From "Fifty Years of Genetics" Ed. by J. Jinks (suppl. to Heredity) 1969.

M. Feldman

PLANT GENETICS IN THE SERVICE OF MAN

RALPH RILEY

Plant Breeding Institute, Cambridge

Proceedings of a Symposium held at the 160th meeting of the Genetical Society on the 50th Anniversary of its Foundation. Held on 9-11 July 1969 in the University of Reading.

1. Introduction

In his inaugural lecture on election to a Professorship of Biology in the University of Cambridge, William Bateson (1908), after discussing Mendelian segregation, complementary gene action and coupling said: " Someone will say, perhaps, this is all very well as a scientific curiosity, but it has nothing to to with real life. The right answer to such criticism is of course the lofty one that science and its applications are distinct, thus the investigator fixes his gaze solely on the search for truth and his attention must not be distracted by trivialities of application. But while we make this answer and at least try to work in the spirit it proclaims, we know in our hearts that it is a counsel of perfection. . . . No practical dog-breeder or seedsman can see the results of Mendelian recombination without perceiving that here is a bit of knowledge he can immediately apply. . . .

" There is no lack of utility and direct application in the study of Genetics. . . . If we want to raise mangels that will not run to seed, or breed a cow that will give more milk in less time, or milk with more butter and less water, we can turn to Genetics with every hope that something can be done in these laudable directions."

This was the confident prediction of Bateson, the founder of this Society, within eight years of the rediscovery of the Mendelian work. My task today is to consider what has in fact been achieved in what Bateson called " these laudable directions " after nearly 70 years of genetics. Necessarily, however, my account will be episodic because of the many species with which the breeder is concerned and the numerous genotypic structures that are represented among them. Many interesting and valuable examples of genetic manipulation have had to be excluded.

2. The problem

I suppose that I need not elaborate on the dire prognostications of the demographers that are a continual spur to plant breeders and plant geneticists. It is enough to say that the present population of the world is about 3,500 millions, whereas it was 1,000 millions in 1850 and 2,000 millions in 1930. It is predicted that by the turn of the century it will have increased to 6,000 millions. Already the world calorie deficit each year is the equivalent of rather more than 30 million tons of wheat, the production of which would need something in the order of 23 million new acres of cultivated land of a fertility corresponding to that of western Europe, and it is estimated that more than half of the world's people go hungry.

Since insufficient new acres are available, the present and future deficits can only be met by improving the productivity of our present crops grown largely on the acres already in use.

Adequate and sometimes quite remarkable yield advances have been

achieved particularly in the period since the 1939-45 war. For example if we look at the yields of a few crops of Britain over this period worthwhile advances are apparent (table 1). Thus in wheat while the yield is 1946-47 was 19·1 cwts. per acre, that in 1966-67 was 31·2 cwts. per acre. Similar increases occurred in barley and oats but those in potatoes and sugar beet, while useful, were less marked.

TABLE 1

Yields in Britain of certain crops between 1946-47 and 1966-67 in cwts. per acre for wheat, barley and oats, and tons per acre for potatoes and sugar beet (from Bell, 1968)

Crop	Season			
	1946-47	1956-57	1960-61	1966-67
Wheat	19·1	24·8	28·5	31·2
Barley	17·8	24·1	25·2	28·7
Oats	16·3	19·4	20·9	24·4
Potatoes	7·1	8·2	8·6	9·7
Sugar beet	10·5	12·2	16·7	14·6

The causes of yield improvements are not of course entirely due to genotypic modification, but there is usually a genotypic component which often determines a phenotypic change that causes a more efficient exploitation of an environment improved in some way by new cultural practises. The genetic procedures employed in much of this breeding work are relatively unsophisticated, often utilising little more than segregational genetics—although its is important to emphasise that even where the genetic basis of the work is simple its conceptual framework will generally have been strongly influenced by a background of genetic knowledge.

I will give some examples from the most widely grown and nutritionally significant crops on a world scale, these inevitably are cereal species.

3. RICE

Rice (*Oryza sativa* $2n=24$) is the staple food of more than half the population of the world and ninety per cent is produced in Asia where hunger is most acute, so that the need for yield improvement is urgent. For this reason the International Rice Improvement Centre was established at Manila, jointly by the Rockefeller and Ford Foundations and the Government of the Philippines. The breeding work of the Institute was aimed at producing a variety for the wet sub-tropics that would remain erect even with the large applications of nitrogenous fertilisers that were essential to make any rapid advance in yield (Chandler, 1969). The necessity for this arises from increased lodging (falling over) that follows the use of nitrogenous fertilisers, and the direct relationship between the days before harvest that lodging takes place and reduction of yield. In the production of the most successful variety, IR 8, the aim was to combine the short strature (100 cm.) of the Formosan variety Dee-geo-woo-gen with the multi-tillering habit, vigour and disease resistance, of the tall Indonesian variety Peta (180 cm.). The genetics of the situation were very simple since the dwarfness of Dee-geo-woo-gen is determined by a recessive allele at a single locus. However,

instead of incorporating this allele by backcrossing, as would have been possible, pedigree breeding and selection were practised (fig. 1), an appropriate segregant was recognised in F_4, and by the 7th generation sufficient

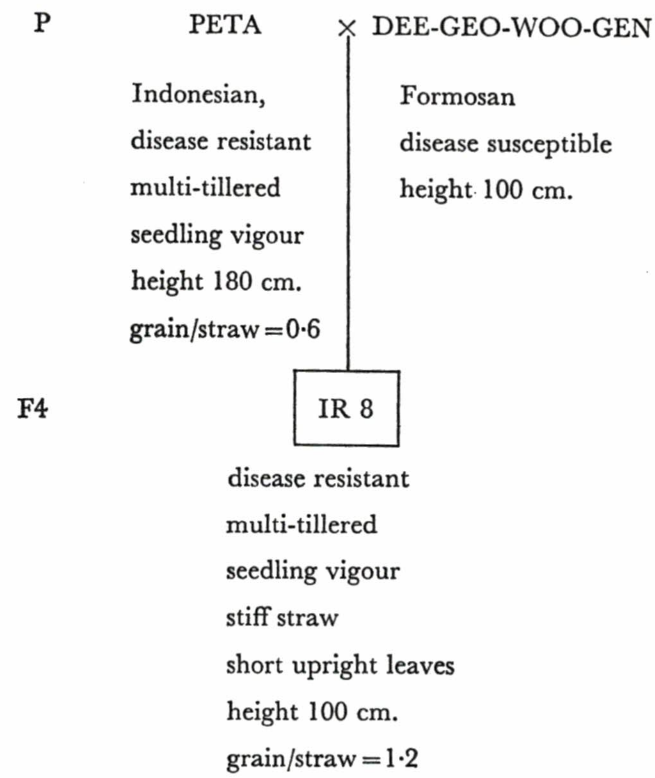


FIG. 1.—The origin of the dwarf rice IR8.

seed was available in the IR 8 lineage for yield testing, with the remarkable results shown in fig. 2. This yield advance arises not only from dwarf stature and consequential fertiliser responsiveness but also from a restructuring of the morphology of the plant so that its leaves are short and upright. This allows for quick run off of rain and in addition for the penetration of sunlight to the lower leaves. For the cloudy monsoon season crop—where performance is limited by insufficient solar radiation, this latter change may be of crucial importance (Chandler, 1969).

More progress is still necessary. IR 8 is dangerously susceptible to some diseases and its grain is unacceptable for culinary reasons to some tropical peoples. Nevertheless, a major change has resulted from simple genetic procedures and this has shown how some of the calorie deficits of the tropics and sub-tropics can be reduced.

4. WHEAT

Similarly dramatic results have arisen from the use of dwarfing genes in *Triticum aestivum* ($2n = 6n = 42$), the common bread wheat. A semi-dwarf variety, known as Norin 10, was taken to the United States from Japan soon

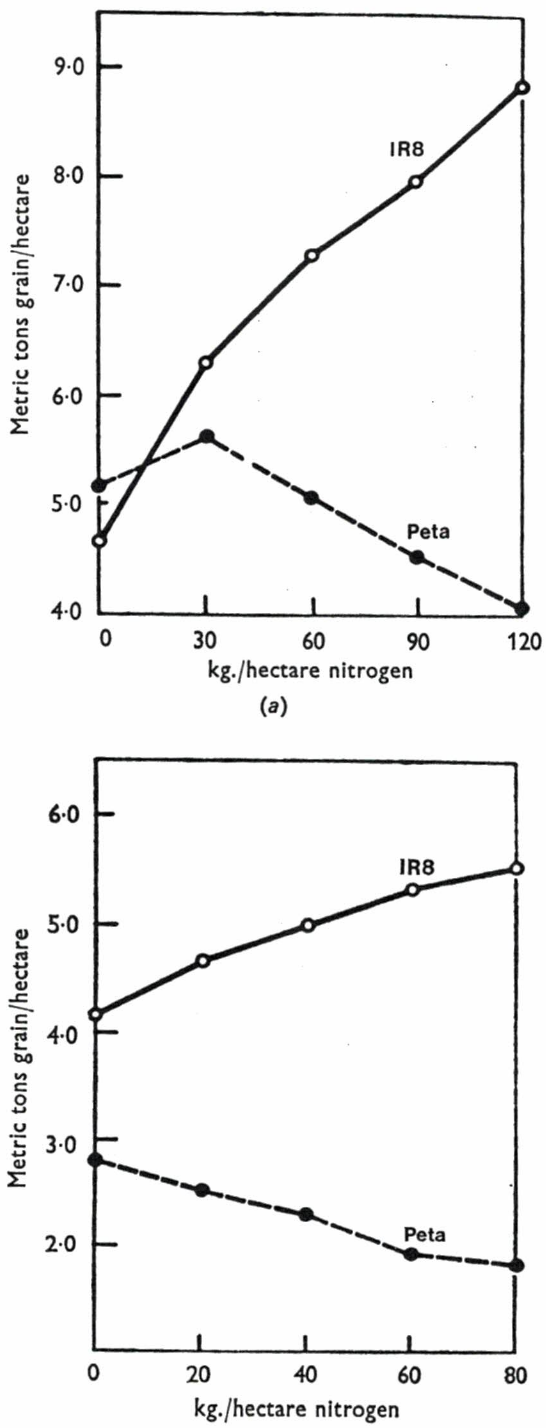
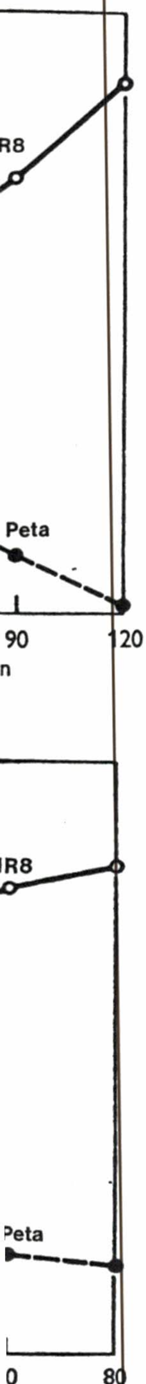


FIG. 2.—The yields of IR8 and Peta in the Philippines: (*a*) in the dry sunny season; (*b*) in the cloudy monsoon season (Chandler, 1969).

after the conclusion of the
of Washington State Unive
of Norin 10 to develop var
application without lodging
in this in that semi-dwarf,
10, are now in use in the Pa
However, more startlin
segregants of Vogel's breed
Norman Borlaug for use in
gramme in that country.
in the Mexican work togeth
appropriate disease resistanc
involving straight-forward s
his colleagues to construct g
full array of adaptive chara
I think that part of the s
himself to have been fortuit
stances. In order to speed
material were grown each
was grown on irrigated des
in Sonora State, while 10°
8,500 ft. a summer generati
City, where there is a hea
alternation of selection in
isolation of genotypes with
methods of selecting out g
devised partly under the in
An important aspect of
they are daylength neutral.
for the non-botanists. Ma
delay the initiation of flora
damaged by adverse weathe
temperatures may be nece
genotypes require vernalisa
from running up to flower
formed until the dark period
sown plants may delay flo
many wheat varieties contro
and by photoperiodic respo
have neither vernalisation n
so that they have a short ge
the year in low latitude re
shortly. In addition, it sho
causing semi-dwarfness als
number of tillers and the nu
As a result of the de
varieties, Mexico became se
exports half a million tons o
a scale. The calorie deficit
of the semi-dwarf wheats, t
and their day-length neutra



n the dry sunny season; (b) in
, 1969).

after the conclusion of the Pacific War nearly 25 years ago. Orville Vogel of Washington State University had the idea of using the semi-dwarf habit of Norin 10 to develop varieties that would tolerate high levels of fertiliser application without lodging, and so produce higher yields. He was successful in this in that semi-dwarf, fertiliser-responsive varieties, derived from Norin 10, are now in use in the Pacific Northwest of the United States.

However, more startling achievements emerged when early generation segregants of Vogel's breeding programme were transferred to Mexico by Norman Borlaug for use in the Rockefeller Foundation Agricultural Programme in that country. The semi-dwarf segregants were used as parents in the Mexican work together with a range of other forms chosen to introduce appropriate disease resistance and adaptation. Pedigree methods of breeding involving straight-forward segregational genetics, were used by Borlaug and his colleagues to construct genotypes giving semi-dwarf habits and with the full array of adaptive characteristics.

I think that part of the success of this work would be admitted by Borlaug himself to have been fortuitous, but we can learn from the relevant circumstances. In order to speed the breeding work two generations of segregating material were grown each year. A winter generation, sown in October, was grown on irrigated desert land just above sea-level at Ciudad Obregon in Sonora State, while 10° of latitude to the south and at an elevation of 8,500 ft. a summer generation was sown in May near Toluca, above Mexico City, where there is a heavy summer rain (Borlaug, 1965, 1968). The alternation of selection in such different environments has resulted in the isolation of genotypes with wide environmental adaptation. More rational methods of selecting out genotypes of wide adaptibility have since been devised partly under the influence of these results (Finlay, 1968).

An important aspect of the adaptation of the resulting varieties is that they are daylength neutral. Perhaps I should explain the meaning of this for the non-botanists. Many plants have genetic control systems which delay the initiation of floral organs until these organs are unlikely to be damaged by adverse weather conditions. Thus exposure to a period of low temperatures may be necessary before inflorescences are formed—these genotypes require vernalisation. This prevents plants sown in the autumn from running up to flower before spring. Alternatively flowers may not be formed until the dark period is of a certain minimum length, which for spring sown plants may delay flowering until night frosts are improbable. In many wheat varieties control is exercised both by vernalisation requirement and by photoperiodic response. However, the products of Borlaug's work have neither vernalisation nor photoperiodic requirements to delay flowering so that they have a short generation time and can be sown in any month of the year in low latitude regions. I will return to the significance of this shortly. In addition, it should be noted that genes introduced with those causing semi-dwarfness also appear to enhance yield by increasing the number of tillers and the number of flowers in each spikelet.

As a result of the development of fertiliser-responsive, semi-dwarf varieties, Mexico became self-sufficient in wheat in 1956. Presently Mexico exports half a million tons of wheat per annum, perhaps on too considerable a scale. The calorie deficits are being diminished. The success in Mexico of the semi-dwarf wheats, their wide adaptability of which I have spoken, and their day-length neutrality, led to their being tested in many other low

latitude wheat-growing areas. With minor genotypic adjustment to incorporate resistance to local diseases they have proved to be suited to the North African countries, to Egypt and Turkey and Afghanistan, but particularly to India and Pakistan, where their introduction has been pursued most actively. Truly remarkable yield increases have resulted. West Pakistan

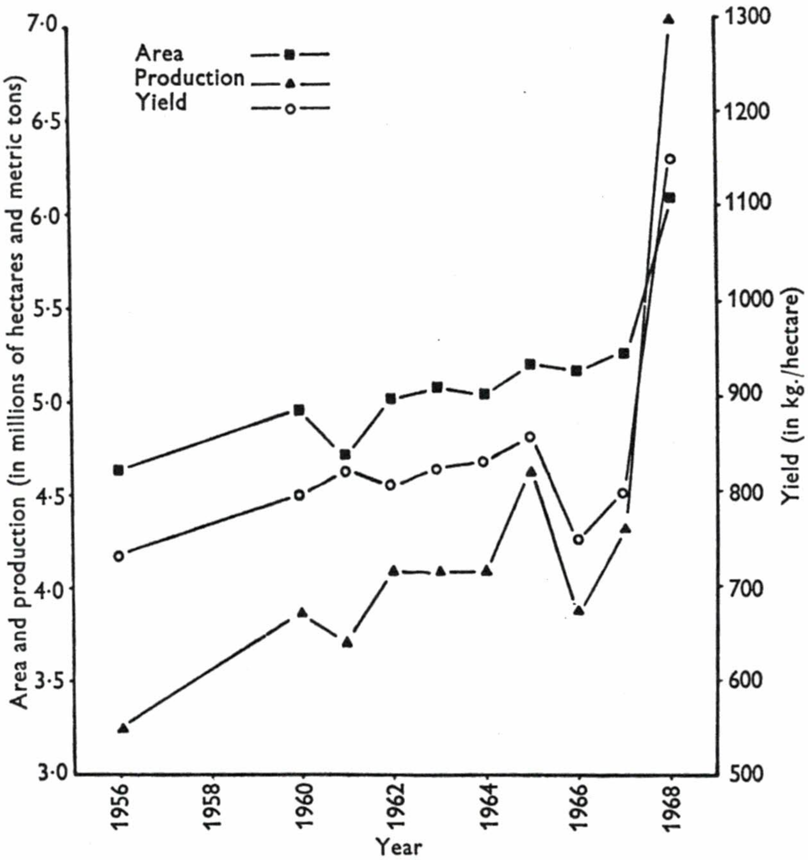


FIG. 3.—Yield, area cultivated and total production of wheat in West Pakistan (Borlaug, 1968).

became self-sufficient in wheat in 1968 (fig. 3), while forecasts of self-sufficiency for India set the date as 1972 (fig. 4). The impact of the day-length neutral, rapidly maturing, wheats is greater than would appear even from these data, since their short life cycle allows regularly for double and sometimes for triple cropping in the course of a year (wheat-rice, wheat-maize, wheat-sorghum, or wheat-mungo beans-maize).

As an aside here it might interest you to contemplate what will be the effect of the exploitation of these new genotypes of wheat and rice in the Peoples Republic of China. While we will all welcome the easing of the burden on the people of China, we can only guess at whether the resulting surplus of productive capacity will cause an increase or a reduction in the competitive attitude to international affairs of their rulers.

Apparently, however, th
a time against population
contribution to this in the

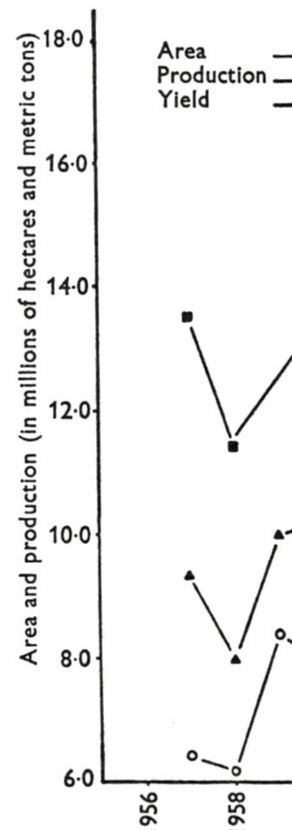


FIG. 4.—Yield area cultivated

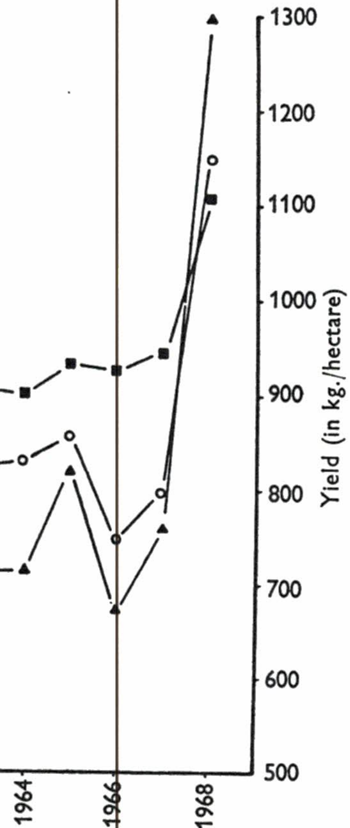
the finesse of quantitative
such characters as height,
insect resistance, that cour
previously limited.

In much crop genetics
resistance to prevailing p
This is because without s
crop would often not have
genetics of disease resistan
in the maintenance of food
interactions of host and pa

I will discuss the relat
and certain fungal pathog

D

or genotypic adjustment to incor-
e proved to be suited to the North
and Afghanistan, but particularly
oduction has been pursued most
es have resulted. West Pakistan



al production of wheat in
g, 1968).

(fig. 3), while forecasts of self-
fig. 4). The impact of the day-
greater than would appear even
allows regularly for double and
e of a year (wheat-rice, wheat-
ans-maize).
o contemplate what will be the
otypes of wheat and rice in the
l all welcome the easing of the
y guess at whether the resulting
n increase or a reduction in the
of their rulers.

Apparently, however, there are prospects that the line may be held for a time against population advance, but it may be noted that the genetic contribution to this in the primary crops, wheat and rice, has not been by

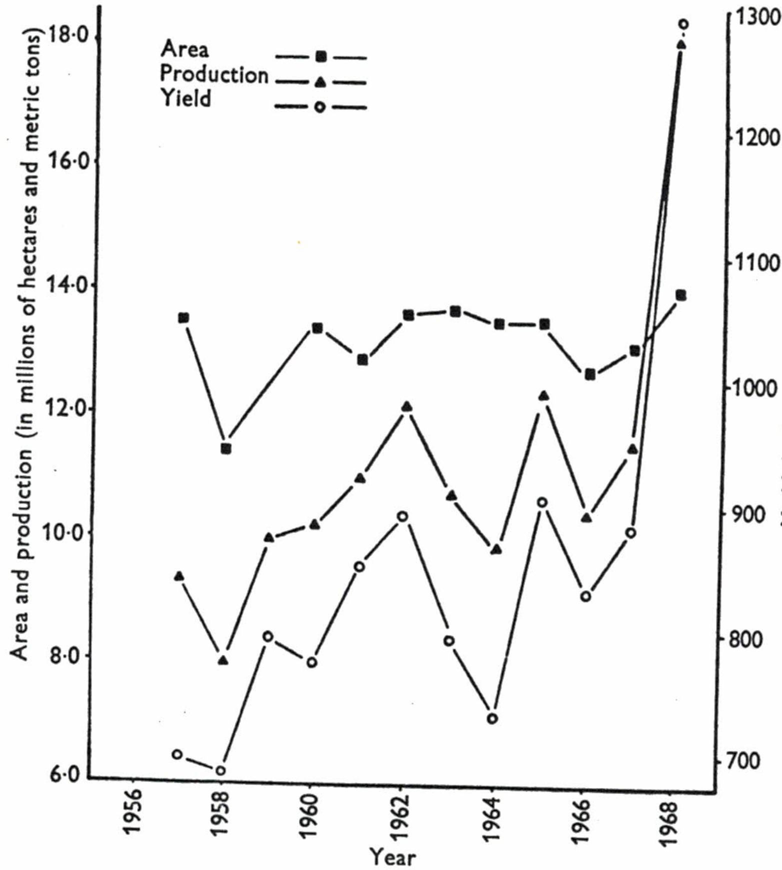


Fig. 4.—Yield area cultivated and total production of wheat in India (Borlaug, 1968).

the finesse of quantitative genetics but by the assembly of genes, affecting such characters as height, maturity time, plant morphology, disease and insect resistance, that counteract environmental factors by which yield was previously limited.

5. Disease resistance

In much crop genetics the modification of the crop genotype to confer resistance to prevailing pathogens has assumed paramount importance. This is because without such resistance continuance of cultivation of the crop would often not have been possible. To crop geneticists, however, the genetics of disease resistance is of great interest not only for its significance in the maintenance of food supplies but also because the genotype-genotype interactions of host and pathogen are intellectually intriguing.

I will discuss the relationships as they exist between the cereal species and certain fungal pathogens, but the models by which the relationships of

host and pathogen are described derive from the work of Flor (1956) on flax and the rust disease of flax. The most significant diseases of cereal species are the rusts and mildews caused by attacks of fungal pathogens. Even when every effort is made to minimise their effectiveness, significant losses arise from these diseases. For example in 1954 stem rust of wheat caused yield losses worth 250 million dollars on the Canadian prairies, while as recently as 1966 the loss of 100 million dollars worth of yield resulted from leaf rust in the same regions (Knott, 1967). Powdery mildew of wheat has been estimated to reduce yield by up to 13 per cent. and yellow rust by between 8 and 20 per cent. in Britain. Thinking in terms of the major food crops, and on a world scale, you can visualise how much food we are losing by fungal depredations.

The form of resistance most commonly exploited by wheat breeders depends upon the presence of major genes. There is allelic variation causing susceptibility or resistance in the host and corresponding allelic variation causing virulence or avirulence in the pathogen (table 2). Usually, but not

TABLE 2

Model to illustrate the relationship between alleles for resistance (R) or susceptibility (r) in the wheat host and alleles for avirulence (V) or virulence (v) in a fungal pathogen (after Knott, 1967)

Host genotype	rr	rr	RR	RR
Fungal genotype	vv	VV	vv	VV
Host reaction	SUSCEPTIBLE —no host resistance	SUSCEPTIBLE —no host resistance	SUSCEPTIBLE —host resistance allele but no interacting fungal allele	RESISTANT —host resistant and interacting fungal allele

invariably, resistance and avirulence are dominant. Consequently the resistance reaction is thought to derive from an interaction of gene products of the dominant alleles. All other relationships between host and pathogen lead to a susceptibility reaction (Knott, 1967).

By and large, by continually introducing new alleles for resistance, cereal breeders have been able to keep the one necessary step ahead of the pathogens (table 3). However, the situation is often desperate. There have, for example, been two major modifications in the genotype of the yellow rust

TABLE 3

Model to illustrate the co-evolution of wheat host and fungal parasite based on two genes in the host and two genes in the fungus. The change in wheat genotypes may result from the introduction of successive varieties (after Knott 1967)

	Initially	Evolutionary change in			
		Host	Pathogen	Host	Pathogen
Host	$r_1r_1r_2r_2$	$R_1R_1r_2r_2$	$R_1R_1r_2r_2$	$R_1R_1R_2R_2$	$R_1R_1R_2R_2$
Pathogen	$V_1V_1V_2V_2$	$V_1V_1V_2V_2$	$v_1v_1V_2V_2$	$v_1v_1V_2V_2$	$v_1v_1v_2v_2$
Host reaction	SUSCEPTIBLE	RESISTANT	SUSCEPTIBLE	RESISTANT	SUSCEPTIBLE
Selection pressure upon	Host	Pathogen	Host	Pathogen	Host

fungus in the last few years in Britain. For about 10 years prior to 1966 the relationship of host and pathogen was stable but in that year a new pathogen genotype known as race 60 became widespread and devastating on certain host genotypes while in 1968 a further rust-race—race 58—arose which was capable of overcoming a resistance allele that had previously been effective. Many have advocated that new resistance genes should never be released singly so that the improbable double modification of the fungus would be necessary to surmount the resistance of the host. However, this is a counsel of perfection and few breeders have the self-restraint necessary to keep a newly discovered resistance gene in the glasshouse until a further new one is discovered with which it can be combined. In addition, this procedure would require an obligation on all subsequent breeders never to separate the two new genes for resistance from each other.

There is at present considerable disenchantment with the major gene form of race specific resistance. Many breeders are scrambling aboard the band wagon that carries the notion that the so called " horizonal " or " generalised " resistance might provide a more stable and permanent solution. As generally discussed, horizontal resistance results from the activities of numbers of genes and may not totally preclude but strictly limit the extent of infection. In practise this type of resistance has been used in few crops and efforts to employ it are going to involve a considerably greater component of population genetics in resistance breeding than has been present hitherto.

6. Duplications

Discussion of breeding for disease resistance gives me the opportunity to mention the problems that arise when it is necessary to have a locus duplicated. This situation may occur for example in inbreeding crops at loci giving disease resistance. If one allele gives resistance to a particular fungal genotype and an alternative allele gives resistance to a different genotype, then no normal homozygote can provide resistance to the full range. A solution to this and similar problems was suggested by Gopinarth and Burnham (1956).

Two interchange stocks must be available in both of which interchange has occurred between the same two chromosomes so that the segment between the different breakpoints includes the region in which the disease resistance locus is situated. Each stock must carry a different allele at this locus. In the F_2 from hybrids between these stocks segregants will occur which are homozygous for both the alleles—that is to say in which the locus is duplicated (fig. 5). If the duplicated segments are sufficiently small so that they do not interfere with meiotic pairing and the related deficiency is trivial in effect the resulting line will be stable for a wider range of resistance than would normally be possible in a homozygote.

Work is in progress to duplicate mildew loci resistance in barley in this way, but we have not yet had the opportunity of examining products with duplications, though material of this type has been developed for other loci.

7. Alien resistance

This consideration of a form of chromosome manipulation in barley leads me to other kinds of manipulation that have been used for disease resistance-

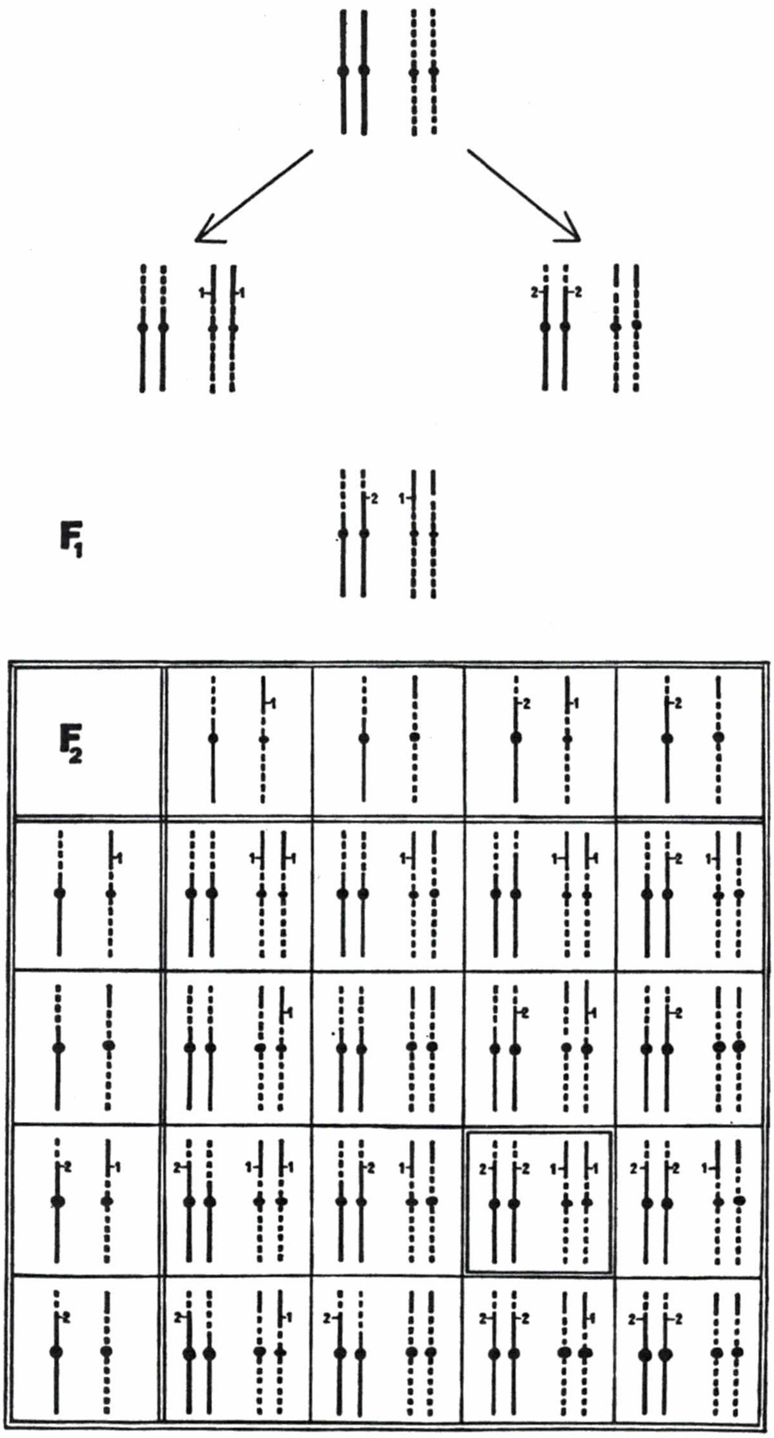


Fig. 5.—The origin of duplicated segments by segregation from interchange heterozygotes carrying different interchanges between the same two chromosomes. The alternative alleles at the locus to be duplicated are labelled 1 and 2 in this model.

loci in wheat. For a c
introduce into the wheat
variation of species in t
and *Haynaldia*. Althoug
resulting hybrids, there is
and of the other parent, c
useful alien genes cannot
somes.

However, it has lon
initiated from the syntheti
to add single pairs of a
chromosomes of wheat (R
of the University of Misso
useful segments of such a
to wheat chromosomes.
alien chromosome, produ
to X-rays or fast neutron,
of the alien chromosome c
to a wheat chromosome.
some backcrossing to clea
segment is made homozy

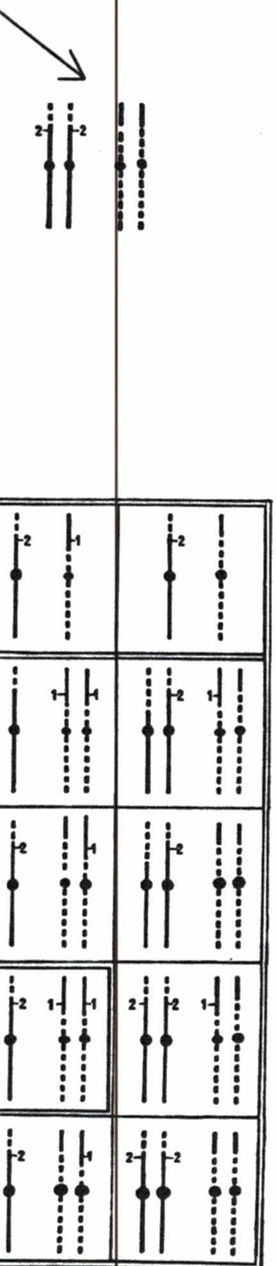
In the first use of thi
chromosome 6B a segmen
ance to leaf rust. The fi
released from Purdue Un
that its name is " Riley 6

Other useful applicati
made by Driscoll (1968)
wheat and by Aristeo Aco
wheat. The stem rust resi
to wheat breeders. Ra
contribution to the limita

8. Alien charac

Subsequent to the int
Sears, other genetic knowl
and potentially superior m
recall that the need for in
of the chromosomes of ali
chromosomes in appropria
pairing in wheat is regula
the long arm of chromosom
(or homoeologous) chrom
from synapsing with each
logous partners (Riley an
removing chromosome 5B
locus, or by forms of ge
situations in which homoe

We reasoned that, if th



n from interchange heterozygotes
o chromosomes. The alternative
l 2 in this model.

loci in wheat. For a considerable period attempts have been made to introduce into the wheat crop agriculturally useful components of the genetic variation of species in the related genera, *Secale* (rye), *Aegilops*, *Agropyron* and *Haynaldia*. Although wheat can be crossed with these species, in the resulting hybrids, there is normally no synapsis of the chromosomes of wheat and of the other parent, consequently recombination does not take place and useful alien genes cannot be transferred straightforwardly to wheat chromosomes.

However, it has long been possible by simple backcross procedures, initiated from the synthetic amphidiploid between wheat and another species, to add single pairs of alien chromosomes to the normal complement of chromosomes of wheat (Riley and Kimber, 1966). It was E. R. Sears (1956), of the University of Missouri, who suggested and applied methods by which useful segments of such an alien addition chromosome could be transferred to wheat chromosomes. The system used is to expose wheat plants with an alien chromosome, producing a beneficial modification of the phenotype, to X-rays or fast neutron, and so to induce interchanges in which a segment of the alien chromosome carrying an agriculturally useful gene is transferred to a wheat chromosome. It may then, of course, be necessary to carry out some backcrossing to clean up the background, after which the introduced segment is made homozygous and is available for agricultural exploitation.

In the first use of this procedure, Sears (1956) introduced into wheat chromosome 6B a segment of a chromosome of *Ae. umbellulata* causing resistance to leaf rust. The first variety in agriculture to use this resistance was released from Purdue University two years ago. I cannot resist telling you that its name is " Riley 67 ".

Other useful applications of radiation induced interchanges have been made by Driscoll (1968) in transferring leaf rust resistance from rye to wheat and by Aristeo Acosta in transferring stem rust resistance from rye to wheat. The stem rust resistance of Acosta's material is still the best available to wheat breeders. Radiation cytology is, therefore, making a useful contribution to the limitation of yield losses in one of the staple food crops.

8. Alien characters introduced by abnormal meiotic recombination

Subsequent to the introduction of the induced interchange system by Sears, other genetic knowledge became available which provided alternative and potentially superior methods of achieving the same objective. You will recall that the need for inducing interchanges arose because of the failure of the chromosomes of alien species to synapse and recombine with wheat chromosomes in appropriate hybrids. In 1957 we discovered that meiotic pairing in wheat is regulated by what we now know to be a single locus on the long arm of chromosome 5B, in such a way that genetically corresponding (or homoeologous) chromosomes of the different genomes are prevented from synapsing with each other—synapsis being confined to fully homologous partners (Riley and Chapman, 1958). However, it is possible by removing chromosome 5B, by using lines carrying mutants of the critical locus, or by forms of genetic interference with its activity, to produce situations in which homoeologues will synapse and will recombine.

We reasoned that, if the activity of chromosome 5B is responsible for the

normal absence of recombination between corresponding homoeologous chromosomes of the different genomes of wheat, then maybe the same activity is also responsible for the failure of synapsis and recombination between the chromosomes of wheat and those of other species that can be put together with wheat chromosomes in hybrid genotypes. Tests proved this to be correct and so the way was opened to transfer alien variation to wheat by recombination (Riley and Law, 1965).

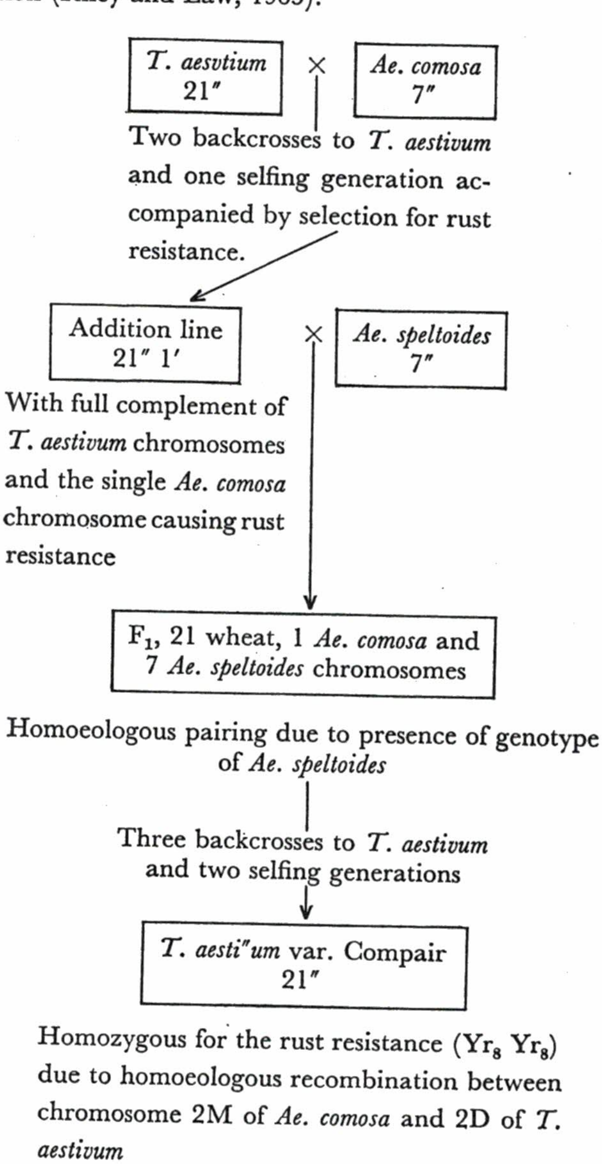


FIG. 6.—The origin of the breeders' variety of wheat " Compair " (Riley, Chapman and Johnson, 1968).

The first product of homoeologous wheat-alien recombination (fig. 6) is the breeders' variety " Compair " in which a segment, causing yellow rust

resistance, has been recon
mosome 2M of the wild g
Johnson, 1968). Interfer
logues was produced by t
dominant to the normal a
gene for yellow rust resista
crops in Western Europe,
of knowledge of the genet
contributing to the alleviat
the genetic control of mei
genetic variation can nov
indeed obtaining advanc
sources.

I cannot discuss the a
Zea mays, in many ways the
Maize follows only wheat
million acres) and in annu
indeed sometimes almost t
people, principally of Cent

The story of yield adva
genetics and represents pe
theory to the direct impro
ment by the removal of l
produce double-cross hybr
present there is a shift aw
Corn Belt. The availabilit
paid to the cultivation of
reducing costs and resulti
Moreover, when single and
generally appear with bett
John Lonnquist that in son
than 40 per cent. of the acr

But this is not the only
the crop, since there is cur
or the products of recurre
may be either simply pheno
combining ability, or on re

By all of these methods c
in North America and Easte
situations genotypic upgrad
The Centro International
relies primarily on a form o
selection to produce populat

10.

However, the aspect of m
found influence on human w

resistance, has been recombined on to chromosome 2D of wheat from chromosome 2M of the wild grass species *Aegilops comosa* (Riley, Chapman, and Johnson, 1968). Interference with the restriction of synapsis to full homologues was produced by the use of *Aegilops speltoides*, a species with an allele dominant to the normal allele on wheat chromosome 5B. The " Compair " gene for yellow rust resistance, Yr_8, is now being incorporated in agricultural crops in Western Europe, Mexico, India and Australia, so that a product of knowledge of the genetics of meiotic chromosome behaviour will soon be contributing to the alleviation of crop losses. Moreover, by interference with the genetic control of meiotic pairing a vast range of potentially useful new genetic variation can now be employed in wheat improvement. We are indeed obtaining advances in yielding ability from the most surprising sources.

9. Maize

I cannot discuss the application of plant genetics without reference to *Zea mays*, in many ways the plant species which is best understood genetically. Maize follows only wheat and rice both in the area planted (about 250 million acres) and in annual production of grain. Moreover, it is the prime, indeed sometimes almost the only, source of nutriment of about 200 million people, principally of Central and Southern America.

The story of yield advance in maize is part of the history of quantitative genetics and represents perhaps the most effective contribution of genetical theory to the direct improvement of yielding ability as opposed to improvement by the removal of limiting factors. The employment of inbreds to produce double-cross hybrids showing marked heterosis is well known. At present there is a shift away from the use of double-cross hybrids in the Corn Belt. The availability of more vigorous inbreds and the greater care paid to the cultivation of crops for the production of single-cross seed are reducing costs and resulting in a shift towards the use of single crosses. Moreover, when single and double crosses are compared some single crosses generally appear with better yields than any double cross. I am told by John Lonnquist that in some of the northern tier of Corn Belt States more than 40 per cent. of the acreage is sown with single crosses.

But this is not the only kind of change in the genotypic composition of the crop, since there is currently some inclination to use synthetic varieties or the products of recurrent selection cycles. These recurrent selections may be either simply phenotypic, or depend upon tests of general or specific combining ability, or on reciprocal tests of combining ability.

By all of these methods corn production has been increased tremendously in North America and Eastern Europe, but in less sophisticated agricultural situations genotypic upgrading of the plant population is less advanced. The Centro International de Mejoramento di Maiz y Trigo in Mexico relies primarily on a form of synthetic resulting from convergent-divergent selection to produce populations with wide adaptability.

10. Maize amino acids

However, the aspect of maize genetics that may well have the most profound influence on human welfare concerns the changes caused in the amino

acid content of the endosperm of the grain following certain allelic substitutions. It has been estimated that 120 million metric tons of protein are consumed annually by the human population of the world, of this 75 per cent. is derived directly from plants and 60 per cent. from cereal species. But because the amino acid composition of these cereal proteins does not coincide with the amino acid composition of our body tissues their overall nutritional value is limited. The essential amino acid that is in relatively low proportion in cereal protein, compared with human body tissue protein, imposes a limit on the nutritional value of the total intake of all amino acids. In cereal grain protein the first three nutritionally limiting amino acids are lysine, methionine and threonine, in that order.

A genetic means of improving the nutritional value of maize grain protein became apparent from discoveries by Mertz, Bates and Nelson (1964) of Purdue University (see also Nelson, Mertz and Bates, 1965). They showed that maize grain which is homozygous for either of the recessive mutants *opaque 2* or *floury 2*, which were first described by Emerson, Beadle and Fraser (1935), has about twice the lysine content of normal maize genotypes (table 4). This depends in part upon the higher proportion of alcohol insoluble glutelin proteins relative to alcohol soluble zeins.

TABLE 4

Amino acid content of defatted endosperm of a normal and two mutant genotypes of maize
(Nelson, Mertz and Bates, 1965)

Amino acid	Genotype		
	Normal	*opaque 2*	*floury 2*
Lysine	1·6	3·7	3·4
Tryptophane	0·3	0·7	0·9
Histidine	2·9	3·2	2·4
Arginine	3·4	5·2	4·3
Aspartic acid	7·0	10·8	10·9
Glutamic acid	26·0	19·8	20·6
Threonine	3·5	3·7	3·6
Serine	5·6	4·8	5·3
Proliine	8·6	8·6	10·0
Glycine	3·0	4·7	3·7
Alanine	10·1	7·2	8·6
Valine	5·4	5·3	5·6
Cystine	1·8	0·9	1·6
Methionine	2·0	1·8	3·4
Isoleucine	4·5	3·9	4·2
Leucine	18·8	11·6	13·9
Tyrosine	5·3	3·9	4·7
Phenylalanine	6·5	4·9	5·4

Feeding trials with monogastric animals show greatly increased growth rates when normal maize is replaced by *opaque 2* maize in the diet (fig. 7). In addition it has been shown that *opaque 2* maize provides a better balanced human diet than normal maize. Dr Alberto Pradilla, of the Universidad del Valle, in Columbia, has shown that children brought to his clinic with the acute protein deficiency syndrome " Kwashiorkor " recovered completely on diets in which all the protein was supplied by *opaque 2* maize. Consequently,

there is every reason to
those elements of South
maize can be removed b
assuring to learn that unl

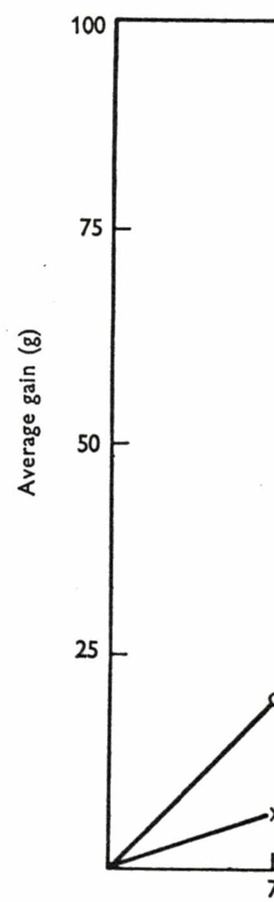


FIG. 7.—Weight-gain of weanl

hybrids will be available
zygous *opaque 2* double-cr
umbia in 1970.

You will not be surpri
America, such as the Ind
long exploited floury type
hausen, 1966). One of th
many parts of South and
and flinty maize genotyp
susceptibility in storage to
ever, these relatively lysin

there is every reason to hope that the nutritional deficiencies suffered by those elements of South American society that depend almost entirely on maize can be removed by the use of *opaque 2* or *floury 2* genotypes. It is reassuring to learn that unlimited supplies of homozygous *opaque 2* single-cross

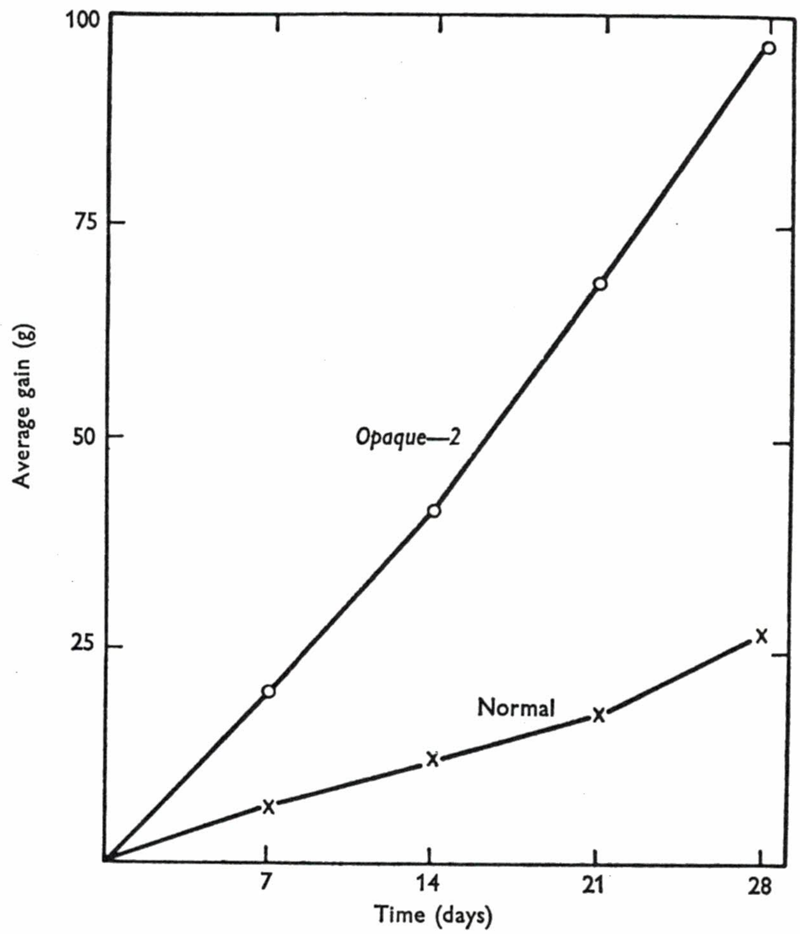


FIG. 7.—Weight-gain of weanling rats fed on *opaque-2* or normal maize (Mertz, Veron Bates and Nelson, 1965).

hybrids will be available in 1971, in Brazil, while large supplies of homozygous *opaque 2* double-cross hybrids will be available for planting in Columbia in 1970.

You will not be surprised to learn that there are communities in South America, such as the Indians of the Chepo area of Panama, who have for long exploited floury types of maize that are relatively high in lysine (Wellhausen, 1966). One of the impacts of North American corn technology in many parts of South and Central America has been the promotion of dent and flinty maize genotypes which have high kernel densities and reduced susceptibility in storage to insect and fungal damage, but low lysine. However, these relatively lysine deficient types will now no doubt be replaced.

The disadvantage of storage damage to the softer *floury 2* and *opaque 2* types of grain would remain were it not that the double homozygote while retaining the high lysine character reverts to the normal texture of the grain (Alexander Lambert and Dudley, 1969).

Of course there would be no point in advocating the use of *opaque 2* and *floury 2* genotypes if yield were to drop. But there is no suggestion of this, indeed, Oliver Nelson tells me that recent results in Illinois show that when a number of normal single-cross hybrids were compared in yield with otherwise similar hybrids derived from parents into which *opaque 2* had been introduced by backcrossing, the yield of the *opaque 2* genotypes was 99·9 of that of the normal genotypes.

There is, therefore, an immediate prospect of improving the nutritional properties of corn, and the impact of this exploitation of genetics on human welfare can hardly be overstated. Naturally, the search is already under way for similar variants in the other cereal species. Johnson, Whited, Mattern and Schmidt (1968) in Nebraska have, up to the present, checked 4,100 wheat genotypes but have as yet found none with dramatically higher contents of lysine. But one feels that now the search is on it is only a matter of time before similar changes will become possible in the nutritional value of the temperate cereals to those which are about to raise the food value of maize.

11. Polyploids

I have already discussed certain kinds of chromosome manipulation that have been used in plant breeding, and in addition, of course, some use has been made of changes in polyploid levels. Synthetic autopolyploids are cultivated in sugar beet, in rye, in red clover and in a few other species. Synthetic allopolyploids are in use in *Brassica* while at the present time there are reports of the imminent release in Canada of a variety of the synthetic allohexaploid species derived from tetraploid wheat and diploid rye.

However, perhaps the most intriguing use of autopolyploidy is that involved in the development of seedless water melon by Kihara and his collaborators (Shimotsuma, 1965). Triploids, which are seedless, are produced by crossing autotetraploids ($2n = 44$) by diploids ($2n = 22$). All of us can, I expect, imagine the delight of eating water melon with no inconvenient seeds.

12. Insect resistance

Another way in which the manipulation of plant genotypes is contributing to our welfare is by helping to reduce the extent to which we contaminate our environment. As a species, for the last two decades, we have been fouling our nests by the use of such substances as the chlorinated hydrocarbons. Their use has been necessary to prevent insect damage to our crops. The danger represented by these hazardous, environment-contaminating substances has recently been demonstrated in a startling manner on the River Rhine. An alternative to their use is to employ plant genotypes that are not susceptible to damage caused by insects. For example, in this country large losses of yield in sugar beet result from infection by the various yellowing viruses, which have aphid vectors. It has been the practice to control these virus diseases by spraying crops with insecticides in order to kill the aphids, so preventing the spread of the virus. However, my colleague,

G. E. Russell, has succeeded in breeding a variety of sugar beet that is tolerant of the virus (Campbell and Russell, 1965; Russell, 1966). This variety, Maris Vanguard, continues to yield at a high rate even though infected with virus, so that the necessity for insecticide spraying is obviated.

True insect resistance has been exploited in many cases, for example in wheat against Hessian fly and sawfly; in lucerne against the spotted aphid, in maize against the European corn borer, and in barley against the greenbug. It is clear that to keep the world sweet, greater efforts to use natural resistance of this kind are needed for without some control of insects—either chemical or genetic—we cannot continue to feed ourselves.

13. Eelworm resistance

Before leaving this topic of crops and the environment, I might refer briefly to the use of eelworm resistant potato varieties, like Maris Piper which was bred by my colleague, H. W. Howard (1965). Maris Piper has a resistance gene derived from *Solanum andigena*. When non-resistance varieties are grown, cysts of the eelworm, which are present in the soil and each of which contains several hundred larvae, are stimulated to hatch by secretions from potato roots. The nematodes invade the roots causing damage and severe reduction in yield. Females in the roots are fertilised and each forms a new cyst, on the surface of the root, which drops off the root into the soil. When the resistant variety Maris Piper is used, the cysts hatch normally and root invasion occurs, but no new cysts are formed. Consequently, as well as being resistant to eelworms, Maris Piper can clean the soil of eelworms—so improving the agricultural environment.

14. New procedures

I have looked at a few examples of the genetic manipulation of plants that have already been carried out or are now in process of realisation. What new procedures can we expect in the future?

One possibility is the production of haploids by the culture of pollen grains. Haploids, derived from eggs which develop parthenocarpically and which are recognised by the use of genetic markers, are already used for speeding the production of inbred lines in maize and in *Brassica oleracea*, and for the isolation of diploids, with simpler patterns of inheritance than the normal autotetraploids, in potato. However, haploids plants can be produced easily from cultivated pollen grains in tobacco (Nitsch and Nitsch, 1969) and have also been produced with difficulty in rice and barley. The development of efficient techniques for haploid production in this way would make it possible to fix the first products of segregation and recombination from heterozygous F_1's in inbreeders to which pedigree methods are usually applied. This would eliminate the several generations that normally elapse in the return to homozygosity.

15. Hybrid cells

But perhaps the most fascinating prospect is the possibility that wider crosses than are possible by sexual means can be made by protoplast fusions. Vertebrate cells can be fused and hybrid cells produced, but fortunately

intact organisms cannot be regenerated from the resulting cultures. By contrast cell suspension and callus cultures of many plant species have been regenerated into entire organisms. However, hybridisation of plant cells is precluded by the cellulose-pectin walls by which they are surrounded which prevent contact between cells. Techniques for the enzymatic removal of the wall have recently advanced considerably and naked protoplasts have been isolated which are viable and capable of resynthesising the cellulose wall, when cellulase is removed from the medium. Nuclear division has been observed in isolated plant protoplasts and there are reasons for believing that protoplast fusions may not be hard to achieve. If this is so it may soon be possible to produce hybrid cells which can be taken into culture and caused to regenerate into complete organisms. In this way a new range of hybrid material may become available to the plant breeder and useful alien genetic variation, from hitherto inaccessible sources, introduced into crop species.

16. Applying genetics

The contrast between what I suppose must be called " pure " and " applied " genetics is that while the former is mainly concerned with analysis the ultimate function of the latter is synthesis. From chemistry all the way to poetry it is easier to analyse than to synthesise, and genetics is no exception. Of course preliminary analysis will often make more obvious the procedures to be used in genetic synthesis, and here there are enormous deficits in our knowledge.

Although the value of the contribution of " disinterested " genetics to the use of the science is obvious, I feel constrained to point out that if as much were known about the dozen or so plant species on which mankind depends as is known about *Escherichia coli*, *Neurospora*, *Aspergillus*, *Drosophila melanogaster* and a few other favoured organisms, there would be better prospects of being able to sustain the population of thirty years hence when we shall be almost twice as many as we are today. Any new knowledge that we can gain about our crop plants is of social significance—it will ultimately be put to work in some way or other.

An enormous task faces plant genetics, yet we must not be daunted by its proportions for I hope that I have been able to show that current achievements are not inconsiderable. It has been proved that, coming back to Bateson's words, " There is no lack of utility and direct application in the study of Genetics ".

17. Summary

1. Consideration has been given to the application of plant genetics in the alleviation of world food shortages. Recent advances that have resulted in the increased productivity of rice and wheat have arisen from relatively simple genetic procedures that have removed limiting factors and made possible the exploitation of improved cultural practices.

2. The genotype-genotype interactions involved in the resistance of plants to diseases were discussed in relation to the manipulation of disease resistance in crop improvement.

3. Chromosome manipulation has made possible the introduction of disease resistance into wheat from related species and the feasibility of duplicating resistance loci is being investigated.

4. The prospects were co
of maize, in terms of the balan

5. Attention was given to
to insect and eelworm resista
hybrid cells.

ALEXANDER, D. E., LAMBERT, R. J. AN
of modified protein maize. *Ne*
national Atomic Energy Agenc

BATESON, W. 1908. *The Methods a*

BELL, G. D. H. 1968. Plant breedi
ments and objectives. *Proc. Ro*

BORLAUG, N. E. 965. Wheat, rust

BORLAUG, N. E. 1968. Wheat bree
Wheat Genet. Symp., 1-36.

CAMPBELL, G. K. G. AND RUSSELL, G
1963-64, 6-32.

CHANDLER, R. F. 1969. Improving

DRISCOLL, C. J. 1968. Alian transfe
Genet. Symp., 196-203.

EMERSON, G. W., BEADLE, G. W. AND
maize. *Cornell Univ. Agr. Expt.*

FINLAY, K. W. 1968. The significan
Genet. Symp., 403-409.

FLOR, H. H. 1956. The compleme
29-54.

GOPINATH, D. M. AND BURNHAM, C.
duplication produced by cro
Genetics, *41*, 382-395.

HOWARD, H. W. 1965. Eelworm-
Agric., *Lond.*, *No. 7*, 2nd Ed. pp

JOHNSON, V. A., WHITED, D. A., MATTE
ment of wheat by breeding. *P*

KNOTT, D. R. 1967. Rust-resista
714-717.

MERTZ, E. T., BATES, L. S. AND NELSO
position and increases lysine co

MERTZ, E. T., VERON, O. A., BATES, L.
opaque-2 maize. *Science*, *148*, 17

NELSON, O. E., MERTZ, E. T. AND BATE
acid pattern of maize endosper

NITSCH, J. P. AND NITSCH, C. 1969.

RILEY, R. AND CHAPMAN, V. 1958.
hexaploid wheat. *Nature*, *182*,

RILEY, R., CHAPMAN, V. AND JOHNSON
in wheat by genetic interferen
Genet. Res., *Camb.*, *62*, 199-219.

RILEY, R. AND LAW, C. N. 1965. Ge
57-107.

RILEY, R. AND KIMBER, G. 1966. T
Breed. Inst. 1964-65, 6-36.

RUSSELL, G. E. 1966. Recent deve
sugar beet. *Acta Agric. Scand.*,

SEARS, E. R. 1956. The transfer o
Brookhaven Symposium in Biology,

SHIMOTSUMA, M. 1965. A survey
Taiwan. *Rep. Kihara Inst. biol.*

WELLHAUSEN, E. J. 1966. The in
Proceedings of the High Lysine Corn
University, pp. 148-160.

e resulting cultures. By
ly plant species have been
/bridisation of plant cells
hich they are surrounded
for the enzymatic removal
nd naked protoplasts have
esynthesising the cellulose
Nuclear division has been
e reasons for believing that
f this is so it may soon be
n into culture and caused
ay a new range of hybrid
er and useful alien genetic
luced into crop species.

be called " pure " and
nly concerned with analy-
From chemistry all the
hesise, and genetics is no
often make more obvious
here there are enormous

disinterested " genetics to
ed to point out that if as
pecies on which mankind
ora, Aspergillus, Drosophila
, there would be better
f thirty years hence when
Any new knowledge that
ficance—it will ultimately

must not be daunted by
how that current achieve-
ed that, coming back to
direct application in the

ation of plant genetics in
vances that have resulted
ve arisen from relatively
niting factors and made
tices.
ved in the resistance of
manipulation of disease

ible the introduction of
es and the feasibility of

4. The prospects were considered of improving the nutritional quality of maize, in terms of the balance of essential amino acids in the grain proteins.

5. Attention was given to the use of induced polyploids and haploids, to insect and eelworm resistance and to the possibilities of exploiting plant hybrid cells.

18. References

ALEXANDER, D. E., LAMBERT, R. J. AND DUDLEY, J. W. 1969. Breeding problems and potentials of modified protein maize. *New Approaches to Breeding for Improved Plant Protein.* International Atomic Energy Agency, Vienna, pp. 55-65.

BATESON, W. 1908. *The Methods and Scope of Genetics.* Cambridge Univ. Press.

BELL, G. D. H. 1968. Plant breeding for crop improvement in Britain: methods achievements and objectives. *Proc. Roy. Soc. B., 171,* 145-173.

BORLAUG, N. E. 965. Wheat, rust and people. *Phytopathology, 55,* 1088-1098.

BORLAUG, N. E. 1968. Wheat breeding and its impact on world food supply. *Proc. 3rd Int. Wheat Genet. Symp.,* 1-36.

CAMPBELL, G. K. G. AND RUSSELL, G. E. 1965. Breeding sugar beet. *Rep. Pl. Breed. Inst. 1963-64,* 6-32.

CHANDLER, R. F. 1969. Improving the rice plant and its culture. *Nature, 221,* 1007-1010.

DRISCOLL, C. J. 1968. Alian transfer by irradiation and meiotic control. *Proc. 3rd Int. Wheat Genet. Symp.,* 196-203.

EMERSON, G. W., BEADLE, G. W. AND FRASER, A. C. 1935. A summary of linkage studies in maize. *Cornell Univ. Agr. Expt. Sta. Mem., 180.*

FINLAY, K. W. 1968. The significance of adaptation in wheat breeding. *Proc. 3rd Int. Wheat Genet. Symp.,* 403-409.

FLOR, H. H. 1956. The complementary genic systems in flax and flax rust. *Adv. Genet., 8,* 29-54.

GOPINATH, D. M. AND BURNHAM, C. R. 1956. A cytogenic study in maize of deficiency-duplication produced by crossing interchanges involving the same chromosome. *Genetics, 41,* 382-395.

HOWARD, H. W. 1965. Eelworm-resistant varieties. *Plant Nematology, Tech. Bull. Minist. Agric., Lond., No. 7,* 2nd Ed. pp. 262-268.

JOHNSON, V. A., WHITED, D. A., MATTERN, P. J. AND SCHMIDT, J. W. 1968. Nutritional improvement of wheat by breeding. *Proc. 3rd Int. Wheat Genet. Symp.,* 457-61.

KNOTT, D. R. 1967. Rust-resistant wheat—an unsolved problem. *New Scientist, 1967,* 714-717.

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, 145,* 279-280.

MERTZ, E. T., VERON, O. A., BATES, L. S. AND NELSON, O. E. 1965. Growth rate of rats fed on *opaque-2 maize. Science, 148,* 1741-1742.

NELSON, O. E., MERTZ, E. T. AND BATES, L. S. 1965. Second mutant gene affecting the amino acid pattern of maize endosperm proteins. *Science, 150,* 1469-1470.

NITSCH, J. P. AND NITSCH, C. 1969. Haploid plants from pollen grains. *Science, 163,* 85-87.

RILEY, R. AND CHAPMAN, V. 1958. Genetic control of the cytologically diploid behaviour of hexaploid wheat. *Nature, 182,* 713-715.

RILEY, R., CHAPMAN, V. AND JOHNSON, R. 1968. The incorporation of alien disease resistance in wheat by genetic interference with the regulation of meiotic chromosome synapsis. *Genet. Res., Camb., 62,* 199-219.

RILEY, R. AND LAW, C. N. 1965. Genetic variation in chromosome pairing. *Adv. Genet., 13,* 57-107.

RILEY, R. AND KIMBER, G. 1966. The transfer of alien genetic variation to wheat. *Rep. Pl. Breed. Inst. 1964-65,* 6-36.

RUSSELL, G. E. 1966. Recent developments in breeding for resistance to virus yellows of sugar beet. *Acta Agric. Scand., Suppl. 16,* 140-143.

SEARS, E. R. 1956. The transfer of leaf-rust resistance from *Aegilops umbellulata* to wheat. *Brookhaven Symposium in Biology, 9,* 1-22.

SHIMOTSUMA, M. 1965. A survey of seedless watermelon breeding and its extension in Taiwan. *Rep. Kihara Inst. biol. Res., 17,* 46-54.

WELLHAUSEN, E. J. 1966. The incorporation of *opaque 2* into tropical varieties of maize. *Proceedings of the High Lysine Corn Conference.* Eds. E. T. Mertz and O. E. Nelson. Purdue University, pp. 148-160.