THE LOCATION OF GENETIC FACTORS AFFECTING A QUANTITATIVE CHARACTER IN WHEAT

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FOR a proper understanding of the genetics of continuous variation, it cannot be doubted that the genes responsible for the control of metrical characters must be isolated so that their individual properties may be investigated. THODAY (1961) has emphasised this point of view and has described methods by which genes of this kind can be located. Essentially these methods involve two steps, the use of marker genes so that small regions of a chromosome can be recognised, followed by progeny testing of the marker classes so that they became classifiable into a number of groups. In this way, it has been possible to explain most of the heritable variation controlling the number of sternopleural chaetae in Drosophila in terms of relatively few factors and locate them with reasonable accuracy on the genetic map (GIBSON and THODAY 1962; WOLSTENHOLME and THODAY 1963; THODAY, GIBSON and SPICKETT 1964; SPICKETT and THODAY 1966).

So far, this technique has been applied extensively to Drosophila only. Markers are, however, known with sufficient frequency in other organisms—for example barley, tomato and maize—so that there is no theoretical reason why such techniques could not also be used in these organisms. Indeed, a study of the genetic factors affecting certain quantitative characters in barley has already been undertaken in which two major genes have been used to mark two regions of a chromosome (FASOULAS and ALLARD 1962).

However, in wheat (*Triticum aestivum*) the extent and availability of suitable markers is not great. The use of markers is complicated also by the polyploid nature of wheat, so that duplicate interactions between marker genes may sometimes present difficulties. On the other hand, the high tolerance of wheat to aneuploidy which permits the use of cytological markers has provided cytogeneticists with two main categories of technique for locating factors on particular chromosomes (SEARS 1953).

The first of these techniques employs the study of F_2 populations derived from crosses between a variety and the 21 monosomics of another variety. Abnormal segregations indicate the chromosome carrying the factor under study. This approach has been used extensively for the location of genes which behave qualitatively (SEARS and RODENHISER 1948; UNRAU 1950; HEYNE and LIVERS 1953; KNOTT 1959).

The second kind of technique involves the substitution of each of the 21 chromosomes from a donor variety for its homologue in a recipient variety. Although

this approach demands a rather lengthy cytological and backcrossing programme, it nevertheless is likely to prove the most efficient way of studying quantitative inheritance in wheat. By this means, it is possible to produce true breeding lines in which individual chromosomes from a donor variety can be assayed in a constant genetic background and compared with the homologue of the recipient. The control of a number of quantitative characters by each chromosome can then be assessed. Material derived by this method has been used by KUSPIRA and UNRAU (1957) and LAW (1965) and has demonstrated that a number of chromosomes participate in the control of quantitative characters such as yield, ear number, grain weight and height.

Both these techniques are concerned with the location of chromosomes rather than the number and the location of the factors carried by them. They are therefore exactly analogous to the genome assays which are a first step in the location of the factors studied by THODAY and his co-workers. For characters which are qualitative in nature, the location of the chromosome responsible is no great disadvantage, since in most cases the F_2 segregation ratios obtained from all the monosomic crosses enable the number of factors to be determined. Quantitative characters are however a different matter and further studies are necessary before the number and type of factors carried by a chromosome can be ascertained. UNRAU (1958) has proposed a scheme using substitution lines by which factors may be located on a chromosome and this will be described in detail below, along with certain modifications which are helpful in studying quantitative characters. The application of this technique to the genetics of chromosome 7B of wheat will then be described.

An alternative technique of studying quantitative characters in wheat in which inbred backcross lines are produced from a cross between two wheat varieties has also been described by WEHRHAHN and ALLARD (1965). By studying the distribution of the backcross lines it was possible to recognise clearly at least four genes controlling the time to ear emergence. This technique may have a number of advantages over those described in the previous paragraphs; in particular the cytological control required in the development of substitution lines is no longer necessary. However, the ability to locate both the chromosome and the factors responsible for the control of quantitative characters, which can be achieved by the substitution technique, should prove to be of greater value, particularly since the basic chromosome structure of wheat into seven homoeologous groups and three genomes is now established (SEARS 1954).

EXPERIMENTAL TECHNIQUE AND MATERIALS

The method used to study the distribution of factors within a chromosome is very similar to that proposed by UNRAU (1958) and later carried out by WEHRHAHN (1961). In this technique, a substituted line is crossed to the recipient variety, so that a single-chromosome heterozygote in a constant genetic background in produced. By backcrossing this genotype as male to the recipient variety, monosomic or nullisomic for the chromosome being investigated, monosomic progeny can be obtained which will be hemizygous either for a nonrecombinant or recombinant chromosome. On selfing these plants it is possible to obtain euploid individuals which will be homozygous. In this way true-breeding recombinant lines can be produced in only two generations.

However, this approach is restricted since it depends entirely upon the recognition of discontinuities in the variation for the detection of the recombinant and nonrecombinant chromosomes. Where such discontinuities are not so apparent it may be difficult to establish whether recombinantion has occurred. To overcome this difficulty, a control group of chromosomes which provide a measure of the variation due to the nonrecombinant chromosomes alone can be produced. Such a control group can be obtained if the crossing programme illustrated in Figure 1 is carried out. Here both the recipient variety (P_1) and the substitution line (P_2), along with the F_1 between them, are crossed to the female recipient variety, monosomic for the chromosome under study. In this way, monosomic plants can be derived from P_1 and P_2 so that when combined they can only represent a sample of the nonrecombinant chromosomes. It is thus possible to compare two types of sample (i) the parental products, (P_1 +P_2), which are composed of only nonrecombinant chromosomes, and (ii) the F_1 products which are made up of both nonrecombinant and recombinant chromosomes. Thus, if the effects of differential transmission can be discounted, any differences between the two samples must reflect the differences which have resulted from recombination.

It is apparent, if euploid plants are derived from the monosomics developed by these procedures, that the parental products should be exactly the same as the recipient variety and the substituted line. Consequently, it could be argued that there is little reason to carry out these procedures since the initial parental material in themselves will provide an estimate of the variation due to nonrecombinant chromosomes. However, there are two reasons for avoiding this alternative: (i) It may be more convenient in many cases to work on the monosomics and

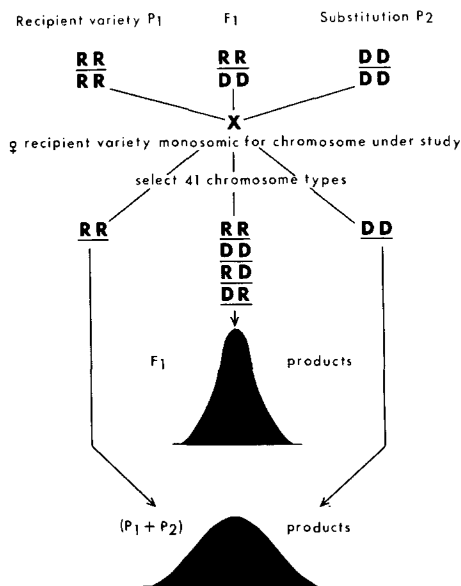

FIGURE 1.—Scheme used for the detection of recombination in *Triticum aestivum*, when intervarietal chromosome substitutions are employed. *RR* and *DD* refer to the chromosomes from the recipient variety (P_1) and the substituted chromosome of the donor variety (P_2), respectively. *RD* and *DR* represent the recombinant chromosomes produced by crossing over between them. The parental products ($P_1 + P_2$) provide an estimate of the variation due to the nonrecombinant chromosomes alone, *RR* and *DD*. The F_1 products give an estimate of the variation due to both nonrecombinant and recombinant chromosomes, *RR*, *DD*, *RD* and *DR*. Thus the $V_{(P_1 + P_2 \text{ products})} - V_{(F_1 \text{ products})} = V$ due to recombination. The diagram indicates the differences in variance expected when the genes involved are in coupling.

their unselected progeny so that the lengthy and laborious cytological selection required in the production of euploids can be avoided. It is therefore necessary to have the control group of chromosomes in a monosomic condition also. (ii) If euploids are considered desirable then a control may be particularly useful, since, although an extensive backcross programme may have taken place in the production of the substitution line, factors from the donor variety may still be present in the background (WEHRHAHN 1961). The variation observed among the F_1 products could then result in part from the segregation of genes carried by chromosomes other than the substituted chromosome. However, the products from the substituted line should show a similar segregation, so that a check of background effects can be made if a control is used; moreover, an estimate of the variation due to such genes should also be possible.

The use of telocentrics: Telocentric chromosomes are available for all the chromosomes of wheat. It is possible therefore to investigate the distribution of genetic factors within a single arm of a chromosome (UNRAU 1958) and in some cases map genes with respect to the centromere (SEARS 1963; DRISCOLL and SEARS 1965). To undertake this, procedures are carried out similar to those described above, but in this case telocentric lines belonging to the recipient variety are used, so that recombination can only take place on one arm of the chromosome.

Materials: The substitution line involving chromosome 7B of the variety Hope in the recipient variety Chinese Spring was used in this investigation. The line was produced by DR. E. R. SEARS and had undergone five backcrosses to the recipient parent in its development. Hope 7B was initially chosen because it was known that this chromosome carried the dominant gene (*Pc*) for purple culm (KUSPIRA and UNRAU 1958) and the line itself differed from Chinese Spring in a number of quantitative characters.

Two experiments have been conducted using this material with the aim of studying the genetic control of a number of characters. This paper describes the results obtained for the character time to ear emergence.

Both experiments are based on the mean of the selfed progeny of monosomics derived in the manner already described. The first experiment investigates the variation obtained when complete chromosomes are allowed to recombine. The second experiment involves the telocentric for the long arm of chromosome 7B from Chinese Spring, so that recombination on this arm alone can be studied.

Further details are given where necessary in the description of the results.

RESULTS

Experiment 1: In this experiment five seeds obtained from monosomics derived by the procedures already described were sown in pots and grown in the greenhouse. When the ears from at least three out of the five plants appeared above the flag leaf, the family was scored for ear emergence. In most cases duplicate cultures were sown and a good agreement was found between them. In 14 cases, however, duplicates were not available, so that the observations described here are based on the means of the two replicates.

The distribution curves of days to ear emergence for 20 lines derived from the parental products (9 from Hope 7B and 11 from Chinese Spring) and for 81 lines derived from the F_1 products are shown in Figure 2.

The parental products give a mean of 12.90 ± 1.71, whereas the F_1 products have a mean equal to 12.20 ± 0.72. There is therefore little difference in the means obtained from the two samples. This indicates that there is no evidence for gene interaction assuming that recombination between genes controlling ear emergence is taking place. The system observed behaves additively. Nor is there evidence that a differential transmission of genes will affect the interpretation

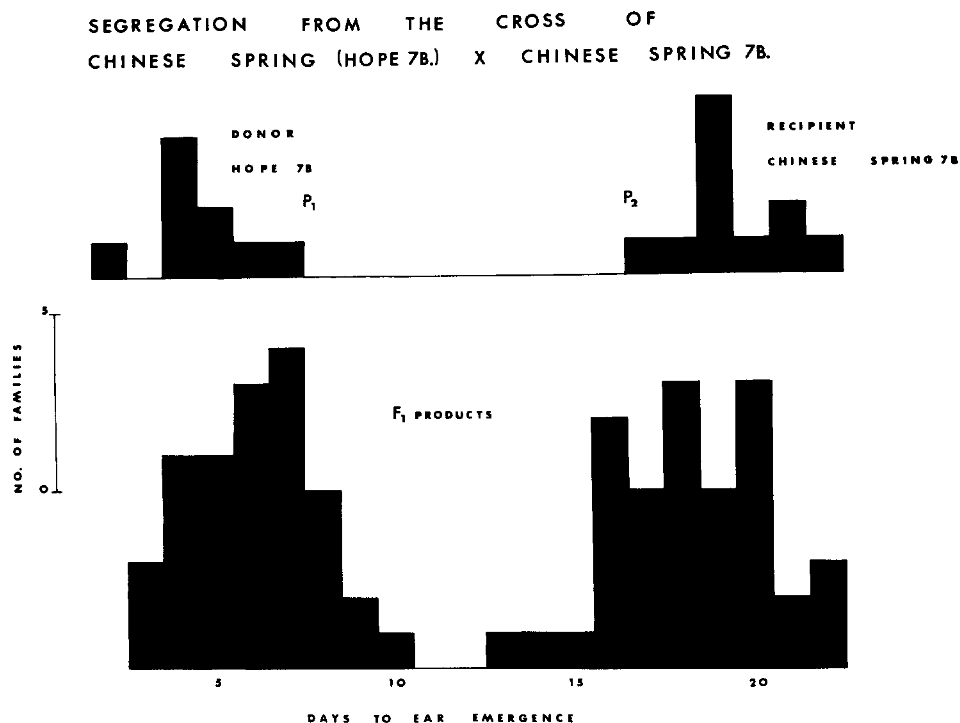

FIGURE 2.—Distribution curves of days to ear emergence for the families derived from (1) the cross of the hybrid between the substitution line, Chinese Spring/Hope 7B, and the recipient variety, Chinese Spring, onto the monosomic of chromosome 7B, (F_1 products); and (2) the crosses of Chinese Spring/Hope 7B and Chinese Spring separately, onto the same monosomic, (P_1 and P_2). The days to ear emergence refer to the commencement of emergence in the population.

of the data, despite the fact that the parental products themselves are biased in favour of chromosome 7B from Chinese Spring. These two complications have therefore been ignored.

It is clear that the bimodality shown by the parental products is found among the F_1 products also. A single factor which may be a single gene or a closely linked block of genes, and which produces an appreciable effect on the time of ear emergence, can therefore be detected.

The bimodal groups obtained for the F_1 products are however closer to each other than to those of the parental products. This is also indicated by the variances obtained from the two distributions. Overall the parental products give a variance of 58.70, whereas the variance of the F_1 products is 41.82. Although these two variances are not significantly different from each other, the smaller variance of F_1 products is expected if coupling linkages between genes affecting the time to ear emergence are being broken down.

This conclusion is supported by the increased variation apparent within each of the modal groups of the F_1 products compared with the variation within each

TABLE 1

The breakdown of the variation observed in Experiment 1

Item	S.S.	df	M.S.	V.R.	P
Parental products *vs.* F_1 products	7.91	1			
Parental products:					
Chinese Spring 7B *vs.* Hope 7B	1079.51	1			
Within modal group variation	35.79	18	1.9883	3.9507	0.01–0.001
F_1 products:					
F_1 modal groups	2725.29	1			
Within modal group variation	620.56	79	7.8852		
Total	4469.06				

of the parental groups. The breakdown of the total variation into its components in Table 1 shows this clearly. Here the within modal group variation of the F_1 products is significantly greater than the variation occurring within the two modes of the parental products. At least two factors affecting this character can consequently be proposed to explain the variation observed. One factor of large effect, which ensures that a bimodality is still observed among the F_1 products, and a second factor of much smaller effect.

The possibility that other factors are also present cannot of course be excluded. However, the ability to produce true breeding lines from this kind of material may allow other factors to be distinguished by means of progeny tests in a manner similar to that conducted by THODAY and his colleagues.

The assertion that the bimodality obtained among the F_1 products arises from the segregation of a single factor which has large effects on ear emergence enables conventional linkage studies to be conducted with other factors which also produce discontinuities. The Hope 7B chromosome, as mentioned previously, carries a single dominant gene (*Pc*) which produces a purple coloration of the culms. Plants were classified for this character as the experiment was carried out. Segregation within families did not occur, so that the presence of *Pc* on chromosome 7B, first concluded by KUSPIRA and UNRAU (1958), was amply confirmed. The segregation of *Pc* with respect to the factor, designated *E*, with a large effect on ear emergence is given in Table 2.

The analysis of the observed ratios indicates that *Pc* and *E* are linked (linkage

TABLE 2

Classification of the F_1 *products in terms of the gene* (Pc) *and the factor controlling the time to ear emergence* (E)

Nonrecombinants		Recombinants		
Pc E	*pc e*	*Pc e*	*pc E*	Total
34	28	13	6	81

$P = 19/81 = 0.2346 \pm 0.0471$.

$\chi^2_{(1)} = 22.8$, $P<0.001$) and give an estimate of recombination of $P = 0.2346 \pm 0.0471$. The assertion that E is also found on chromosome 7B is therefore confirmed by this result.

Experiment 2: This experiment involved the study of F_1 products in which recombination was confined to the long arm of chromosome 7B only. To do this the substituted line containing chromosome 7B of Hope was crossed to a Chinese Spring plant, ditelocentric for the long arm of the same chromosome. The resulting F_1 was therefore heterozygous for the long arm only and hemizygous for the short arm of Hope 7B. By backcrossing this F_1 as male to the monosomic in the manner already described, 35 monosomic and 13 monotelocentric plants were obtained. These plants were then selfed and the progeny sown in pots in a controlled environment chamber maintained at a temperature of approximately 18°C and under a regime of continuous light. The experiment took the form of two completely randomized blocks. Two seeds were sown in each pot and the measurements of time to ear emergence were based on the mean of these two plants.

At the same time some of the derivatives from Experiment 1 were also included. These were two lines from each of the parents and ten lines from the F_1 products. By this means, comparisons could be made between three types of treatment (i) a control in which both chromosome arms had effectively undergone no recombination, (ii) a backcross, involving the telocentric, in which recombination had occurred on only the long arm, and (iii) a backcross, involving the complete chromosome, in which recombination had taken place on both arms of the chromosome.

One further cross should also be possible, namely, the cross involving the short arm of chromosome 7B. In this way the comparisons envisaged in this experiment would be orthogonal and the effect of recombination within each of the arms of chromosome 7B could be separated clearly. Unfortunately, at the time this experiment was conducted, the short arm of 7B was not available as a telocentric, so that this useful addition could not be carried out. Experiments are now under way to accommodate this deficiency.

Nevertheless, the three comparisons that are possible in this experiment may still be sufficiently adequate for the study of the factors controlling the time to ear emergence.

The distribution of the means for each of the families studied in this experiment is given in Figure 3. Because replicates were grown, it is possible to break down the variation shown in Figure 3 into components and carry out statistical tests between them. Accordingly the analysis of variance for this data is presented in Table 3.

A number of points are evident. For the derivatives which have involved the telocentric chromosome in their crossing schedule, *Pc* is found only when the complete chromosome is transmitted and not among those families carrying the long, armed, telocentric chromosome. Crossing over has therefore not produced a redistribution of *Pc*. This suggests strongly that it is the short arm and not the long arm of chromosome 7B which carries this gene and also that the telocentric

TABLE 3

Analysis of variance for days to ear emergence in Experiment 2

Item	S.S.	df	M.S.	V.R.	P
a. *Total variation*					
Blocks	4.10	1			
Genotypic variation	10365.28	61	169.9226	22.3303	< 0.001
Error	441.35	58	7.6095		
Total	10810.73	120			
b. *Genotypic variation*					
1. Parental products					
Variation associated with *Pc* and *pc*	612.44	1	612.4400	599.3060	0.01–0.001
Remainder	2.19	2	1.0950		
Total	614.63	3			
2. F_1 products					
Variation associated with *Pc* and *pc*	2.83	1	2.8300	0.0208	not significant
Remainder	1090.94	8	136.3675		
Total	1093.77	9			
3. F_1 telocentric products					
Variation associated with *Pc* and the telocentric condition	7530.44	1	7530.4400	314.6770	< 0.001
Remainder	1100.81	46	23.9307		
Total	8631.25	47			
Variation between 1, 2 and 3	25.63	2	12.8150		
Grand Total	10365.28	61			

families are in fact deficient for this locus. Furthermore, there is no indication that the bimodality in ear emergence times found in the first experiment occurs among the monosomic and monotelocentric derivatives of this cross. The factor *E*, producing large effects on the time to ear emergence, must therefore be present on the deficient or short arm also.

This lack of bimodality could of course arise from the fact that different environments were used in the two experiments. However, a bimodal distribution is clearly shown in the ten monosomic families which represent material in which recombination has occcurred on both arms. Consequently differences in environment can be discounted.

There is strong evidence therefore for placing the two factors, *Pc* and *E*, on the short arm of chromosome 7B. Only one consideration prevents this evidence from becoming conclusive and this refers to the assumption that the experiment involving the telocentric chromosome has not reduced recombination on the long arm. If this assumption is incorrect then *Pc* and *E* could still be on the long arm but the reduction in crossing over between them would ensure that an apparent linkage of these two factors with the short arm would be observed. A spurious classification could thereby be achieved. The results of the short arm telocentric crosses may resolve this situation. For the moment however the evidence is consistent with the hypothesis that *Pc* and *E* are located on the short arm of chromosome 7B.

Considerable variation exists within the complete and telocentric chromosome

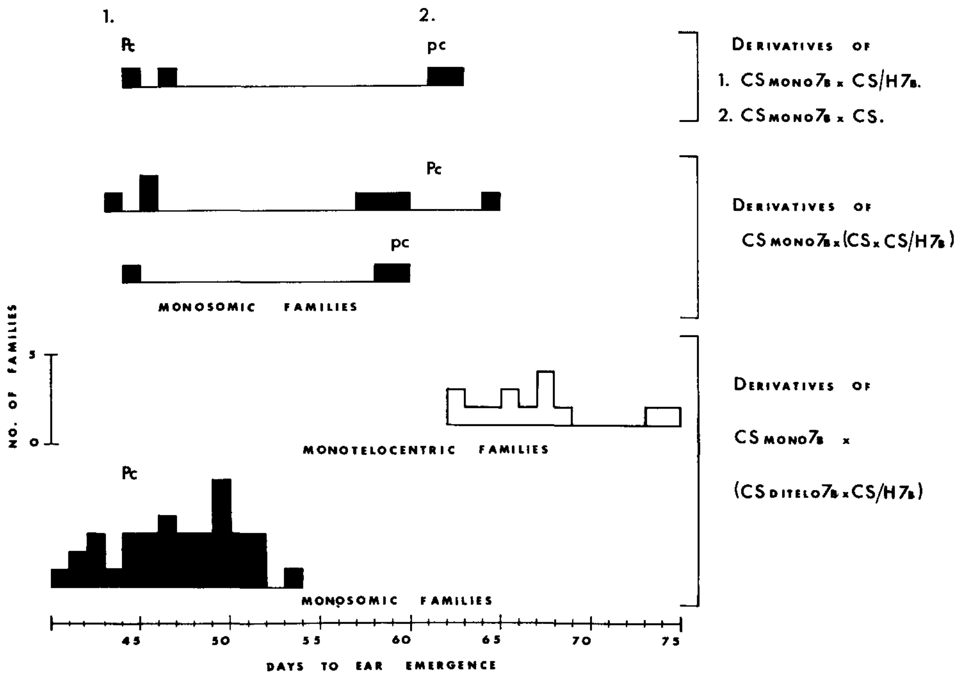

FIGURE 3.—Distribution curves of days to ear emergence for the families derived from three sets of crosses onto Chinese Spring, monosomic for chromosome 7B. Open histograms refer to families carrying the telocentric for the long arm of chromosome 7B. Solid histograms refer to families carrying the complete 7B chromosome. Days to ear emergence relate to the number of days from the start of the experiment.

classes despite the fact that the factor E controlling ear emergence is responsible for the larger differences between them. Indeed, the remainder variation for the cross involving the telocentric chromosome given in the analysis of variance is significantly greater than the error variation ($P < 0.001$). Consequently a factor or factors affecting the time to ear emergence is or are segregating when recombination has been allowed to take place on the long arm of chromosome 7B.

The evidence from the second experiment is therefore entirely consistent with the conclusions arrived at earlier. At least two factors affecting ear emergence are segregating, one of which (E) can be mapped with respect to the gene *Pc*. Furthermore, the second experiment indicates strongly that E along with *Pc* is located on the short arm of chromosome 7B and that a second factor of smaller effect is most probably found on the long arm of the same chromosome.

It is of interest to mention also that the presence of the factor E on the short arm of chromosome 7B of Hope means that the comparison between the complete chromosomes carrying E and the telocentric chromosomes is concerned with the difference between this factor and its absence. This being so, the action of this region of the chromosome cannot be amorphic. Similarly, since the monotelocentric families give a mean = 67.51 and the control plants carrying chromosome

7B of Chinese Spring give a smaller mean of 62.38, the allele or alleles carried by this chromosome cannot be amorphic either. Thus, the factor E and its alleles appear in this instance to be concerned with the creation of products which bring about earliness in ear emergence rather than its delay. This is in agreement with other evidence in wheat (SEARS 1954) which shows that the time to maturity of nullisomics is consistently greater than that of euploids. This would not be the case if some genes are responsible for lateness *pe se*. Although this evidence cannot be regarded as extensive, it nevertheless suggests that the control of ear emergence times in wheat is concerned with gene products which accelerate rather than inhibit or retard the processes leading to ear emergence.

DISCUSSION

It may not be surprising that ear emergence is the only quantitative character reported in higher plants which has so far proved amenable to the kinds of analysis described above. Ear emergence is generally found to have a high heritability, so that the recognition of the factors responsible for this character may not be so difficult as other quantitative characters which have smaller heritabilities. Nevertheless, an important feature of the technique described above is the ability to produce recombinant and nonrecombinant lines. There is thus no reason, with sufficient replication and progeny testing, why factors influencing characters with much smaller heritabilities should not be capable of recognition.

Whether the extension of this technique to the genetic analysis of other characters will result in a bias due to the recognition of factors which have only large effects must await its application. It is probable that a number of genes will have such small effects because they perform functions which are only peripheral to the character being studied; in this event they may be difficult to isolate. However, as THODAY (1961) has pointed out, it is only by an extensive attack on the genes controlling quantitative characters, that assertions such as this can be tested. There may be all gradations of genes controlling these characters, alternatively there may be distinct groups of genes in the way proposed by MATHER (1949), the genes of evolution with relatively small effects plus the major genes around which the genotype is built. Only by carrying out experiments to isolate and characterise the genes concerned can such questions be answered.

A wide range of factors are now known to control the time to ear emergence in wheat. Many differ considerably in the magnitude of their expressions. Thus chromosome 5D has often been associated with the differences occurring between spring and winter varieties (MORRISON 1960; TSUNEWAKI and JENKINS 1961; TSUNEWAKI 1962; DRISCOLL and JENSEN 1964). It is probable that the gene of large effect observed by WEHRHAHN and ALLARD (1965) and which accounted for 80% of the heritable variation is carried by this chromosome. Numerous other chromosomes and factors having smaller effects than this are also known. It should be possible therefore to study this wide range of genes, already available for analysis in wheat, in order to investigate the number of classes into which the genes controlling the character can be placed. Furthermore, it should

also be possible with the extension of these techniques to other characters to carry out similar surveys. The consequences of such comparisons should be highly informative from the point of view of past selective histories and should be of considerable value to plant breeders whose interest is in future selective possibilities.

It is clear also that the technique described here using cytological markers and those used by THODAY and his co-workers and WEHRHAHN and ALLARD, provide the necessary means for isolating many of the genetic factors involved in quantitative inheritance. It should therefore be possible to supplement the biometrical analyses of conventional genetics by investigating the specific contributions of some of the relevant loci. In this way a greater understanding of the genetics of continuous variation should be possible.

The isolation of factors which affect quantitative characters may also allow the study of the developmental effects of these factors either individually or in combination. This possibility has been suggested by THODAY (1961) and informative experiments on the developmental differences between the factors controlling sternopleural chaetae in Drosophila have already been conducted by SPICKETT (1963). In wheat, as mentioned in a previous paragraph, the number of known factors controlling ear emergence is extensive; moreover, many of these are now available in substitution line material. It should therefore not be difficult to study the developmental differences for which these factors are responsible. Indeed, MORRISON (1960) has already indicated that some of the factors responsible for ear emergence can be differentiated by their ability to respond to either cold treatment or light. The way is consequently open to the exact study of the developmental genetics of ear emergence time in wheat.

I wish to thank MR. A. J. WORLAND and MISS B. J. SMOLNY, B.Sc., for their assistance in carrying out these experiments.

SUMMARY

The techniques used in locating genetic factors controlling quantitative characters in wheat by means of inter-varietal substitution are described. These techniques were used to show that chromosome 7B of the variety Hope differed from that of Chinese Spring by at least two factors which controlled the time to ear emergence. One of these factors, *E*, produced such large effects that it was possible to classify the genetic segregation qualitatively. In this way, a recombination value of 23% was obtained between *E* and a gene for purple culm (*Pc*) carried by the same chromosome. The use of a telocentric chromosome for the long arm of chromosome 7B provided strong evidence for placing both *Pc* and *E* on the short arm and at least one factor of small effect on the long arm.

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