha-amylase content, and be resistant to premature germination at harvest.

Milling quality is a strongly heritable character, which is little affected by growing conditions and can readily be combined with high yield. Resistance to premature germination is also a heritable character, though the design of suitable testing procedures presents some difficulties, and there is no reason why the high endogenous alpha-amylase levels associated with such varieties as Maris Huntsman should not be avoided in breeding.

But protein content is negatively correlated with grain yield and is much dependent on the way in which the crop is grown. Indeed, the protein yield per hectare of modern varieties is little greater than that of varieties cultivated forty years ago (Table 1), but has been diluted by much increased yields of carbohydrate.

In order to combine high yield with grain of good quality, it has therefore been necessary to select varieties with grain protein of improved quality. An empirical assessment of protein quality can be obtained by the sodium dodecyl sulphate (SDS) precipitation test (Axford, McDermott & Redman, 1978). In this test, small samples of wholemeal flour are shaken up in a solution of SDS and lactic acid, and allowed to settle in a graduated cylinder. The solution causes the long molecules associated with good-quality protein to uncoil, forming gel-like particles of a starch-protein complex which settle much more slowly than those associated with poorer-quality proteins. The test is very rapid and is almost independent of the protein content of the sample. Only 4 g of grain are required for each test, so that estimates of quality can be obtained from part of the seed of single F_2 plants, introducing a level of precision previously unknown in breeding for baking quality in wheat.

The wheats of good bread baking quality bred at the Plant Breeding Institute are all derived from the Canadian variety Red Fife (Fig. 2), and it has been de-

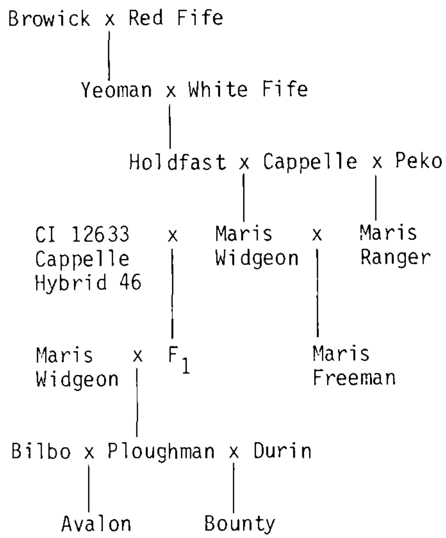

Fig. 2. Pedigrees of wheats of good bread-baking quality bred at the Plant Breeding Institute, Cambridge.

monstrated by polyacrylamide gel electrophoresis that this quality is associated with two protein bands of high molecular weight in the glutenin fractions of all these varieties (Payne, Corfield & Blackman, 1979). This raises the possibility of finding alternative good-quality varieties in which grain quality is determined by different proteins which might be combined with those already identified to produce varieties showing transgression for improved grain quality. A range of such varieties has now been identified, and their quality proteins are being combined in our latest breeding programmes (Payne et al., 1981).

The expansion of winter barley

Future advances in plant breeding are greatly dependant on integrated research in which knowledge of breeding technology and plant genetics is combined with experience in other disciplines, such as physiology and plant pathology. This is well illustrated by consideration of the expansion of the winter barley crop during the past ten years, and by the steps taken by breeders to find varieties to meet the increased demand.

Under circumstances of complete disease control, it has been found in Britain that the high-yielding 2-row winter barleys Igri and Sonja give the best yields when sown in early September, but that when sown in November or early in the New Year, these varieties yield at about the same level as good-quality malting varieties such as Maris Otter and Halcyon. More detailed investigation showed that when sown early, Igri and Sonja established rapidly and produced large ear primordia, though the number of ears per m^2 was somewhat lower than in early sown crops of Maris Otter or Halcyon. This early vigour was correlated with grain size and resulted in the very high yields of Igri and Sonja. But when sown later these varieties produced fewer tillers of which few survived to form ears and were unable to compensate for this by increased ear or grain size, so that there were no significant varietal differences in yield (Sage & Roffey, 1981).

Early sown crops of winter barley may be exposed to damage if the ear primordia are too far advanced before the onset of low winter temperatures. This was investigated by Kirby & Appleyard (1981), who compared a range of winter and spring varieties sown successively from early September. They found that the ear primordia of true winter barleys, such as Igri and Sonja, developed relatively slowly. From an early September sowing, these varieties had reached the glume primordium stage with about 45 spikelet primordia by mid December, and developed little further during the next 8-10 weeks. But spring varieties developed more quickly, so that the embryo ear was almost fully formed by mid December, and was therefore very subject to winter damage, though the less advanced ears obtained from a mid October sowing suffered little damage.

These observations help the plant breeder to define the crop ideotype for which he should select. They indicate the importance of grain size in obtaining a vigorous plant establishment, enabling the crop to take advantage of good autumn growing conditions. But the variety should be able to tiller adequately even if not sown early, and the rate of ear primordium developent must not be so rapid as to expose the young ear to excessive winter damage.

All these considerations may be of purely academic importance if due attention is not paid to the pathological problems associated with the winter barley crop. The most important of these arise from the so called 'green bridge' effect, whereby infection from ground keepers of one year's spring barley spreads to early sown plots of the next year's winter barley. It was at one time considered that the diseases most likely to be transferred in this way were powdery mildew, *Rhynchosporium* and barley yellow dwarf virus, but recent experience has shown that net blotch (*Pyrenophora teres*) may be of even greater importance, and that strains of eyespot virulent on winter barley may also be important. The problems facing the breeders undoubtedly represent a challenge which would have appealed to Dr. Feekes.

Plant pathologists in Germany, the Netherlands and Britain have taken the initiative in dealing with the powdery mildew problem by suggesting that some sources of resistance should be used by winter barley breeders alone (Schwarzbach, 1982). It is to be hoped that all European breeders will follow their lead; and that the disease may be checked by integrated control, in which chemicals are used to limit losses on varieties showing moderate levels of infection. There are however disquieting reports of forms of the fungus which are insensitive to triadimefon and it is also reported that this chemical may exacerbate losses due to net blotch.

The cost of disease control, and the need to apply insecticides to prevent the spread of barley yellow dwarf virus, has caused many farmers to think again about the desirability of growing large areas of winter barley. At the same time the spread of barley yellow mosaic virus, carried by a soil-borne saprophytic fungus, is making it impossible to grow winter barley on may farms. It thus seems that the rapid expansion of winter barley is unlikely to continue. But the crop will undoutedly be widely grown and will continue to offer many problems for joint attention by the breeder, physiologist and plant pathologist.

Improvements in the logistics of breeding

The improvements achieved in recent years in both yield and grain quality make further advances more difficult so that it is necessary for the breeder to refine his selection techniques in order to improve the precision with which he can identify the best material in his programme. Many of these changes have been associated with the introduction of better sowing and harvesting equipment or with the development of computerised systems for data recording in the field, or for recording and analysing data from yield trials. Such techniques enable the breeder to handle more material, and to make more sophisticated tests and measurements on it, but they do little to change the basic techniques of selection, which continue to be based on the pedigree and pedigree trial systems as originally described by Nilsson Ehle in 1910. The increase in scale of operations may be illustrated by reference to the winter wheat programme at Cambridge, where we normally make some 600 crosses each year, introducing where possible new genetic variability by using selections developed in breeding programmes at stations throughout the world. Up to 2000 F_2 plants are grown from each cross, giving an F_2 population of over a million plants from which we hope to obtain, after ten years of selection, one or possibly two varieties recommended for use in British agriculture.

One of the problems in obtaining such varieties derives from the need to ensure that new varieties achieve the standards of uniformity and stability required in the EEC. But many of these difficulties may be avoided in future by the use of the dihaploid technique, at present only applicable to barley, but possibly available for wheat in future. In using this technique, a new selection is crossed with *Hordeum bulbosum.* In the resultant hybrid, the chromosomes derived from *H. bulbosum* abort, giving a haploid plant, which is then treated with colchicine to give a fully homozygous diploid. The technique can be used at any stage in a selection programme, but we find it most useful to apply it to the progenies of F_2 plants which have been selected on the basis of easily observed pathological and morphological charaters. It is of course necessary to ensure that dihaploid progenies are not exposed to outpollination during subseqeunt multiplication.

Longer-term prospects

The possibility of transferring DNA between widely differing species has recieved much publicity in recent years, and we have given considerable thought to the possibilities of introducing such techniques into our programmes. We have also recently established a laboratory at the Plant Breeding Institute to study the possible use of recombinant DNA techniques for the isolation and characterisation of plant genes, and to investigate methods by which useful genes may be transferred between species or genera to provide plants with valuable new genetic properties.

There seems little doubt that these techniques will play a significant and important part in breeding technology in the next ten or twenty years. But it is not at present clear which characters can most usefully be transferred between species. Although simply inherited genes determining resistance to pests and diseases could usefully be transferred, new physiologic races of pathogen capable of overcoming such resistance could be a limitation. At the same time, such obviously valuable characters as the capacity to fix atmospheric nitrogen or to use the C_4 photosynthetic pathway are dependent on complex interacting enzyme systems, with corresponding complex genetic control which may be very difficult to handle by DNA transfer between organisms. The most suitable candidates for DNA transfer thus appear to be simply inherited physiological characters, such as the *Rht* dwarfing genes in wheat, which might be usefully transferred to barley, or genes associated with high-quality grain protein which might be transferred to wheat from alien species in the Triticinae, or elsewhere.

Conclusion

I have in this lecture attempted to review the plant breeder's contribution to the very great changes in cereal productivity which have taken place during the past thirty years, and to indicate the importance of plant pathologists and plant physiologists both in achieving these advances and in indicating the ways in which further progress can be made. The period considered covers the greater part of Dr. Feekes' work with the cereal crop, and there are few aspects of its improvement with which he has not been concerned during this time. It is therefore a pleasure to dedicate this review to his memory.

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