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PLANTS: OFF-THE-PEG OR MADE-TO-MEASURE*

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Initial pattern of plant improvement

SOMETHING LIKE 10,000 years ago our ancestors first began to adopt a settled agricultural life instead of the wandering existence they had previously followed as hunters and gatherers. Of course the change to a predominantly agricultural life must have been gradual—occurring in some areas earlier and in others later. In addition, total dependence upon the harvest of cultivated crops, rather than upon the gathered produce of untended plants of forest and plain, was probably only accomplished over an extended period. Indeed even now in Britain we have not totally abandoned the gathering of wild produce. The delicious bilberry pies cooked in local Yorkshire kitchens, from fruit picked on the Pennine moorlands, testify to the continuing usefulness of plant produce collected from the wild. Elsewhere present-day gatherers seek out blackberries, sloes, rose hips, elderberries and a host of other fruits, while the blueberry provides a national dish for our American friends. However, although we have not entirely abandoned gathering wild produce, there are now few people anywhere in the world who obtain their staple foods from the wild.

The production of food crops continues to be, as always, our most important industrial activity. The nature of this activity is determined by the kinds of crops bequeathed to us by our ancestors and by the ways in which we can modify these crops better to satisfy our needs. Some plant species more or less surrendered themselves into agricultural bondage by the freedom with which they grew in the disturbed areas round human dwellings. However, relatively few species were chosen to become crops from the profusion of nature, by the early agriculturalists. The number was limited because few species that were amenable to cultivation provided useful produce that was easily harvested and stored.

These were the plants that, in the metaphor of my title, were taken off-the-peg of nature. Immediately that they were taken into cultivation man began by unconscious selection to tailor them to fit his needs better. The mere acts of sowing and reaping are selective and, as a result of these and all the basic farming practices, genotypes better suited to the conditions of agriculture were favoured in the initially heterogeneous populations. Crop plants, more or less as we know them today, emerged from several millenia of such unintentional selection. In the process they often became so different from their wild progenitors that they were incapable of persisting out of an agricultural environment.

Selection took place not only within but also between species and some, such as *Chenopodium album* and *Polygonum lapathifolium*, were discarded and are no longer cultivated. Possibly such species were rejected because they responded inadequately to agricultural selection. Certainly plants that survived for long as crops were shaped to meet man's needs by the selective favouring of genotypes that gave more—or more certain—yields, and that were better suited to agriculture.

While the initial shaping of the genetic fabric of crop species resulted from unintentional selection —and this process is still significant in moulding crops—conscious acts of choice became significant probably quite early in the development of agriculture. Obviously we can only guess at the rigour of the selection practised by our early farming ancestors, but it seems likely that it was severe because crop plants evolved rapidly. In parts of the world where primitive forms of agriculture

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are still carried out, extreme care is apparently taken over the source and choice of seeds for the next crop. Stringent selection is possible because of the close observation of, and feel for crops. Detailed, almost individual, knowledge of his plants is feasible for a farmer working under primitive conditions in a way that the modern grower, tending large areas by machine, would find it hard to imagine. Much of the tailoring of crop plants to their present forms was accomplished in this apparently crude manner, and the more we consider the extent of the adaptation of our crops to cultivation the more must we wonder at its effectiveness.

Much more deliberate selection was carried out in the eighteenth and nineteenth centuries, especially following the spread of understanding of the theory of natural selection. From these activities selected varieties arose that were genetically purified, multiplied and widely disseminated. A good example of this process—and moreover one with a Yorkshire background—was narrated by the famous nineteenth-century selectionist S. D. Shirreff. It concerns the establishment of the wheat variety Squarehead which originated from a single prolific and high-yielding plant spotted in a field of Victoria wheat in Yorkshire in 1868 by a man called Taylor. From 1870, Squarehead was grown and sold by C. Scholey of Goole, who may in part have been responsible for its discovery. By the 1880's Squarehead had spread to Scandinavia, France, Germany, Holland and Belgium. This illustrates the way in which ease of transport enabled talented and creative selectionists—able to pick out promising variants—to exercise influence over crops well beyond their own localities. Much of the detailed shaping of the crop forms used today resulted from the efforts of these selectionists.

Finally, in outlining the history of the development of plant improvement, mention must be made of hybridization. Breeding by hybridization and selection has been carried out in many of our most important crop species for a little over 100 years. In wheat for example the first attempts at hybridization were made by Knight at the end of the eighteenth century and wheat hybrids were demonstrated at the Great Exhibition of London in 1851.

Hybridizers of cultivated plants make use of rearrangements, in the derivatives of their programmes, of the characters that distinguish the parental forms. They also look for expressions of beneficial characters that surpass those of either parent. In the segregating generations following hybridization they select, for further propagation, plants with arrays of characters that approximate to the ideal they have set themselves. This fashioning of a more acceptable pattern of plant depends upon recombination and segregation of the chromosomes of the initial parents at meiosis in the hybrids and their derivatives.

Great progress in the genetic improvement of cultivated plants has resulted from the complementary procedures of hybridization and selection and elaborate methods have been designed to increase the probability of obtaining the desired variants from such programmes. Much current plant breeding makes use of these painstaking procedures and a good deal of the steady rise in arable productivity derives from their application. However, since they are fairly well understood I will not discuss them further, concentrating instead upon some more unusual and complex approaches.

In its pursuit of more valuable cultivated forms, plant breeding is not concerned with the enunciation of new principles from nature, but—in a broad sense—with the modification of our environment; so it is not science but technology. However, it employs knowledge gained from numerous scientific disciplines, and many plant breeders are forced to apply scientific method in order to provide themselves with the knowledge necessary for the attainment of specific breeding objectives. The ever-increasing use of scientific understanding, and the employment of refined techniques derived from science and mathematics, are enabling plants to be modified in ways previously impossible. In order to help us to understand this—and to illustrate our improved capacities to make plants to fit our measurements—I will outline a few examples.

Fashioning the product

A great deal of current work on crop improvement has been stimulated by the more precise definition of the use to be made of the harvested product. Some definitions have been formulated because of extensions of the manner in which crops are used. For example we no longer simply require peas—but peas suitable for this freezing or that canning process—no longer potatoes but potatoes for crisping, for chipping and freezing and so on. This diversification in use is being met by the development of genotypes yielding products that fit the various user requirements.

Of much the most profound significance, in terms of the adjustment of crop products to user requirements, are the recent discoveries concerning the inheritance of amino acid composition in maize. In a major scientific breakthrough Mertz, Bates and Nelson,[6] of Purdue University, showed that homozygosity for either of the mutant alleles *opaque-2* (o_2) or *floury-2* has the effect of approximately doubling the lysine and tryptophane content of maize grains (Table 1). The significance

TABLE 1

AMINO ACID CONTENT OF NORMAL AND *opaque-2* MAIZE AS g/100 g OF PROTEIN[8]

Amino acid	*Normal*	*Opaque-2*
Lysine	1·6	3·7
Tryptophan	0·3	0·7
Histidine	2·9	3·2
Arginine	3·4	5·2
Aspartic acid	7·0	10·8
Glutamic acid	26·0	19·8
Threonine	3·5	3·7
Serine	5·6	4·8
Proline	8·6	8·6
Glycine	3·0	4·7
Alanine	10·1	7·2
Valine	5·4	5·3
Cystine	1·8	0·9
Methionine	2·0	1·8
Isoleucine	4·5	3·9
Leucine	18·8	11·6
Tyrosine	5·3	3·9
Phenylalanine	6·5	4·9
% Protein	12·7	11·1

of this discovery is that the low concentrations of these amino acids normally limit the nutritional value of maize to monogastric animals such as men and pigs. The nutritional advantage of *opaque-2* over normal grain is illustrated from an experiment carried out with rats by Mertz and co-workers[7] in Fig. 1. Similar benefits occurred when *opaque-2* maize was used to feed children.[9]

I am sure that in this hungry world I need not labour the advantages of removing the nutritional limitations to the usefulness of maize that are consequent upon the use of such mutants. High lysine maize stocks, with high yields, high overall protein contents and appropriate combinations of agronomic characters, are now being bred in the U.S.A. But it is in some of the under-developed countries—where malnutrition is common—and where maize is used directly as human food that the discoveries made at Purdue University will have the greatest impact. In this case making the crop measure up to our needs may be one of the most useful contributions that technology can make to the food and population problem.

As a footnote to these comments on high lysine maize it is sobering to recall that the *opaque-2*

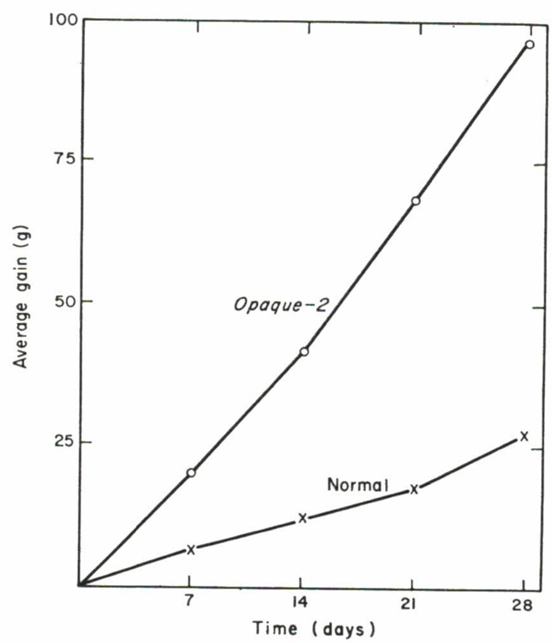

FIG. 1. A graph to show the average weekly gains of weight of rats fed on *opaque-2* high lysine maize or normal maize.[7]

and *floury-2* mutants have been known to maize genetics for about 40 years. The recognition of their true significance and potential value required the perception of Dr. Nelson and his colleagues and the availability of amino acid auto-analysers. Searches are now being made for similar genetic variants in other cereal species including the temperate cereals, wheat and barley. Success in these searches could also have profound effects in correcting disequilibria in the world's nutrition.

Indeed, breeding plants with nutritionally advantageous proportions of amino acids may be the most important detailed fashioning that our crops can undergo.

It might be interesting to consider another example of a detailed adjustment of crop products made possible by greater appreciation of the needs of the user. This concerns the oil produced from the seeds of rape (*Brassica napus* $2n=4x=38$), a rapidly expanding crop in Canada. Rape oil is used as an industrial oil, when high linolenic and erucic acid contents are valued. It also has a use as an edible oil—for margarine, shortening and salad oil—when low erucic and eicosenoic acid contents and high oleic and linoleic contents are preferred.

Little progress could be made in the adjustment of the fatty acid content of rape seed by breeding until rapid chemical methods became available that permitted large-scale screening. However, with the application of gas chromatography Downey[2] and his colleagues at the Canada Department of Agriculture Research Station, at Saskatoon, found that they could easily select for fatty acid content. Determinations were made from one cotyledon removed from the embryo and the remainder of the seed was germinated and planted. In this way the zero erucic acid variety, Canbra, was quickly established. Moreover, in Canbra, other favourable changes in fatty acid composition were the low level of eicosenoic acid and the high levels of oleic and linoleic acid contents, although selection had not been exercised directly for these components (Table 2).

Canbra, which was tailored to their needs, is now benefiting margarine and salad-oil processors.

TABLE 2

COMPARISON OF PERCENTAGE FATTY ACID COMPOSITION IN SEEDS OF RAPE (*B. napus*) VARIETIES TANKA AND CANBRA[8]

Fatty acid	*Tanka*	*Canbra*
Palmitic	3·7	4·8
Palmitoleic	0·4	0·5
Stearic	1·2	2·4
Oleic	15·7	63·1
Linoleic	15·2	19·4
Linolenic	9·3	9·0
Arachidic	0·9	trace
Eicosenoic	9·2	0·8
Erucic	44·4	0

TABLE 3

GENOTYPIC CONSTITUTIONS OF *B. napus* POSTULATED TO DETERMINE VARIOUS LEVELS OF ERUCIC ACID CONTENT[1]

% *Erucic acid*	*Genotype*
0	aa bb
9–10	Aa bb aa Bb
18–20	AA bb Aa Bb aa BB
27–30	Aa BB AA Bb
36–40	AA BB

In addition, studies of the inheritance of erucic acid content have shown that it is probably controlled by two independent loci (Table 3). Consequently, it seems that erucic acid content could be stabilized at the 0 per cent, 18 to 20 per cent or 36 to 40 per cent levels—the upper range providing oils suitable to industrial use. This example illustrates the precise adjustment of a product to the requirements of its processors that becomes possible when applied genetics is sustained by rapid methods of chemical assessment.

'Instant' crops

So far, I have emphasized the gradual nature of the evolution of crop plants and indicated the detailed refinements that can result from the activities of plant breeders. Now I would like to discuss an example where the scale both in terms of the speed and of the magnitude of change is a complete contrast. This concerns combinations of wheat with rye that have recently been interesting cerealists.

The most widely cultivated wheat species is *Triticum aestivum*—the bread wheat—an allohexaploid with 42 chromosomes. Allotetraploid wheats with 28 chromosomes, such as *T. durum*—the macaroni wheat, are also of considerable importance however. Cultivated rye, *Secale cereale*, is a diploid with 14 chromosomes and for long cereal breeders have cherished the notion of combining the high productivity, and grain quality, of wheat with the vigour and hardiness of rye. This resulted in the extensive study of 56-chromosome synthetic allo-octoploids derived from the cross, *T. aestivum* × *S. cereale*. However, in these forms the genetic complements of the parental species do not combine to operate in an integrated manner, so that despite extensive breeding work no worthwhile crop has been developed.

In the last decade interest turned instead to 42-chromosome allohexaploids derived from crosses like *T. durum* × *S. cereale*. The chromosome number of this so-called *Triticale* species is not new since it is the same as that of bread wheat. Hybridization between *Triticale* forms of independent origin, followed by selection, has resulted in the production of genotypes that are at least of sufficient merit to demand further work.

A variety of *Triticale* bred by Kiss[4] is now grown on a farm scale on the very sandy soils of the Kecskemét area of the Hungarian Plain. It replaces rye as a higher yielding cereal species, tolerant of low fertility conditions. To Kiss must therefore be given the credit of being the first person in historical times to bring a new cereal species into cultivation. In addition, however, workers at the University of Manitoba, Winnipeg, are using the hexaploid *Triticale* in breeding, and their varieties are also grown on a farm scale in southern Manitoba.

A unique interest of some workers with *Triticale* is the provision of a new type of grain from which whisky can be distilled. This is of obvious concern in regions where rye whisky is favoured, and many thousands of proof gallons of *Triticale* whisky are maturing at the present time. Proof of the whisky will be in the tasting, and seven years is a long wait, but the future of *Triticale* does not depend upon this alone. Its future will ultimately be determined by its yields relative to those of the other temperate cereals, by its hardiness, vigour and disease resistance, as well as by the quality of its grain, of which whisky flavour is only one component. However, from what I have said about *Triticale* I hope that I have demonstrated that plant breeders are not only interested in making small-scale—although very important—adjustments to existing crops, but also concern themselves in the investigation of 'instant' crops.

The up and down of chromosome numbers

In order to adjust the structure of crop plants, or to make improvement easier, the plant breeder occasionally changes their chromosome numbers. The procedures involved employ principles derived from cytogenetics and indeed sometimes partly copy situations found in nature in other species. An example of this relates to the normal condition of bananas and an artificially maintained condition of some water-melons.

The fruit of the edible banana develops parthenocarpically, failing to set seeds for a number of reasons, one of which is that the most widely grown cultivars are triploid.[14] The seedlessness of the fruit is of considerable importance in relation to the edibility of the pulp and triploidy plays a significant rôle in this character, although of course it also means that useful cultivars must be vegetatively propagated.

The water-melon (*Citrullus vulgaris* $2n=22$) is a native of tropical Africa although it is now widespread outside temperate and arctic areas. As you are probably aware, the numerous seeds do not detract from the enjoyment of eating water-melon but they can certainly make it inconvenient. It occurred to Dr. H. Kihara, of the Japanese Institute of Genetics, that this inconvenience might be removed if triploid water-melons were produced. This notion, which relies upon employing genotypes analogous to those of banana, was so successful that triploid seedless water-melons are now produced in Japan, California, Taiwan (for export to Hong Kong) and Bulgaria (for export to central Europe).

The essentials of the system employed are that seed-producing, 44-chromosome, autotetraploid stocks are produced from normal diploids by colchicine treatment. Tetraploid–diploid crosses are tested to determine which parental combinations give good triploid offspring and seed stocks of the selected parents are multiplied and grown together. Then tetraploid ♀ × diploid ♂ crosses are made on a large scale by hand-pollinations to produce seeds from which 33-chromosome seedless triploids are grown[13]. By lifting the chromosome number to the triploid level, therefore, an alteration is made that considerably enhances the product.

Breeders of other crops have found a reduction rather than an increase in chromosome number to be valuable. This applies to certain work with the potato, *Solanum tuberosum*, which is a tetraploid species with 48 chromosomes. Because of its largely autotetraploid nature, seed setting is variable and often very low in the potato. Autotetraploidy and the accompanying low fertility makes new variation that arises by sexual reproduction difficult to exploit in breeding work. However, Hougas, Peloquin and Ross[3] and their colleagues at the University of Wisconsin conceived the notion of circumventing this by reducing the potato to the 24-chromosome diploid (or polyhaploid) state. This was accomplished by making pollinations on to normal potatoes with pollen parents so marked genetically that seedlings could be recognized that derived from seeds that had developed without fertilization.

Haploids, produced in this way, in addition to displaying the simple disomic inheritance of diploids, are often vigorous and fertile. Consequently the potato can be bred as though it were a diploid and then restored to the tetraploid level by colchicine treatment if this is essential to obtain agriculturally adequate yields. However, even this is not certain, for it now appears that the potato is capable of producing acceptable yields of tubers at the 24-chromosome haploid level.[10] Reductions in polyploidy are used only rarely in manipulating plant genotypes but the work with potatoes shows that it is an interesting means of shaping some crop species.

Imported characters

Occasionally wild relatives of cultivated species have genetic attributes that it would be useful to incorporate in the cultivated form. The plant breeder's task is then to transfer this variation and so to build up crops with characters imported from foreign sources. Such characters have been widely used and have contributed real benefit to the cultivated species.

I shall describe two examples of the transfer of useful characters between species to illustrate the kinds of procedures that are used. The first concerns the garden delphinium and is chosen in part for its aesthetic qualities although it is also of real merit as an exercise in plant breeding. The garden delphinium (*Delphinium elatum*) is a tetraploid species with 32 chromosomes, and its flowers range from white to deep blue in colour. Horticulturalists have been intrigued by the notion of obtaining red or yellow delphiniums especially as there are some related species with flowers in these colours. The related 16-chromosome diploid species *D. nudicaule* and *D. cardinale* are respectively orange- and red-flowered.

The successful transfer of the red coloration of these species to garden delphinium was achieved by Dr. R. A. H. Legro[5] of Wageningen in the Netherlands. The procedure used is depicted in Fig. 2 and involved first the hybridization of *D. nudicaule* and *D. cardinale*. The chromosome number of the hybrid was doubled using colchicine to produce a synthetic allotetraploid with orange flowers. The synthetic tetraploid was crossed with the natural tetraploid *D. elatum* and selection was practised for colouring, spike-shape and so on, in the generations derived from the resulting hybrids. After five generations of selection acceptable delphiniums with red and orange inflorescence were obtained and are being described under the general name 'University Hybrids'.

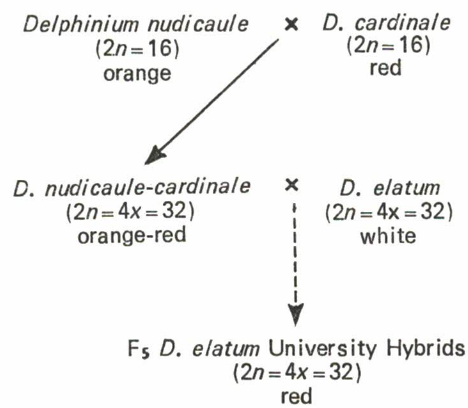

FIG. 2. The origins of the red-flowered delphiniums produced by Dr. R. A. H. Legro.[5]

The second example of alien variation transferred to a cultivated species, concerns the introduction by myself and my colleagues of disease resistance from the wild grass *Aegilops comosa* into bread wheat. One of the major diseases of wheat in western Europe is yellow rust, caused by the fungus *Puccinia striiformis*. *Ae. comosa*, a 14-chromosome diploid from the eastern Mediterranean, is resistant to this disease and our task has been to transfer this resistance to wheat.

Hybrids, between wheat and *Ae. comosa*, and their derivatives were backcrossed with wheat and rust-resistant derivatives, in each generation, were again backcrossed with wheat (Fig. 3). The out-

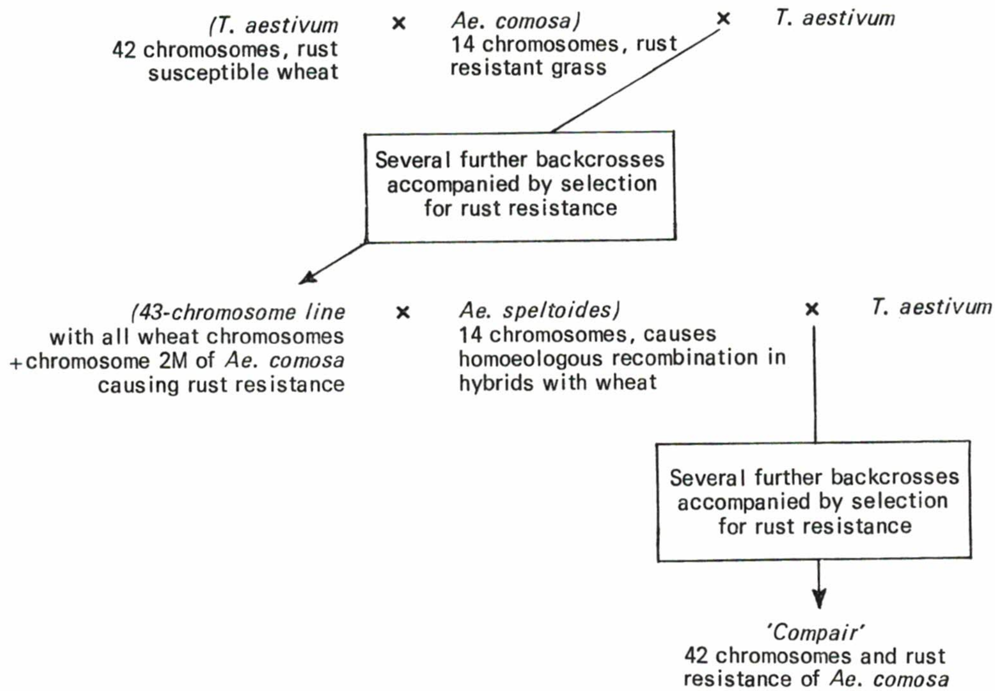

FIG. 3. The origin of the wheat form 'Compair' which has the yellow rust resistance of *Aegilops comosa*.

come of this programme was the isolation of a rust-resistant line that had the unchanged chromosome complement of wheat with, in addition, the single chromosome—designated 2M—of *Ae. comosa* determining rust resistance. From this work it could be concluded that in normal circumstances this *Ae. comosa* chromosome did not pair at meiosis and recombine with any wheat chromosome. Consequently, the region of the chromosome causing rust resistance could not be incorporated in wheat by conventional breeding methods.[12]

From our earlier work with wheat we were aware that genetically related, or homoeologous, chromosomes are prevented from recombining because of the activity of a particular gene on chromosome 5B.[11] We reasoned that, if the activity of this gene were removed or suppressed, the alien chromosome 2M would recombine with its homoeologues in the wheat complements and in this way the rust-resistance gene could be introduced into wheat. This plan was carried out using the genetic activity of another wild grass, *A. speltoides*, to suppress the activity of the 5B recombination-preventing gene. Consequently chromosome 2M, with its rust-resistance gene, was given the opportunity of recombining with wheat chromosomes.

Another backcrossing programme was carried out, again accompanied by selection for rust resistance, the outcome of which was the isolation of a line that, apart from its rust resistance, is perfectly normal wheat. Because it carries a pair of rust-resistance genes from *Ae. comosa* we call this line 'Compair'. In the construction of 'Compair', wheat parents were used that allow for a rapid turnover of generations but are not suited to farm use. However, the present situation is that 'Compair' can be easily used by breeders as a parent in the production of varieties that combine an alien form of rust resistance with other desirable agricultural properties. Thus a hole in the genetic cover of a crop has been patched with a gene from a wild species.

The plant tailor

I have discussed in outline a number of examples in which breeders have rejected the kinds of plants provided by nature or by their predecessors and have altered them to fit the needs of the grower or user. This is a technology in which success can be gained by the exploitation of understanding obtained from such sciences as agricultural botany, genetics, cytology and from plant evolution, chemistry and pathology. Important characteristics of plant breeders are the optimism to believe that a worthwhile end will result from a prolonged programme of work and the persistence to carry through the programme. To those who successfully complete programmes of the kind I have discussed, however, comes the enormous satisfaction of having adjusted a small part of nature to their wishes and to the benefit or pleasure of the world at large.

References

1. DOWNEY, R. K. (1963): 'Oil quality in rapeseed', *Can. Fd Ind. June 1963*, 1–4.
2. DOWNEY, R. K. (1966): 'Towards an improved rapeseed'. *Agric. Inst. Rev. March–April 1966*, 1–4.
3. HOUGAS, R. W., PELOQUIN, S. J. and ROSS, R. W. (1958): 'Haploids of the common potato', *J. Hered.* **47**, 103–7.
4. KISS, A. (1966): 'Kreuzungsversuche mit *Triticale*', *Züchter*, **36**, 249–55.
5. LEGRO, R. A. H. (1965): 'Delphinium breeding'. In *Genetics Today*, ed. by S. J. Geerts, vol. 2, pp. li–lv. Oxford: Pergamon Press.
6. MERTZ, E. T., BATES, L. S. and NELSON, O. E. (1964): 'Mutant gene that changes protein composition and increases lysine content of maize endosperm'. *Science*, N.Y. **145**, 279–80.
7. MERTZ, E. T., VERON, O. A., BATES, L. S. and NELSON, O. E. (1965): 'Growth of rats fed on *opaque-2* maize,' *Science*, N.Y. **148**, 1741–2.
8. NELSON, O. E. (1966): 'Mutant, genes that change the composition of maize endosperm proteins', *Fedn Proc. Fedn Am. Socs exp. Biol.* **25**, 1676–8.
9. NELSON, O. E. (1967): 'A mutant gene that influences the synthesis of protein in the endosperm of maize', *Genetica agr.* **21**, in press.
10. PELOQUIN, S. J., HOUGAS, R. W. and GABERT, A. C. (1966): 'Haploidy as a new approach to the cytogenetics and breeding of *Solanum tuberosum*'. in *Chromosome Manipulations and Plant Genetics*, ed. by R. Riley and K. R. Lewis, pp. 21–8. Edinburgh and London: Oliver & Boyd.
11. RILEY, R. (1960): 'The diploidisation of polyploid wheat', *Heredity*, **15**, 407–29.
12. RILEY, R., CHAPMAN, V. and MACER, R. C. F. (1966): 'The homoeology of an *Aegilops* chromosome causing stripe rust resistance', *Can. J. Genet. Cytol.* **8**, 616–30.
13. SHIMOTSUMA, M. (1965): 'A survey of seedless watermelon breeding and its extension in Taiwan', *Rep. Kihara Inst. biol. Res.* **17**, 46–54.
14. SIMMONDS, N. W. (1959): *Bananas*. London: Longmans.