CHROMOSOME VARIATION FOR LOCI CONTROLLING EAR EMERGENCE TIME ON CHROMOSOME 5A OF WHEAT

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SUMMARY

Substitutions of chromosome 5A from different varieties into the variety Chinese Spring had differential effects on the ear emergence time of this variety. A model of three genetic factors was capable of explaining the genetical relationships between these chromosomes but it was not possible to distinguish whether these were three separate loci or three separate components of the *Vrn* 1 locus, located on this chromosome. The results suggest, however, that close adaptation of ear emergence times and vernalisation requirement is possible by genetical manipulation of this variation.

1. INTRODUCTION

INVESTIGATIONS of the genetical control of ear emergence time in bread wheat, *Triticum aestivum* ($2n = 6x = 42$) using monosomic analysis on the one hand and chromosome substitution lines on the other, have shown that major effects are associated with chromosomes 5A and 5D (Unrau, 1950; Kupsira and Unrau, 1957; Halloran and Boyde, 1967; Law, 1968, 1972; Maystrenko, 1974). These same investigations have shown that these effects are synonymous with the response to vernalisation treatments; these chromosomes being important determinants of the spring-winter polymorphism of wheat.

Conventional genetic analysis by Akerman and Mackey (1949) and Pugsley (1971, 1972) have shown that spring habit is controlled by at least four independent, dominant loci with large effects, any one of which is able to reduce the requirement for vernalisation. These loci have been designated *Vrn* 1, 2, 3 and 4 and the aneuploid analyses have equated *Vrn* 1 and *Vrn* 3 with the effects of chromosomes 5A and 5D, respectively.

More detailed analysis of the genetical control of ear emergence time using substitutions of chromosomes 5A and 5D from the variety Hope into the variety Chinese Spring by Law, Worland and Giorgi (1976) showed that a single factor located distally on the long arm of both chromosomes was responsible for the variation between these substitution lines and the recipient. They equated these factors with the *Vrn* 1 and *Vrn* 3 loci. However they also found that substitutions of chromosome 5A from other varieties into Chinese Spring had differential effects on the ear emergence time of this variety. Either, therefore, a multiple allelic series exists at the *Vrn* 1 locus, or more than one factor controlling ear emergence time is carried on this chromosome, these being homozygous with respect to the Hope/Chinese Spring difference.

The present paper presents a more detailed analysis of the variation between these different 5A chromosomes and examines the genetical relationship between them.

2. MATERIALS AND METHODS

Substitution lines of chromosome 5A from the varieties Cappelle-Desprez, Hope, Timstein and *Triticum spelta* into Chinese Spring were chosen for investigation. These substitution lines represent a range of ear emergence times, earlier and later than euploid Chinese Spring. The Cappelle-Desprez and *T. spelta* substitution lines were developed at the Plant Breeding Institute and the Hope and Timstein substitution lines by Dr E. R. Sears at the University of Missouri, U.S.A.

The four substitution lines plus Chinese Spring were crossed reciprocally in all combinations and selfed to produce a 5×5 diallel.

The F_1 progeny of these crosses was sown in a randomised block design in a constant environment room. One plot of four plants of each parental line and one plot of four plants of each reciprocal cross were grown in each of two blocks. The plants were grown under a regime of continuous light at 20°C and ear emergence times recorded.

3. RESULTS

Variation between blocks and reciprocal crosses and block interactions was found to be non-significant, so that in the analyses presented the data have been averaged over reciprocals and blocks and the sums of squares of these effects pooled.

Table 1 shows the mean ear emergence times of each genotype, measured from the sowing date. Clearly there are large differences between the 5A chromosomes with respect to their effect on ear emergence on a Chinese Spring background. The analysis of variance of these data (table 2) confirms this and further shows that significant differences are exhibited both between the substitution lines and the hybrids, and between the means of the two groups.

TABLE 1
Mean ear emergence times (days from sowing)

	Chinese Spring (CS)	CS (<i>Triticum spelta</i> 5A)	CS (Hope 5A)	CS (Timstein 5A)	CS (Cappelle- Desprez 5A)
Chinese Spring	64.59	52.00	54.56	62.38	67.00
CS (<i>Triticum spelta</i> 5A)		45.88	50.00	55.88	60.50
CS (Hope 5A)			50.34	53.36	61.31
CS (Timstein 5A)				61.92	66.00
CS (Cappelle-Desprez 5A)					72.25

Parental mean = 60.63.

Hybrid mean = 58.80.

TABLE 2
Analysis of variance

Item	d.f.	M.S.	P
Between genotypes	14	703.39	<0.001
Between parental lines	4	1305.53	<0.001
Between hybrids	9	498.53	<0.001
Parental lines <i>v.</i> Hybrids	1	138.59	<0.001
Pooled Error	181	4.70	
Total	195		

These results confirm those obtained by Law *et al.* (*loc. cit.*) about the differential effects of different 5A chromosomes and in the present study the chromosomes may be ranked in order of "earliness" as *Triticum spelta* 5A, Hope 5A, Timstein 5A, Chinese Spring 5A and Cappelle-Desprez 5A.

The significance of the Parental lines *v.* Hybrids item in the analysis of variance suggests that the hybrids exhibit potence with respect to the "early" chromosomes. The dominance relationships of the different chromosome combinations can be examined in detail by calculating the deviation of each hybrid from its mid-parental value. The values obtained are shown in table 3. Significant potence is exhibited in only three crosses, those of Chinese Spring (CS) $\times$ CS (*Triticum spelta* 5A), CS $\times$ CS (Hope 5A), and CS (Timstein 5A) $\times$ CS (Hope 5A). In each case potence is in the direction of the early chromosome. This is in agreement with the results of Law *et al.* (*loc. cit.*) and Pugsley (1971).

TABLE 3
Potence relationships

	CS (<i>Triticum spelta</i> 5A)	CS (Hope 5A)	CS (Timstein 5A)	CS (Cappelle- Desprez 5A)
Chinese Spring	-3.24*	-2.90*	-0.88	-1.42
CS (<i>Triticum spelta</i> 5A)		+1.90	+1.98	+1.44
CS (Hope 5A)			-2.77*	+0.02
CS (Timstein 5A)				-1.09
CS (Cappelle-Desprez 5A)				

Probability: * = 0.05-0.01.

In order to investigate further the relationships between these chromosomes it is possible to set up models including different numbers of factors and to describe each of the parental lines in terms of whether they carry the + (late) or - (early) component of a factor. The validity of such models can be tested by least squares fitting techniques on the generation means.

From the data in table 1 the five 5A chromosomes can be roughly classified into three groups, according to their ear emergence times. *Triticum spelta* and Hope, constitute an "early" group, Timstein and CS an "intermediate", and Cappelle-Desprez a "late" group. Similarly within the first two groups the difference between *Triticum spelta* and Hope on the one hand, and Timstein and CS on the other are similar in magnitude. Thus it is possible to specify the differences between the five chromosomes in terms of three factors. First a factor whose + and - components specify the difference between the "early" plus "intermediate" genotypes and Cappelle-Desprez. Secondly a factor whose components specify the difference between the "early" and "intermediate" genotypes; and thirdly a factor whose components specify the differences within the first two groups. If these factors are arbitrarily called f_1 , f_2 and f_3 respectively, then each chromosome can be defined as carrying the + or - components of each factor (table 4). In genetical terms the + and - components can be taken as the two alleles at each of three separate loci, although of course, in the present case they cannot be identified as such. Nevertheless, the above model can be tested by conventional least squares fitting techniques on the observed mean ear emergence times of the five genotypes. Four parameters are necessary to

parental lines. Equally the small dominance effects would suggest that heterozygous $\times$ heterozygous effects would not be large. However homozygous $\times$ heterozygous (j) interactions may be the cause of failure of the model.

Models of different " j " type interactions were fitted to the data and a minimum of three extra parameters was needed to sufficiently explain the observed variation (table 6). This ten-parameter model gives a satisfactory fit to the observed data.

TABLE 6
Model fitting on parental lines and hybrids

Parameter	7- parameter model	10-parameter model
$\hat{m}$	61.11***	61.13***
$\hat{d}_1$	5.39*	4.80**
$\hat{d}_2$	6.48*	7.84***
$\hat{d}_3$	0.74 n.s.	1.52*
$\hat{h}_1$	0.24 n.s.	-0.36 n.s.
$\hat{h}_2$	-0.88 n.s.	0.31 n.s.
$\hat{h}_3$	-0.35 n.s.	0.26 n.s.
j_{12}	—	2.07 n.s.
$j_{13} = j_{31}$	—	1.06 n.s.
$j_{23} = j_{32}$	—	-1.91*
	$\chi^2_{[8]} = 27.4^{**}$	$\chi^2_{[5]} = 0.16$ n.s.

Probability: * = 0.05-0.01;
 ** = 0.01-0.001;
 *** = < 0.001.

4. DISCUSSION

The three factor model proposed provides a satisfactory explanation of the "multiple allelism" of these 5A chromosomes from different varieties. Interestingly, on this model, two crosses, namely CS $\times$ CS (*Triticum spelta* 5A) and CS (Hope 5A) $\times$ CS (Timstein 5A) have the same genetical expectations. In fact, the analysis of variance of the raw data for these two crosses fails to detect any difference between them.

However it is not possible from these data to discover whether the three factors are three separate loci or three components of the same locus, for example different mutational sites. To do this it is necessary to examine segregants from these hybrids. A particularly sensitive method of detecting recombination was used by Law *et al.* (*loc. cit.*) where the recipient monosomic for the chromosome in question was used to derive homozygous products from hybrids between CS and CS (Hope 5A). They detected no recombinants but as can be seen from table 4, none are expected on the present model since these lines only differ by the factor f_2 . To detect recombination requires, of course, that the parental lines differ by at least two factors and the cross of CS (Cappelle-Desprez 5A) $\times$ CS (Hope 5A) should be particularly efficient in this respect since recombinant lines containing all three + components are expected. Such lines would be later than either the parental lines or the hybrid, and chromosomes of this type may already exist in extreme winter wheats.

On the model proposed here the *Triticum spelta* 5A is the "earliest" possible chromosome. This chromosome would be particularly potent if transferred into winter wheats, transforming them into spring-type wheats

because of their much reduced vernalisation requirement. This can easily be done using the chromosome substitution techniques described by Law and Worland (1973) and may have important consequences in plant breeding and also in providing valuable stocks for looking at the underlying physiological and developmental processes associated with ear emergence and vernalisation requirement.

The variation between the different 5A chromosomes contrasts with the variation found for chromosome 5D by Law *et al.* (*loc. cit.*), where they detected fewer variants. However their evidence of the homology of the genes *Vrn 1* and *Vrn 3* on 5A and 5D through their use of alien substitution lines would suggest that similar variation to the 5A variation may be found for 5D. They also suggested that CS (Hope 5D) was equivalent to CS (Cappelle-Desprez 5A), and CS5D was an "early" chromosome equivalent to either Hope 5A or *T. spelta* 5A. If this is so, then recombinants should have been observed from the cross of CS with CS (Hope 5D) if the three factors hypothesised in this paper are distinct and easily separable loci. No recombinants were found from this cross (Law *et al.*, *loc. cit.*), suggesting that the genetic description of the variation on chromosome 5A relates to either a tightly linked group of genes or different components of the *Vrn 1* locus. The genetic validity of the three factor model may thus be difficult to establish except that it may be possible to identify the different variants predicted by the model among other substitution lines of chromosome 5A in CS.

Using the wide variation evidently available on chromosome 5A and 5D it should be possible to finely adjust the ear emergence times of a spring sown variety to achieve close adaptation to different environments. Similar adaptation of winter sown varieties to different vernalisation treatments should also be possible so that a wide adaptation to different environmental conditions could be achieved using one basic variety if desired.

5. REFERENCES

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