M. Feldman

Chromosomal Location of Genes for Some Quantitative Characters of Wheat Using Chromosome Substitution Lines

M. SASAKI,* M. MORIYASU,* R. MORRIS,† AND J. W. SCHMIDT†

* Faculty of Agriculture, Tottori University, Tottori, Japan.
† Department of Agronomy, University of Nebraska, Lincoln, Nebr., U.S.A.

The technique and the significance of using chromosome substitution lines in studying the genetics of quantitative characters of polyploid organisms have been described and developed by SEARS (1953), UNRAU *et al.* (1956), KUSPIRA and UNRAU (1957) and LAW (1965, 1966). This paper deals with the results of a study on the chromosomal locations of genetic factors affecting some quantitative characters when chromosomes of the hard red winter wheat variety 'Cheyenne' were substituted singly into the spring variety 'Chinese Spring'.

MATERIALS AND METHODS

The Cheyenne disomic substitution lines in Chinese Spring used in this study were developed at the University of Nebraska (MORRIS *et al.*, 1966). Four backcrosses to Chinese Spring were made for all the chromosomes except 2A(II) and 2D (three backcrosses). There is some doubt about the identity of the substituted chromosomes in the lines for 2D, 1D, and 4D. Therefore, the redevelopment of these lines is in progress.

All the substitution lines, along with the parents Cheyenne and Chinese Spring as checks, were grown at Tottori, Japan in the crop season of 1965-1966. Three-week-old seedlings grown in a nursery bed were transplanted into the field. All lines were planted in single-row plots 60 cm apart and 1 m long, and plants were placed 10 cm apart in the row. Ten plants were used for each plot in a randomized block design with four replicates. The data for each of the characters studied were taken on the mature plants after harvesting. Culm length, internode length, flag leaf length and width, flag leaf sheath length, spike length, number of spikelets per spike, seed fertility (number of kernels per spike) were measured using a leading culm of each plant.

RESULTS AND DISCUSSION

The effects of substituting each Cheyenne chromosome for the homologous Chinese Spring chromosome in Chinese Spring background were compared with

TABLE 1. Expression of 14 wheat characters in 21 Cheyenne disomic substitution lines and Cheyenne (Cnn), shown as difference between each line and Chinese Spring (Cns), the recipient variety, 1966.

Line	Culm. length cm	Internode length 1st[1] cm	2nd cm	3rd cm	Flag leaf Length cm	Width mm	Sheath length cm	Spike Length cm	No. spikelets	No. kernels	Seed fertility	No. tillers	1000-Kernel weight g	Yield per plant g
1A	−3.0[2]	−3.3*	−2.9*	−0.6	0.0	+1.1	−2.6**	−0.1	+0.9	+3.8	+0.05	−2.6	−0.6	−0.6
1B	−1.5	−1.3	−2.1	−0.7	−1.1	−0.8	−2.5**	−0.4	+1.2*	+0.8	−0.07	−2.6	+2.2	+1.0
1D	−1.6	0.0	−1.5	−1.0	−0.6	−0.1	−2.2*	−0.6*	+0.8	+0.4	−0.12	−1–7	−0.7	−0.9
2A[3]	−4.4	+2.6	−1.9	−2.0	+1.1	+1.7*	−1.0	0.0	−1.0	−0.5	+0.05	−0.3	+0.3	−0.2
2B[3]	+12.5**	+5.0**	−0.4	+1.9	+0.1	0.0	−1.5	−0.7*	+1.7**	+2.5	−0.10	+0.3	−6.3**	−0.8
2D	−6.9*	−0.1	−3.3*	−2.3*	−0.8	−1.4	−2.3**	+0.6*	+0.8	−0.9	−0.15	+0.1	−0.1	+3.8
3A	−3.7	−2.1	+1.0	−0.4	−0.7	+1.7*	−2.1*	−1.2**	−0.6	−4.2	−0.15	+0.4	+0.3	+3.0
3B	−12.2**	−2.3	−1.0	−1.0	−0.1	−0.1	−1.7*	−1.1**	−0.3	−3.7	−0.20*	−2.1	+4.8**	+1.7
3D	−10.8**	−1.7	−3.5*	−3.7**	−0.5	0.0	−2.2*	−0.7*	0.0	0.0	−0.02	−1.8	−3.7**	−0.7
4A	−2.9	−2.8	−1.6	+1.1	−2.0	+0.6	−2.7**	−0.9**	+0.1	−5.4	−0.27**	−0.4	+8.9**	+4.2
4B	−6.0*	−2.0	−4.1**	−1.0	−1.4	+1.0	−3.3**	−0.1	+1.8**	+0.3	−0.15	−0.7	−0.6	+0.4
4D	−6.7*	−3.4*	−4.1**	−2.6*	−3.8**	−0.5	−3.4**	−1.0**	+1.1	−0.9	−0.15	−1.0	+0.5	+2.4
5A	−6.7*	−4.2**	−1.0	−0.3	−3.2*	+0.6	−2.5**	−1.2**	+1.1	+1.5	−0.05	+1.9	−1.7	+1.3
5B	+0.5	+0.3	−0.2	+0.6	−2.1	−0.4	−1.9*	−0.3	+0.2	−1.6	−0.12	−2.4	+1.7	−0.2
5D	−5.0	−5.5**	−1.8	−0.8	−5.4**	−0.9	−4.0**	−0.9**	+0.4	−3.8	−0.25*	−1.4	−1.0	+1.2
6A	−16.1**	−0.8	−4.7**	−3.9**	−3.3**	−2.1**	−1.0	−0.4	−1.7**	−6.9	−0.20*	−2.8	−7.7**	−1.4
6B	+0.9	−1.3	−1.8	+0.3	−2.3	+2.2**	−3.4**	+0.3	+1.7**	+7.7*	+0.10	+0.5	−0.8	+6.0*
6D	−3.2	+0.5	−3.5	−2.0	−1.8	+0.7	−1.5	−0.3	0.0	−3.9	−0.20*	−3.5*	+4.7**	+2.3
7A	+0.6	+1.5	−1.3	−1.0	−0.4	+0.6	+0.7	+0.2	+2.2**	+6.0	0.00	−2.8	+1.3	+1.7
7B	+2.9	+3.2*	−0.9	−1.0	−0.9	+0.5	−3.6**	+0.1	+2.1**	+7.5	+0.10	−1.0	+1.0	+5.3*
7D	−2.9	−1.5	−2.5	−0.2	−2.0	+1.7	−3.1**	−0.2	+2.9**	+4.0	+0.08	+0.5	−0.5	+2.9
Cnn	+8.2**	+15.1**	−4.6**	−3.1**	−1.4	−3.1**	−1.2	+1.8**	−0.8	−14.4**	−0.55**	−0.1	+5.8**	−3.1
Cns	101.5[4]	37.8	29.4	18.5	26.6	13.6	22.4	7.9	22.1	51.2	2.35	17.4	31.8	18.2
LSD (5%)	5.4	3.1	2.7	2.2	2.5	1.6	1.7	0.6	1.2	7.7	0.20	3.2	2.3	4.8
LSD (1%)	7.2	4.1	3.6	2.9	3.3	2.0	2.3	0.8	1.5	10.2	0.26	4.3	3.0	6.4

[1] First internode below spike.

[2] Positive or negative numerals are the difference of measurements between Cns as a check and each of the substitution lines or Cnn.

[3] 2A=II, 2B=XIII.

[4] Mean values of four replicates. * Significant at the 5% level. ** Significant at the 1% level.

the recipient variety Chinese Spring. An analysis of variance was made for each character using each plot mean of all the substitution lines. The differences between Chinese Spring as a check and each of the substitution lines or Cheyenne, using the means of four replicates, are shown in Table 1.

Most of the substitution lines showed an increase in some characters and a decrease in others as a result of chromosome substitution regardless of whether the character in question was significantly larger or smaller in Cheyenne than in Chinese Spring. For example, the culm length of Cheyenne was significantly longer than that of Chinese Spring, but only the 2B(XIII) Cheyenne substitution line had significantly longer culms than Chinese Spring. Substitution lines 2D, 3B, 3D, 4B, 4D, 5A and 6A had significantly shorter culms than Chinese Spring. Such a significant increase or decrease in culm length of the substitution lines cannot be attributed entirely to the Cheyenne chromosomes substituted. The differences between Chinese Spring and the substitution lines are due to the total effects of the differences between the substituted Cheyenne chromosomes and the Chinese Spring counterparts in regard to the additive effects of whole chromosomes, including non-allelic interactions of genes on those chromosomes. In addition, between-chromosome interactions can occur when a single pair of Cheyenne chromosomes is substituted into a genetic background having 20 pairs of Chinese Spring chromosomes.

At the moment, however, the substitution effects which show a significant departure from the recipient variety Chinese Spring will be treated as the genetic effects of the chromosomes substituted. In Table 2 are presented only the substitution lines with significant departures in character expressions from those of Chinese Spring.

It is of interest that the significant deviations from Chinese Spring for various characters were all negative for 8 of the 21 substitution lines (1A, 1D, 3D, 4D, 5A, 5B, 5D, and 6A). The significant substitution effects of Cheyenne chromosomes were also all negative for the following characters: second and third internode lengths, flag leaf length, flag leaf sheath length, and seed fertility. All these characters were inferior in the donor variety Cheyenne compared to those of Chinese Spring.

On the contrary, though the yield per plant of Cheyenne was lower than that of Chinese Spring, the significant substitution effects of chromosomes 6B and 7B were all positive. This is shown in Table 3, where substitution lines having higher yielding ability than Chinese Spring are given together with data on yield components. The increase in yield of lines 6B and 7B was mainly attributed to the increase in number of spikelets per spike without a decrease in seed fertility. Accordingly, these two lines were significantly or nearly significantly higher in number of kernels per spike. On the other hand, the yield increase of line 4A, though not statistically significant, was caused merely by the significant increase of 1000-kernel weight, whereas seed fertility decreased significantly. This situation has often been reported in the case of varietal

TABLE 2. Chromosomes with significant substitution effects on character expression of Cheyenne disomic substitution lines, and performance of Cheyenne, 1966.

Line	Culm length	Internode length			Flag leaf			Spike						Yield per plant
		1st	2nd	3rd	Length	Width	Sheath length	Length	No. spikelets	No. kernels	Seed fertility	No. tillers	1000-Kernel weight	
1A		−[2]	−				=							
1B							=		+					
1D							−	−						
2A[1]						+								
2B[1]	++	++						−	++				=	
2D	−		−	−			=	+						
3A						+	−	=						
3B	=						−	=			−		++	
3D	=		−	=			−	−					=	
4A							=	=			=		++	
4B	−		=				=		++					
4D	−	−	=	−	=		=	=						
5A	−	=			−		=	=						
5B							−							
5D		=			=		=	=			−			
6A	=		=	=	=	=			=		−		=	
6B						++	=		++	+				+
6D											−	−	++	
7A									++					
7B		+					=		++					+
7D							=		++					
Cnn	++	++	=	=		=		++		=	=		++	

[1] 2A=II, 2B=XIII [2] +, ++, or −, =: Positive or negative differences were significant at the 5% and 1% levels, respectively.

variations in many crops, but the fact that it occurs as a chromosome-to-chromosome variation attracts our attention from the point of view of plant breeding. It might be of interest to develop a double disomic substitution line of Cheyenne chromosomes 6B, 7B and others that are largely responsible for yield components.

TABLE 3. Relationships between yield per plant and some yield components in some higher-yielding substitution lines than Chinese Spring, 1966.

Line	Yield per plant gr	No. spikelets per spike	No. kernels per spike	Seed fertility	1000-kernel weight gr	No. tillers
6B	+6.0[1]*	+1.7**	+7.7*	+0.10	−0.8	+0.5
7B	+5.3*	+2.1**	+7.5	+0.10	+1.0	−1.0
4A	+4.2	+0.1	−5.4	−0.27**	+8.9**	−0.4
2D	+3.8	+0.8	−0.9	−0.15	−0.1	+0.1
3A	+3.0	−0.6	−4.2	−0.15	+0.3	+0.4
7D	+2.9	+2.9**	+4.0	+0.08	−0.5	+0.5
4D	+2.4	+1.1	−0.9	−0.15	+0.5	−1.0
6D	+2.3	0.0	−3.9	−0.20*	+4.7**	−3.5*
Cnn	−3.1	−0.8	−14.4**	−0.55**	+5.8**	−0.1
Cns[2]	18.2	22.1	51.2	2.35	31.8	17.4
LSD (5%)	4.8	1.2	7.7	0.20	2.3	3.2
LSD (1%)	6.4	1.5	10.2	0.26	3.0	4.3

[1] The difference between Cns as a check and the substitutions. [2] Mean values of four replicates.
* Significant at the 5% level. ** Significant at the 1% level.

In Table 4 are given the phenotypic and genotypic correlations estimated between characters, and heritability values estimated for each character, treating the 21 different substitution lines as a group. In this case very high genotypic correlations were obtained for yield per plant and both number of spikelets per spike and 1000-kernel weight (0.99 and 0.89, respectively). The relationships between these characters did not exactly run parallel with each substitution line, such as 6B, 7B or 4A as already mentioned above. The genotypic correlation between yield per plant and seed fertility showed a negative value of — 0.62, whereas the phenotypic correlation of 0.51 was positive. Genotypic correlations between yield per plant and some other characters are illustrated diagrammatically in Figure 1.

Furthermore, it is valuable to note that a high negative genotypic correlation of r = — 0.85 was obtained between yield and flag leaf length. In this connection, TANAKA (1965) showed that, under intensive cultivation of rice, a high assimilatory efficiency was inherent in plants with a relatively small number of short and erect leaves that minimize mutual shading.

TABLE 4. Estimated phenotypic and genotypic correlations and heritability values of 14 different characters for the 21 Cheyenne disomic substitution lines treated as a group, 1966.

Character	Culm length cm	Internode length 1st[1] cm	Internode length 2nd cm	Internode length 3rd cm	Flag Leaf Length cm	Flag Leaf Width mm	Flag Leaf Sheath length cm	Spike Length cm	Spike No. spikelets	Spike No. kernels	Seed fertility	No. tillers	1000-Kernel weight g	Yield per plant g
Culm length		1.82[1]**	1.37[3]**	1.41**	.60**	.06	.34**	.27**	−.87	.55**	.49**	.31**	−.60	.40**
	(.52)[2]	.19	.52	.85	.35	.03	−.15	.06	.21	.61	.09	−.67	.66	−.51
Internode length 1st			.70	.49**	.86**	.04	.70**	.30**	.36**	−1.55	.08	.36**	.17	.46
		(.50)	.09	−.02	.83	−.01	.41	.23	.08	2.27	.02	.10	−.59	−.52
2nd				.96**	.36**	.06	.41**	.07	.38**	.90**	.01	.70**	.80**	.89**
			(.25)	.57	.26	.03	−.10	.36	.01	−.10	−.03	1.12	.05	−.55
3rd					.29	.06	.14	.11	.47**	.72**	.07	.69**	.43**	.68**
				(.38)	−.13	.04	−.31	−.13	.30	.20	−.03	−.02	.27	−.06
Flag leaf: Length						.02	.64**	.16	.14	.58**	.06	.29**	.23*	.25*
					(.27)	−.02	.03	.18	−.07	.33	.04	−.30	.09	−.85
Width							.03	.04	.04	.08	.07	.05	.03	.06
						(.42)	−.03	.01	.01	.03	.04	.06	.03	0.5
Sheath length								.11	−.02	.27**	.06	.19	.08	.20
							(.36)	.07	−.42	−.38	−.04	−.92	.01	−1.51
Spike: Length									.23*	.39**	.10	.10	.01	.23*
								(.53)	.07	.21	−.24	−.39	.03	.03
No. of spikelets										.89**	.06	.09	.08	.42**
									(.29)	.59	−.30	.21	−.00	.99
No. of kernels											.90**	.17	−.03	.32**
										(.24)	.15	−.88	−.18	−.75
Seed fertility												.36**	−.00	.51
											(.07)	.28	−.03	−.62
No. of tillers													−.16	.18
												(.02)	−.43	2.38
1000-kernel weight														.59**
													(.46)	.89
Yield per plant														(.01)

[1] Upper numerals in each row are phenotypic and lower ones, genotypic correlations. [2] Numerals in parentheses on the diagonals are heritability values from respective genetic and error variances on a plot basis. [3] Those which are larger than r = 1.00 are assumed to be due to a sampling error. *, ** Significant at the 5% and 1% levels, respectively.

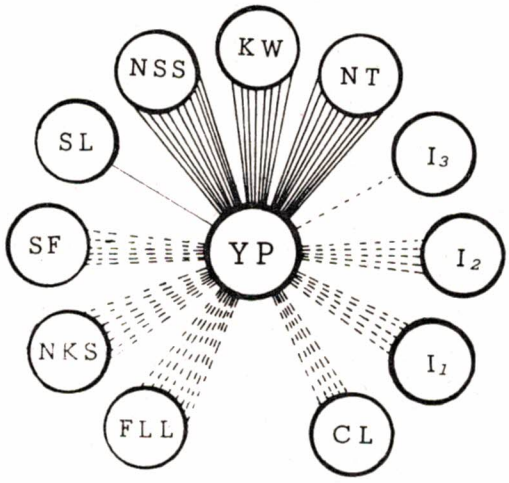

FIG. 1. A diagrammatic illustration of positive (solid line) and negative (broken line) genotypic correlations between yield per plant (YP) and various characters for Cheyenne disomic substitution lines. Abbreviations are as follows: CL = culm length; I_1 I_2 and I_3 = length of first, second and third internodes below spike, respectively; NT = number of tillers; KW = 1000-kernel weight; NSS = number of spikelets per spike; SL = spike length; SF = seed fertility; NKS = number of kernels per spike; FLL = flag leaf length.

Further genetic and environmental variance components are being investigated.

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