53. Studies on the Right- and Left-Handedness of Spikelets in Einkorn Wheats. VI. Polygenic Analysis in a Species Cross

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In the preceding papers of this series, it has been reported that the expression ($\bar{C}$ value) of the right- and left-handedness of spikelets in wheats is controlled by a polygenic system. Since 1951 we have been working on a crossing experiment between two species of Einkorn wheats in order to investigate in detail the genetic nature of this character. The materials used were *Triticum monococcum flavescens* (P_1), *Triticum aegiopoides boeoticum* (P_2), and the derivatives of the hybrid between them; their $\bar{C}$ values are shown in Table I.

Table I. Number of plots and means of $\bar{C}$ values in the cross between two Einkorn wheats

Generation		P_1		P_2		F_1		F_2		F_3		B_1		B_2		B_{1S}		B_{2S}	
Block		I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II
I	No. of plots planted	6	6	6	6	6	8	16	16	122	137	10	10	7	7	10	10	24	17
II	No. of plots observed	3	5	0	1	3	6	3	10	28	38	5	5	3	5	4	3	4	5
III	Mean of $\bar{C}$ value (%)	78.25		88.20		93.38		87.23		84.93		86.71		90.54		82.93		89.80	

Experiment and Analysis. In 1951 the first cross between the two species was made, and in the autumn of 1953 all materials necessary for the analysis were planted in duplicated randomized-blocks. The generations included in the present experiment, the number of plots (each plot comprising ten plants at the beginning of the experiment), and the mean values for each generation are represented in Table I in which the values of reciprocal crosses were pooled, since the deviations between them were non-significant.

The mean values. The frequency distributions of the $\bar{C}$ values in various generations are plotted on the cumulative probability in Fig. 1. The F_1 shows extreme heterosis in the $\bar{C}$ value of 93.38%, while the selfed F_2 and F_3 generations show a remarkable retrogression toward the mid-parental value of 83.23% and the first back-crossed generations toward the midway of the corresponding parents, as expected from Mendelian inheritance. These retrogressions of

generation means are contained in the left side column of Fig. 1. A considerable skewness is found in the distribution of F_1 plants.

The scaling. In the polygenic analysis it is indispensable to test the adequacy of the scale to be used in the measurement of phenotypes. In the present analysis the adequacy of $\bar{C}$ value as the scale was tested by the following two criteria: first, the genic effects must on the average be simply additive, and secondly, the contribu-

Fig. 1. The distribution of $\bar{C}$ values in various generations and generation means

tion made by the genotype must be independent from that of environment (Mather, 1948). The first criterion was tested by the comparison of the mean measurements of various segregating generations. The results of this test will be found in Table II a, in which $\bar{B}_1 = 1/2 (\bar{P}_1 + \bar{F}_1)$, $\bar{B}_2 = 1/2 (\bar{P}_2 + \bar{F}_1)$, and $\bar{F}_2 = 1/4 (\bar{P}_1 + \bar{P}_2 + 2\bar{F}_1)$ are tested.

The test of conformity with the second criterion is equivalent to that of variance-ratios between two non-segregating generations of different genotypes. The tests of variance-ratios will be found in Table II b. The results shown in Table II give no proof in respect of the inadequacy of the $\bar{C}$ values as the scale for the present polygenic analysis, except for the slightly significant discrepancy between the variances of the $\bar{P}_1$ and $\bar{F}_1$. Therefore, the $\bar{C}$ values may be regarded as an adequate measurement in spite of the skewness observed in the frequency distribution of $\bar{F}_1$ plants.

The partitioning of the second degree statistics into their components. In general a polygenic segregation causes an increase of variances and the occurrence of covariances between the parents and

Table II. Scaling tests

a) Additiveness			b) Independency		
Formulae	Block I	Block II	Combination	Variance ratio	
				Block I	Block II
$A=2\bar{B}_1-\bar{P}_1-\bar{F}_1$	-0.46 ± 9.08	-6.50 ± 6.37	$V_{\bar{P}_1}/V_{\bar{F}_1}$	2.08	—
$B=2\bar{B}_2-\bar{P}_2-\bar{F}_1$	—	1.50 ± 11.83	$V_{\bar{F}_1}/V_{\bar{P}_1}$	—	$9.08^{*)}$
$C=4\bar{F}_2-2\bar{F}_1-\bar{P}_1-\bar{P}_2$	—	1.68 ± 18.21	$V_{\bar{P}_1}/V_{\bar{F}_1}$	1.65	1.65
			$V_{\bar{P}_2}/V_{\bar{P}_1}$	—	1.52
			$V_{\bar{P}_2}/V_{\bar{F}_1}$	—	2.50

*) Significant.

their offspring. In the second column of Table III the expected constitutions of variances and covariances found in the present experiment are shown in terms of D, H, E_1 , and E_2 which designate the sums of contributions of homozygous loci, heterozygous loci, environmental effects on individuals, and means of plots to the variation. The observed values of the statistics are shown in the third column of Table III, and are also given in the pooled forms over Block I and Block II on the account of insufficient information in each block caused by a great number of missing plots.

Table III. The observed and expected values in the crossing experiment of two Einkorn wheats

Statistics	Expected constitution of variance and covariance	Observed	Expected	Deviation
V_{P_1}		30.311		
V_{P_2}		57.200	36.85411	-6.22911
V_{F_1}		26.086		
Pooled	$E_1 =$	30.625		
$V_{\bar{F}_1}$		13.311		
$V_{\bar{F}_1}$		26.036	16.24262	3.85538
Pooled	$E_2 =$	20.098		
V_{F_2}	*) $\frac{1}{2}D + \frac{1}{4}H + E_1 =$	74.372	66.20552	8.16648
$V_{B_1} + V_{B_2}$	*) $\frac{1}{2}D + \frac{1}{2}H + 2E_1 =$	106.554	114.68152	-8.12752
$V_{\bar{F}_3}$	*) $\frac{1}{2}D + \frac{1}{16}H + E_2 =$	35.957	36.87761	-0.92061
$\bar{V}_{F_3}$	*) $\frac{1}{4}D + \frac{1}{8}H + E_1 =$	50.977	51.52981	-0.55281
$W_{F_2/\bar{F}_3}$	*) $\frac{1}{2}D + \frac{1}{8}H =$	10.113	23.54046	-13.42746
$V_{\bar{B}_{1S}} + V_{\bar{B}_{2S}}$	$\frac{1}{2}D + \frac{1}{8}H + 2E_2 =$	54.555	56.02570	-1.47070
$\bar{V}_{B_{1S}} + \bar{V}_{B_{2S}}$	$\frac{1}{2}D + \frac{1}{4}H + 2E_1 =$	110.497	103.05963	7.43737
$W_{B_1/\bar{B}_{1S}} + W_{B_2/\bar{B}_{2S}}$	$\frac{1}{2}D + \frac{1}{4}H =$	37.964	29.35141	8.61259

*) Formulae according to K. Mather (1948).

From the ten equations in the second column in Table III, each consisting of the expected constitution and the observed value of the statistics, the following values of D, H, E_1 , and E_2 were calculated by the least squares method: $D=35.459\pm 17.031$, $H=46.488\pm 37.781$,

$E_1=36.854\pm4.907$, and $E_2=16.243\pm4.766$. The heritable portions in the variances and the covariances were also calculated as follows: $\frac{1}{2}D+\frac{1}{4}H=29.351\pm12.717$, $\frac{1}{2}D+\frac{1}{2}H=40.974\pm20.721$, $\frac{1}{2}D+\frac{1}{16}H=20.635\pm8.837$, $\frac{1}{4}D+\frac{1}{8}H=14.675\pm6.358$, and $\frac{1}{2}D+\frac{1}{8}H=23.541\pm9.737$.

As to the relative magnitude of the four components of variation, it is a remarkable fact that in the present experiment the contribution of heterozygous loci is considerably large, compared with the results obtained by other investigators in various plants (Mather, 1948, and Copp and Wright, 1952). But the value of H cannot be reliable because of its large standard error. The expected values of various statistics are given in the fourth column of Table III and also compared schematically with the observed values in Fig. 2.

Fig. 2. Variation of the $\bar{C}$'s in Einkorn cross

The middle column of each statistics is the observed value, the left the expected value calculated from the statistics of all generations, the right the expected value calculated from the statistics, consisted of same linkage terms in D and H. The right column in V_{F_2} , V_{F_3} , and W_{F_2/F_3} represents the expected value calculated from the statistics excluding all the others (D is minus), and that in $V_{B_1}+V_{B_2}$, $V_{B_1S}+V_{B_2S}$, and $W_{B_1/B_2S}+W_{B_2/B_2S}$ the expected value excluding other statistics (H is minus).

Table IV. General formulae of D and H taking linkage in consideration

Statistics	D	H
$V_{F_2}^*$	$S(d^2)+2Sc[(1-2p)d_ad_b]$ $-2Sr[(1-2p)d_ad_b]$	$S(h^2)+2S[(1-2p)^2h_ah_b]$
$V_{F_3}^*$	„	„
W_{F_2/F_3}^*	„	„
$\bar{V}_{F_3}^*$	$S(d^2)+2Sc[(1-2p)^2d_ad_b]$ $-2Sr[(1-2p)^2d_ad_b]$	$S(h^2)+2S[(1-2p)^2(1-2p$ $-2p^2)h_ah_b]$
$V_{B_1}+V_{B_2}^*$	$S(d^2)+2Sc[(1-2p)d_ad_b]$ $-2Sr[(1-2p)d_ad_b]$	$S(h^2)+2S[(1-2p)h_ah_b]$
$V_{B_1S}+V_{B_2S}$	$S(d^2)+2Sc[(1-2p)d_ad_b]$ $-2Sr[(1-2p)d_ad_b]$	$S(h^2)+2S[(1-2p)h_ah_b]$
$\bar{V}_{B_1S}+\bar{V}_{B_2S}$	$S(d^2)+2Sc[(1-p)(1-2p)d_ad_b]$ $-2Sr[(1-p)(1-2p)d_ad_b]$	$S(h^2)+2S[(1-p)(1-2p)^2h_ah_b]$
$W_{B_1/B_2S}+W_{B_2/B_2S}$	$S(d^2)+2Sc[(1-2p)d_ad_b]$ $-2Sr[(1-2p)d_ad_b]$	$S(h^2)+2S[(1-2p)h_ah_b]$

p: Recombination value, c: Coupling, r: Repulsion

d: Contribution of homozygous loci, h: Contribution of heterozygous loci

* The asterisked formulae were taken from K. Mather (1948).

The linkage relation. The presence of linkage does not change the mean values of various generations but changes the values of D and H as shown in Table IV. The detection of linkage was tested by the analysis of variance as follows. The total sum of squares was calculated from the deviations in Table III, and this included both sums of squares due to the variation of the various linkage terms shown in Table IV and due to the variation within the variances and covariances consisting of the same linkage terms in each of D and H. In the present experiment there are two such groups; one V_{F_2} , $V_{\bar{F}_3}$, and $W_{F_2/\bar{F}_3}$, and the other $V_{B_1} + V_{B_2}$, $V_{\bar{B}_{1S}} + V_{\bar{B}_{2S}}$, and $W_{B_1/\bar{B}_{1S}} + W_{B_2/\bar{B}_{2S}}$. The estimates of D and H in each of these two groups are calculated by the least squares method with the following estimates of E_1 and E_2 : in the former group $D = -9.017$, $H = 173.992$, $E_1 = 33.004^*$, and $E_2 = 28.845^*$, and in the latter $D = 77.798$, $H = -19.281$, $E_1 = 36.667^*$, and $E_2 = 15.433$ in which only the asterisked values are statistically significant at 5% level.

The expected variances and covariances of these groups are represented in Fig. 2. The sum of squares of the deviations between the expected and the observed values in each group corresponds to the error sum of squares. Therefore, two analyses of variance for the test of linkage were made as follows.

Selfed generations					Backcrossed generations				
Items	S.S.	D.F.	M.S.	P	Items	S.S.	D.F.	M.S.	P
Linkage	392.341	5	78.468	0.3 > P > 0.2	Linkage	246.612	5	49.324	0.1 > P > 0.05
Error	107.177	1	107.177		Error	252.906	1	252.906	
Total	499.518	6			Total	499.518	6		

The results of both analyses of variance are not significant, and, therefore, we cannot assume the presence of linkage in the present experiment.

Conclusions. (1) Throughout this experiment the $\bar{C}$ value was used as the adequate scale to measure the expression of R/L-handedness of spikelets.

In the first report of this series, Kihara et al. (1951) assumed that the determination of the right- and left-handedness was controlled by the threshold reaction. As the $\bar{C}$ value is a mean of concordance proportions which are the direct measure of R/L-handedness, the transformed value of the $\bar{C}$ into *probit* may be regarded as a more adequate scale in the polygenic analysis. In fact, the distribution of the F_1 plants can be put into a more normalized distribution by the probit transformation. But the transformed scale into probit may not be as convenient as the usual percentage scale $\bar{C}$, as found in this experiment in which

the $\bar{C}$ values give direct representation of the character.

(2) The number of segregating generations used in this experiment is larger than that reported in experiments carried out by other workers. Besides the two parental strains, F_1 , F_2 , and F_3 -families, backcrosses and selfed backcross generations were used.

In this way insufficient information in each generation due to a number of missing plots was compensated.

(3) The genetic portion in variances of various generations was found to be significant, and the heritability of F_2 generation in broad sense was about 44.33%. As shown in Fig. 2, the non-heritable portion of variation was found to be large, compared with the genotypic component.

This may have been caused by the following two facts: First, a wide variation of this character was due to environmental fluctuations and second, experimental systematic errors caused by adverse field conditions in the winter of 1953. As reported in the fourth paper of this series, the variation range of the $\bar{C}$ value due to nutritional conditioning amounted to about 20% which could cover nearly half of the whole distribution range of the present experiment.

In addition, the field conditions were so adverse that about 70% of the originally planted materials were degenerated. Consequently it may be understandable that the environmental variance was considerably larger than the genotypic one.

The adverse conditions may be also responsible for the magnitude of the standard error of D and H. If the duplication of the randomized-blocks was retained, the standard errors could be reduced so that the magnitudes of D and H would have been significant.

(4) The numbers of effective factors were estimated by several methods. The largest estimate was 2.3 and the smallest 0.6. But the values were not always reliable.

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