

RECENT DEVELOPMENTS IN PLANT-BREEDING.

O. H. FRANKEL, Wheat Research Institute, Christchurch.

THE object of this paper is to review some recent trends in genetic research which clearly point to new possibilities in economic plant-breeding. It is therefore not intended to report on actual breeding results, but rather on the fundamentals of some breeding methods to be. Thus, some of this is what the Germans call "Zukunftsmusik," music of the future ; and whilst a number of economic plant-breeding stations in various countries are actively engaged in this pioneering work, in many parts of the world, and for most crops, there is still a great deal of progress in store from the utilization of the present methods of selection among natural variants or amongst progenies from varietal crosses. Again, most of this work has been carried out on other than pastoral plants, since most of these are thoroughly unsuitable for genetic experimentation : references are made later to the applicability of these new ideas to pasture-plant breeding. The lines of advance to be touched upon can be summed up as follows :-

(1) A fuller realization of the tremendous amount of variation exhibited by cultivated plants, and of the value to the plant-breeder of comprehensive collections of the natural plant resources of his crops. In 'short, we are beginning seriously to make the best of what Nature herself has provided for us.

(2) The combination in one form of characteristics borne by closely related species. Species crosses, until quite recently largely a preserve of theoretical genetics, are now becoming the foundation of large-scale breeding-schemes in the great plant-breeding institutions of the Continent, the Soviet Union, and North America.

(3) The creation of entirely *new* types--i.e., the production of new variants which are not merely selections from, or recombinations of, naturally occurring units, but which, in their chromosomal constitution or balance, are novelties in the true sense of the word. Frequently such new creations deserve and receive specific rank.

WORLD COLLECTIONS OF CULTIVATED PLANTS, AND THEIR UTILIZATION IN PLANT-BREEDING.

Comprehensive botanical surveys and collections of cultivated plants are of recent origin. Not until the work of Russian, German, and American botanists of the last ten or fifteen years became known was the average plant-breeder conscious of the tremendous scope of variation prevailing in most crop plants. Usually - h e restricted his field of vision: to local types- and to a more or less rudimentary collection of foreign forms haphazardly acquired through correspondence and exchanges with other institutions. Whilst only too many stations have not yet progressed beyond this stage, the most advanced institutions endeavour to obtain collections representing comprehensively the forms occurring in all parts of the earth. This goes hand in hand with the fullest recognition of the value of material indigenous to one's own country. But frequently it is found that desirable characteristics absent in native material are

exhibited by some foreign types. There is, for example, the resistance to frost, drought, and fungoid diseases so strongly possessed by some South American potato species which became known to the world only within the last few years. In some instances such importations may be of direct benefit, such as some Abyssinian barleys in Northern Russia ; others possess some valuable characteristics but are lacking in others, such as the highly resistant potato species mentioned above, many of which are low yielders and/or short-day plants. All the same; they may prove invaluable for crossing purposes.

One may say safely that outside Russia and the United States of America a full realization of these Possibilities has been restricted to a comparatively small number of individual stations and of individual crops. Only now are we becoming truly conscious of the fact that not only our own crop plants possess an enormous range of variation, far beyond that exhibited in our own particular part of the world, but also that those strange genera and species which we may introduce for breeding purposes are equally composite. There is no such thing as using for breeding purposes "*Triticum durum*," or "*Phleum alpinum*," or "*Solanum andigenum*," pure and simple, without preliminary trials with a comprehensive range of the multitudinous forms of these species : just as our own crops, they are highly composite conglomerations of more or less widely differing units, amongst which the most advantageous have to be selected deliberately, and not by the chance factor of obtaining a few odd forms from some collector or other.

It will be generally realized that in New Zealand so far hardly any serious attempts in this direction have been made. Whilst it may justly be claimed that in most crops, and particularly in pasture-plants, selection and hybridization amongst indigenous and other available forms will go a long way, there is every likelihood that introduction, for direct use or for hybridization, may in some instances facilitate a short-cut otherwise impossible. At the very least it would help to build up knowledge and material for further progress once the native possibilities are exhausted. I can imagine, for instance, to mention only a trivial example out of hundreds of possible ones, that some of the species of *Lolium* indigenous to the Black Sea countries, which I saw in the Leningrad Herbarium, might conceivably be useful in combination with our own types, for some of the lighter land in Canterbury.

Systematic, planned introduction is, in my opinion, a task for a systematic botanist with ecological leanings ; at the same time he should secure the co-operation of geneticists, ecologists, and plant pathologists. However, the utilization of the material is secondary to its acquisition, and this—outside the Soviet Union—is still a tortuous problem. It is to be hoped that the New Zealand initiative planned for the forthcoming Science Conference in London will lead to co-operative action on an Imperial basis.

CROSSES BETWEEN CLOSELY RELATED SPECIES.

Only a comparatively short time ago, species crossing was the preserve of fundamental genetics. None but the most advanced institutions contemplated or even started its application in economic

work. To-day it is included in the breeding-programmes of the large majority of plant-breeding institutions. In some instances—as the sugar-cane breeding in the Dutch East Indies—striking successes have already been achieved.

In crosses of the type contemplated here the parents possess similar chromosome complements, so that fertility in the progeny is either complete or very high. From the genetic point of view there is often little or no difference between this type of inter-specific cross and the varietal crosses 'within one and the same species that have been practised for over thirty years. From the plant-breeder's angle, however, they open up the possibility of combining widely different morphological and physiological characteristics. A few examples will serve to illustrate these possibilities.

Early maturity in the tomato is of course a highly desirable characteristic. *Lycopersicum racemigerum* is much earlier than *L. esculentum*, the cultivated tomato, but it has small, insignificant fruits. Attempts to combine the valuable characteristics of both these species are at present being made in Germany.

In the course of producing for the northern regions of the Soviet Union early-maturing and high-producing wheat varieties, resistant to the fungoid diseases prevalent in a wet climate, the utilization of macaroni wheats, *Triticum durum*, has loomed large. However, these are plants of a warmer and drier climate. The recently discovered *T. persicum*, with an equal chromosome number, is highly resistant to cold and wet, is also rapidly-maturing and exceedingly resistant to mildew. The attempt is now being made to combine all these useful characteristics, and, if successful, will open up for wheat-production vast areas at present barren.

The recent potato-work in Kussia has already been mentioned. A careful survey of the material which had been obtained by three research expeditions in South and Central America revealed the most promising lines amongst a material of infinite variety. But, as every plant-breeder knows, the success of any crossing-scheme depends not merely upon the parents' visible characteristics, but on their genes, which is a very different thing. Thus it is possible to obtain amongst the progeny of highly promising parents only a very small number of useful segregates. The Russians, recognizing the wisdom of having many irons in the fire, are utilizing not one or two, but a very large number of varieties belonging to several *Solanum* species, in combination with a number of the best cultivated varieties of potato. This is large-scale work in which millions of hybrid plants are at the disposal of the geneticists in charge. The Russian plant-breeders are convinced that plant-breeding, if it is to be successful, has to be conducted on a proper footing.

Large-scale breeding-schemes for the solution of difficult but economically important tasks are in progress in various countries; many among them resort to species crossing. The work at the Kaiser Wilhelm Institute, Müncheberg, near Berlin, in connection with the breeding of vines and fruit-trees resistant to fungoid and insect pests, may serve as an example of the carefully planned, long-range schemes which are a new and significant feature of modern plant-breeding.

In vines the objective is the production of varieties immune to the vine mildew (*Peronospora viticola*) and the vine louse (*Phylloxera devastatrix*), in apples and pears immunity to the *Fusicladium* disease.

In both instances, the cultivated forms do not include immune types, but such are to be found among wild relatives. Thus species crosses are resorted to, and a vast seedling-material obtained every year. These are repeatedly infected, and on each occasion any sign of disease suffices for the elimination of affected seedlings. In the course of several years' work fifty thousand immune individuals were found amongst the millions of vine seedlings treated with *Peronospora* spores. These are now being infected with the vine louse, and the doubly immune ones are taken to an institution in Western Germany, in the vine-growing districts, where further resistance tests are conducted under the ecological conditions of vine-growing. Those passing through this test are handed over to a viticultural institution, to be tested there for their viticultural characteristics, quality, flavour, &c. This work is well on the way, and with the continuous flow of increasing material the breeders are confident of final success. The *annual* expenditure on sprays to fight these vine pests is about £2,000,000 to £3,000,000, most of which will be saved in the event of success.

In apples the first generation is now coming into bearing. Disease immunity is satisfactory, but apparently the size of the fruits approximates too much to that of the wild parent. Hence back-crosses to the cultivated parent become necessary, similar to those applied in the Russian potato-work, or in our own wheat-work.

Whilst in the pasture grasses a large number of inter-specific and inter-generic crosses are on record, not many amongst them point to economic possibilities. *Lolium perenne* × *L. temulentum* (Jenkin, 1935) or *Phalaris arundinacea* × *P. tuberosa* (Jenkin and Sethi, 1932) may be quoted as examples of hybrids which can be easily obtained and the fertility of which can be restored by back-crossing to one of the parents. Jenkin suggests two economic applications of crosses between *Lolium temulentum* and *L. perenne*: (1) *L. temulentum* is self-fertile and does not exhibit loss of vigour on inbreeding, both of which characters could be usefully combined with the productive characteristics of *L. perenne*: (2) *L. temulentum* could be used as a "detector" for *L. perenne* individuals heterozygous in various characteristics.

It is highly probable that there may be other specific or generic combinations which will prove economically important. There is still a wide field for survey and research.

In the province of leguminous plants there is likely to be a field for interspecific crosses, amongst others, in the genera *Trifolium* and *Medicago*. Ufer (1933) reported on crosses *Medicago falcata* × *M. gaetula*, a species of lucerne from North Africa, the object of which was the production of a drought-resistant lucerne for poorer soils. Altogether the possibility must not be overlooked of producing, by means of species crosses, races adapted to the more extreme ecological conditions. In the clover-s, as well as in the grasses, they may provide means of radically improving some of the poorer pasture-lands in this Dominion.

ON THE ORIGIN OF POLYPLOID FORMS.

In the previous section reference has been made to recombinations of genes belonging to more or less closely related parent forms. Such work can be described as a reshuffling of existing material: it is employed to establish new and better combinations of *existing* units.

But genetic research of recent years has given us a lead on the next step—the formation of altogether new forms, with a new kind of chromosomal constitution or balance.

In an ever-increasing number of cases it has been found that in species or genera which are so widely separated that their hybrids, when produced, as a rule are sterile, sporadically a fully fertile hybrid individual appears. In every case this has been shown to be due to chromosomal reduplication. The result is an entirely new structure, with a new range of variation, and with new possibilities of development.

The classical example is that of *Primula Kewensis*. The hybrid *P. floribunda* × *P. verticillata* is completely sterile; but a single fertile shoot has been found on three occasions. Its progeny combines characteristics of both parents and breeds true. For all aspects and purposes it is a new species, called *Primula Kewensis*. Both parents and the sterile hybrid have eighteen chromosomes, but *P. Kewensis* has thirty-six. The sterility of the eighteen chromosome hybrid is due to the fact that the corresponding chromosomes of floribunda and verticillata are too different—they cannot pair in the prophase of the meiotic division. After doubling, however, each floribunda chromosome meets another floribunda, each verticillata another verticillata chromosome. Balance is reestablished, but on a different plane: the new set consists of both verticillata and floribunda components.

Similarly, from a cross between *Brassica oleracea* (the cabbage) and *Raphanus sativus* (the radish), among sterile hybrids with eighteen chromosomes arose a fertile one with thirty-six, the new form Raphano-Brassica. More fertile specific hybrids with chromosome doubling have been produced since in the genus *Brassica*, and in Russia, in Denmark, and in England at Cambridge attempts are being made to produce new economically valuable, polyploid Brassicas from this material.

Not in every case are both parents equal in chromosome number. A notable example of this kind is the cross of rye, with fourteen chromosomes, and bread-wheat, with forty-two, which as a rule produce a hybrid with twenty-eight chromosomes, which is sterile with its own pollen but fertile with wheat pollen. As far back as 1888, Rimpau produced this hybrid. However, Rimpau's plant was fertile, and its origin was not understood until less than a year ago Lindschau and Oehler found that Rimpau's hybrid did not possess twenty-eight chromosomes, as the well-known sterile wheat-rye hybrids, but fifty-six. It is curious that in the first inter-generic cross of this nature chromosome reduplication should have occurred. A similar case is recorded from Russia.

In pasture-plants two interesting examples of species formation by chromosome doubling have been recorded. The British *Phleum pratense* cannot be crossed with American *P. pratense*, but both cross with *P. alpinum*. From the cross *P. alpinum* × British *P. pratense*, a hybrid was obtained which among 500,000 flowers gave four viable seeds. These gave rise to fertile plants, fertile also with the American *P. pratense*. The explanation is this: British *P. pratense* has fourteen, *P. alpinum* has twenty-eight, their hybrid twenty-one, and the four fertile progeny plants forty-two chromosomes, the same as the American *P. pratense*. In this way a new species had been constructed, probably analogous to the American variety.

The other case of chromosome reduplication in a species hybrid was reported by Nilsson in the hybrid *Festuca arundinacea* x *F. gigantea*. Here again a new species with the doubled-chromosome number arose.

The question arises whether chromosome reduplication in species hybrids can be caused at will or whether for its appearance one has to depend on chance. Quite recently, Dorsey, by using a technique developed by Randolph in maize, succeeded in obtaining chromosome reduplication in wheat, in rye, and in wheat-rye hybrids by heat treatment. I was shown similar attempts at Svalof. Here there seems to be a hopeful new avenue. The production of polyploid parts of diploid individuals is no new idea. Jorgenson recently developed the technique of obtaining polyploid shoots from a callus tissue in the tomato. By decapitating young tomato plants it is comparatively simple to obtain a fairly high proportion of tetraploid shoots. This technique was recently applied to several Brassica species. In *Brassica Napus* tetraploid shoots have also been produced by low-temperature treatment. Altogether there are many signs that these mechanisms will be useful tools in the hands of the experimental geneticist.

Polyploidy frequently is associated with larger cell and organ size, and therefore with larger productivity. But equally important is the wider variability and adaptability usually exhibited by polyploids in comparison with their diploid relatives. This, however, is not without exception, since, for example, the cultivated barley and the sugar-beet are diploid, some of their wild relatives tetraploid, or white clover has thirty-two chromosomes, the more productive red clover fourteen. But as a rule it can be safely claimed that polyploidy has been a powerful tool for the domestication of crop plants. There is no reason why further steps in this process should not be taken deliberately under the influence of man. It is possible, for example, that in genera which so far have not developed polyploidy, such as the genus *Lolium*, undreamed of possibilities are still in store. This genus, as was pointed out by Jenkin, presumably owes its range of distribution to a large amount of gene mutation. There is a chance of great and radical improvement if polyploidy could be added to it. At the Plant-breeding Station, Svalof, a large Department has as its chief task the production of polyploid races in *Phleum*, *Dactylis*, *Triticum*, and others.

Artificial induction of mutations by means of X-rays, treatment with heat, cold, or chemicals, has produced a large array of gene mutations and structural chromosome changes in various organisms. Apart from one reported case of a specially winter-hardy form of wheat which originated in Russia, I am not aware of any "useful" new form produced in this manner. Whilst the last word has not yet been said on the possibilities of causing gene mutations, this seems to be at present a less-hopeful-line of advance than those indicated above.

To sum up : Whilst selection and hybridization with the use of indigenous material has not nearly been brought to exhaustion-point, further progress in plant-breeding is in sight through the systematic utilization of world resources, the application of species crosses, and the induction of polyploidy, with the new range of variation it offers.

DISCUSSION.

Mr. Cockayne : While Dr. Frankel was giving us this interesting *résumé* of what man is trying to do under controlled conditions (which is what Nature herself has done under more or less uncontrolled conditions), it occurred to me as

fitting that Dr. Frankel has brought up the matter of species-crossing and species-hybridizing and the development of new species, because New Zealand has been in that field for many years past, and it becomes fairly clear why that small amount of observational work that my father did in regard to species-crossing under Nature in New Zealand led to such considerable interest throughout the world. Nature has successfully and extensively carried out species-crossing in her own material and by herself. It would not be very inappropriate if in New Zealand we did develop along the same lines by human endeavour. Nature to a large extent here has shown us the way. The great institutions are showing us how it can be done under the control of geneticists, physiologists, and others, and it would be well if we did at some not distant date work along this line from the fundamental standpoint, and join up with work on a similar line that is being done in other parts of the world.

Professor Peren : I should like to congratulate Dr. Frankel. He has given an interesting and very stimulating short talk. I think that as a result of an efficient extension service farmers in this country are probably in closer touch with the scientific work than the farmers in other parts. At the same time, we must not neglect the foundation head. One does hope that as the years go by many will be found to carry out more fundamental work on our particular problems in this country.

Mr. Paton : Is it possible that during the ages through which the world has passed cosmic rays have varied both in intensity and character, and that this has had an influence on mutation and hybridization, and even in evolution itself.

Dr. Frankel . Work on plants does not yet make it sufficiently clear what are the connections between various rays and mutation.

Mr. Levy : I wish to compliment Dr. Frankel on his paper. If new plants could be introduced or new plants could be made that would fit in with certain of the ecological habitats and conditions which man can modify, there is no question that the work itself would be invaluable.
