Theor. Appl. Genet. 59, 145-152 (1981)

Genetic Studies of Frost Resistance in Wheat

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Summary. Genetic studies of frost resistance were performed on various wheat varieties using diallel, F_2 monosomic and substitution analysis.

A six-parental cross including reciprocals was carried out, and F_1 hybrids and their parents were used for the freezing tests under controlled conditions. Both the general combining ability (GCA) and the specific combining ability (SCA) were significant, indicating additive and non-additive gene action in the inheritance of frost resistance. The high GCA:SCA ratio revealed a preponderance of additive genetic variance. No significant reciprocal differences were found between the reciprocal crosses. The variance/covariance graphical analysis indicated the partial dominance of frost sensitivity. Frost sensitive varieties had the largest number of dominant genes, while frost resistant varieties had the highest proportion of recessive genes. The magnitude of the additive component of variation was higher than that of the dominance component, and the overall measure of the degree of dominance was smaller than one, so average dominance is incomplete. The increasing and decreasing alleles are not equally frequent at all loci. In this set of wheat varieties the values of narrow and broad heritability are relatively high.

F_2 monosomic analysis of the winter wheat variety 'Arthur' crossed with the monosomics of 'Chinese Spring' revealed that the average frost resistance of all the 21 monosomics was lower than that of the disomic. F_2 monosomic hybrids 5A, 2B, 4B and 5D proved to be relatively frost resistant, while monosomics 3A, 3B and 6D were the most sensitive.

The control of frost resistance in the set of chromosome substitution lines of the variety 'Cheyenne' into 'Chinese Spring' (with the exception of 2B) indicated that the genes responsible for the frost resistance of 'Cheyenne' are localised in chromosomes 5A, 7A, 4B, 5B, 4D and 5D.

The genetic basis of frost resistance and problems of analysis are discussed.

Key words: Wheat – Frost resistance – Diallel cross – F_2 monosomics – Substitutions

Introduction

The inheritance of frost resistance was studied early in this century by Nilsson-Ehle (1912), who crossed two winter wheat varieties intermediate in winter hardiness and found transgressive segregation for the character. He concluded that winter hardiness behaved similarly to other quantitative characters controlled by polygenes. Similar results were later reported in winter wheat by Hayes and Aamodt (1927), Worzella (1935) and Salmon (1933).

An eighteen-parent diallel cross of barley, which was tested for winter hardiness in six field locations and under controlled conditions, was analysed by Rohde and Pulham (1960) and re-analysed by Eunus et al. (1962). Dominant and recessive genes controlled winter hardiness. Jenkins (1969) tested a five-parental oat diallel for frost resistance under controlled freezing conditions. In one severe freezing test, frost resistance was largely determined by recessive genes. Under less severe conditions his data indicated that resistance was controlled by dominant genes. Muehlbauer et al. (1970), Quisenberry (1931) and Worzella (1935) similarly reported that dominant genes controlled winter hardiness under mild winter conditions, while lack of dominance was found under more severe conditions.

The inheritance of frost resistance was studied in detail in winter wheat by Gullord (1975) and Gullord et al. (1975). The material of two complete diallels, one with six and the other with four parental genotypes, was tested together with the F_2 and backcross populations under both high and low intensity freezing. Frost resistance was assessed in terms of lower peripheral crown meristem (root) regrowth on a 0 (dead) to 5 (undamaged) scale. The data showed that frost resistance is controlled by partially dominant genes which are mostly additive in their effect. Some or all of the genes found to control frost resistance under low intensity freezing may very likely be different from the dominant genes found to control resistance under high intensity freezing. No reciprocal differences were found in either of the diallels tested under any level of freezing intensity.

0040-5752/81/0059/0145/$ 1.60

A seven-parent diallel cross of winter wheat was tested for frost resistance by Puchkov and Zhirov (1978). Frost resistance estimated as percentage survival at −18° C was found to be controlled mainly by an additive-dominance system. Dominant genes acted in the direction of lower frost resistance and recessive genes in the direction of higher levels of resistance. The analysis showed insignificant reciprocal differences in the F_1 hybrids.

F_2 monosomic analysis of frost resistance was studied by Goujon et al. (1968) at the coleoptile stage using a monosomic set of 'Chinese Spring' and six varieties of winter and spring types of wheat. They found that chromosomes 5A, 2D and 5D carried the genes for frost resistance, while chromosomes 7A and 1B were responsible for frost sensitivity. These findings were later confirmed by Sutka and Rajki (1978, 1979), but the latter found that chromosomes 6A, 2B, 3B, 6B and 4D were also involved in the determination of frost resistance in the winter wheat varieties 'Mironovskaya 808' and 'Rannyaya 12'.

Puchkov and Zhirov (1978) found significant differences between populations from monosomics and disomics in chromosomes 5A, 1B, 4B, 1D, 4D, 5D and 6D of F_3 populations of 'Bezostaya 1' monosomics × 'Albidum 114', and in chromosomes 7A, 1B, 2B, 4B, 4D and 5D 'Bezostaya 1-Albidum 114' substitution lines after the third backcross. In both tests, chromosomes 4B, 4D and 5D were shown to have the greatest influence on frost resistance, while chromosome 6A was associated with the lowest level of resistance.

The study of substituted chromosomes of 'Cappelle-Desprez' into the variety 'Chinese Spring' showed that frost resistance was determined by three chromosomes: 7A, 4D and 5D (Law and Jenkins 1970). Genetic control of frost resistance in the set of chromosome substitution lines of the variety 'Cheyenne' into 'Chinese Spring' indicated that the genes responsible for frost resistance were localised in the chromosomes of homoeologous group 5 (Jenkins 1971).

Since experiments on frost resistance have been performed under different conditions, on various genetic materials and in different stages of development, it is very difficult to compare and draw general conclusions from the data obtained in frost resistance tests by different authors.

The present paper describes three experiments designed for a detailed study of the genetic basis of frost resistance, using various genetic materials and using the frost testing method devised in the Martonvásár phytotron for the special purpose of genetic analysis.

Materials and Methods

The following materials were used for testing frost resistance:

Experiment I

A six-parental diallel cross including reciprocals was completed in the field in May 1977. A spring variety 'Chinese Spring' (1), which is relatively frost sensitive, and five winter wheat varieties with different levels of frost resistance, 'Bezostaya dwarf' (2), 'Mironovskaya 808' (3), 'Tom Thumb' (4), 'Rannyaya 12' (5) and 'Sava' (6), were used as parents. At the beginning of tillering, seedlings of F_1 and their parents were used for the freezing test.

Experiment II

All the 21 monosomics and the disomic of 'Chinese Spring' were crossed with the winter wheat variety 'Arthur' in the field in May 1977. In the F_1 generation, monosomics were selected by counting the number of chromosomes in cells taken from root-tips and from the anthers. The monosomics were then self-pollinated in the field in May 1978. The root-tips and anthers were stained by the Feulgen method. Seedlings of F_2 monosomics and disomics were used for the freezing test. The monosomic set of 'Chinese Spring' was developed by Dr. E.R. Sears at the University of Missouri, USA.

Experiment III

The set of 'Cheyenne' substitution lines consists, for each line, of a 'Chinese Spring' background of 20 chromosome pairs plus a different 'Cheyenne' chromosome pair substituted in turn for the corresponding homologous pair of the 'Chinese Spring' complement. The substitution line 2B is absent due to problems with univalent shift. The set of 'Cheyenne' substitutions was developed by Dr. R. Morris at the University of Nebraska, USA. The germinated seeds were sown randomly in wooden boxes; the internal dimensions of which were 39 × 27 × 11 cm. Thirty lines were sown in each box, with 5 plants per line. For each line 75 plants were available for evaluation in experiment I, 90 plants in experiment II, and 45 plants in experiment III. Seeds germinated for 2 days in petri dishes were sown in a 4:1 mixture of good quality garden soil and sand. At first the plants were watered with tap water; then, from the second week onwards, with Volldünger nutrient solution. During the hardening period the plants were given less nutrient solution, and during freezing they were not watered at all. Then after freezing they were again given the optimum quantity of nutrient required for regrowth. The plants were raised and hardened in Conviron PGV units, frozen in C units and placed in a GB unit for recovery. In the PGV units the boxes were re-randomised each week. Both PGV and GB units are plant growth chambers (walk-in types) in which the temperature, the illumination, the length of day and, to some extent, the light quality can be adjusted and controlled. C units are frost-testing chambers in which the temperature can be adjusted from −20° C to +20° C but they have no illumination. Before freezing the plants were subjected to a programme of gradually decreasing temperature. This programme was originally worked out by Rajki (1980) and was then simplified and modified for the purposes of this genetic study (Table 1). Hardening took place in the 6th week for 7 days with a 20-hour day and day/night temperatures of +2°/−2° C. After hardening, the boxes were transferred from the PGV units to the frost testing chamber (C unit), where the temperature was reduced by 2° C an hour from 0° C to −4° C. In this chamber the plants were hardened for another 2 days at −4° C, then the temperature was further reduced to −9° C or −11° C (Experiment III), or to −14° C (Experiment I, II). After 24 hours' freezing without illumination, the tempera-

Table 1. Temperature and daylength programme for raising and hardening

Weeks after germination	Day temperature °C	Night temperature °C	Daylength hours
1st	15	10	12
2nd	10	5	12
3rd	10	5	12
4th	5	0	8
5th	5	0	8
6th	2	−2	20

ture was raised by 2° C an hour to +1° C, and the plants were kept at this temperature for 15 hours. After this the boxes were transferred to a GB unit for recovery at a day temperature of 16° C and a night temperature of 15° C with a 14-hour day for 18 days. The intensity of illumination during the raising and hardening of the plants was Q = 260 μE $s^{-1} m^{-2}$ (15 klx), using Sulvania Gro-Lux/WS fluorescent tubes. After freezing, the leaves were cut off with scissors a few centimetres above the soil, so that regrowth could be more accurately evaluated, and to avoid the risk of infection by fungal diseases. Frost resistance was assessed in terms of regrowth on a 0 (dead) to 5 (undamaged) scale and also as percentage survival.

In the diallel cross the frost resistance test was analysed for general and specific combining ability and reciprocal differences by using Griffing's (1956) method I (parents, one set of F_1 s and their reciprocals are included) and by the method proposed by Keuls and Garretsen (1977). Analysis of variance and estimates of the components of genetic variance were carried out according to the model proposed by Hayman (1954a, b). The variance/covariance graphical analysis was based on the method of Jinks (1954). The narrow- and broad-sense heritability values were estimated by the method described by Mather and Jinks (1971). The experimental data were computed using a Hewlett-Packard 9831A computer, which was also used to plot the figures.

Results

Experiment I

Data for the parents and F_1 hybrids (mean values of 2 replications) are presented in Table 2. The mean frost resistance of the parents revealed that the varieties 'Chinese Spring' and 'Tom Thumb' were the most sensitive to freezing, and the variety 'Mironovskaya 808' was the most frost resistant in this set of wheat varieties. To test the significant differences between the genotypes of both parents and the crosses a one-way variance analysis was carried out, the results of which are summarised in Table 3. Analysis of variance shows that highly significant genotypic differences exist for frost resistance.

In the analysis of variance for combining ability, variance due to the general combining ability (GCA) and specific combining ability (SCA) was significant (Table 4). This indicates the importance of both additive and non-additive gene action in the inheritance of frost resistance.

Table 3. Analysis of variance of parents and F_1 s for frost resistance from a six-parental diallel in hexaploid wheat

Source of variation	df	SS	MS	F
Replication	1	0.41	0.41	
Genotypes	35	91.20	2.61	70.479***
Error	35	1.29	0.04	

*** significant at P = 0.001

Table 4. Analysis of variance for combining ability and reciprocal differences of parents and F_1 hybrids for frost resistance

Source of variation	df	SS	MS	F
General combining ability (GCA)	5	37.4	7.473	202.76***
Specific combining ability (SCA)	15	7.6	0.5066	13.74***
General reciprocal effect (GRE)	5	0.4	0.08901	2.41
Specific reciprocal effect (SRE)	10	0.2	0.03686	
Error	35	1.3	0.03686	

***significant at P = 0.001

Table 2. Mean frost resistance of parents and F_1 hybrids from a six-parental diallel in hexaploid wheat (values are means of 2 replications) and the magnitudes of $[W_r - V_r]$ and $[W_r + V_r]$

Parents	'Chinese Spring'	'Bezostaya dwarf'	'Mironovskaya 808'	'Tom Thumb'	'Rannyaya 12'	'Sava'	$W_r - V_r$	$W_r + V_r$
'Chinese Spring'	**0.000**	0.825	0.685	0.000	0.435	0.060	0.49	0.72
'Bezostaya dwarf'	0.560	**3.420**	1.855	0.410	2.250	1.630	0.52	3.09
'Mironovskaya 808'	0.695	2.780	**4.110**	0.765	2.755	1.935	0.54	3.89
'Tom Thumb'	0.015	0.335	0.605	**0.000**	0.280	0.170	0.37	0.50
'Rannyaya 12'	0.380	2.370	2.510	0.260	**3.170**	1.460	0.61	3.46
'Sava'	0.030	2.030	1.830	0.210	1.690	**0.690**	0.84	2.23
Mean							0.56	2.32
Variance							0.02	2.05

Table 5. General (bottom) and specific combining ability effects for frost resistance

Parents	'Chinese Spring'	'Bezostaya dwarf'	'Mironovskaya 808'	'Tom Thumb'	'Rannyaya 12'	'Sava'
'Chinese Spring'	0.59	−0.24	−0.47	0.65	−0.43	−0.10
'Bezostaya dwarf'		0.97	−0.36	−0.51	−0.04	0.17
'Mironovskaya 808'			1.20	−0.42	0.05	−0.01
'Tom Thumb'				0.69	−0.51	0.10
'Rannyaya 12'					0.92	0.01
'Sava'						−0.18
GCA	−0.893	0.624	0.853	−0.946	0.527	−0.165

SE for GCA = ± 0.051; SE for s_{ij} = ± 0.115; SE for s_{ii} = ± 0.113

The high GCA:SCA ratio (14.6) revealed a preponderance of additive genetic variance. No significant average maternal differences or other reciprocal differences were found between the reciprocal crosses.

Estimates of general and specific combining ability effects are given in Table 5. The parent 'Mironovskaya 808' was a very good combiner for frost hardiness, followed by 'Bezostaya dwarf' and 'Rannyaya 12'; 'Tom Thumb' and 'Chinese Spring' proved to be the poorest general combiners among the varieties studied. The best crosses for frost resistance showed better specific combining ability effects.

The variance (V_r) and covariance (W_r) were calculated for the freezing test, averaged over the reciprocal crosses. The fact that there were no significant differences in the magnitude of ($W_r - V_r$) over arrays, and the presence of a significant correlation between the parental means and the values of ($W_r + V_r$) indicate that the additive dominance model with genes independently distributed among the parents is adequate to describe the variation in frost resistance (Table 2). The significant differences observed in the magnitude of ($W_r + V_r$) over arrays show that there is non-additive genetic variation for frost resistance, which can be ascribed purely to the dominance effects of the genes. The regression coefficient (1.061 ± 0.168) is significantly different from 0 but not significantly different from unity. This also indicates that non-additive genetic variation is present as dominance only. As the values of ($W_r + V_r$) are significantly different and the values of ($W_r - V_r$) are positive, the dominance is incomplete.

The graph (Fig. 1) also showed the partial dominance of frost sensitivity, since the point of interception was above the point of origin. Parents of the recessive arrays generally have good frost resistance, while those of the dominant arrays are frost sensitive. 'Tom Thumb' and 'Chinese Spring' have the lowest W_r and V_r values and contain the largest number of dominant genes, while 'Mironovskaya 808' has the highest values and hence the highest proportion of recessive genes.

The estimates of the genetic components of variation are given in Table 6. The magnitude of the additive component (D) was higher than that of the dominance com-

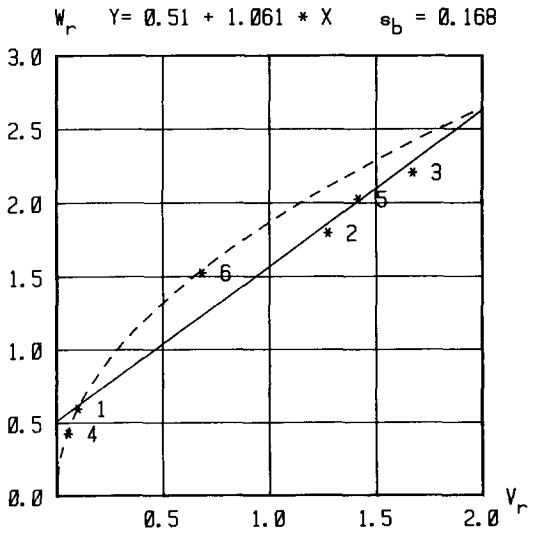

Fig. 1. The regression of W_r on V_r for frost resistance in terms of ratings for a six-parental complete diallel

Table 6. Estimates of the genetic components of variation for frost resistance in a six-parental diallel of wheat

Component	Estimated values
D	3.48*
H_1	1.19*
H_2	1.00*
F	1.21
E	0.04
$\sqrt{H_1/D}$	0.58
$H_2/4\,H_1$, uv	0.22
$\frac{1}{2}F/\sqrt{D/H_1\text{-}H_2/}$	0.89
Heritability	
narrow	81.10**
broad	97.55**

* significant
**highly significant

ponent. Since $D > H_1$ and the overall measure of degree of dominance $\sqrt{H_1/D} = 0.58$, i.e. smaller than one, average dominance is incomplete. The value of $H_2/4H_1$ is less than the maximum of 0.25, i.e. increasing and decreasing alleles are not equally frequent at all loci, so these results suggest an unequal distribution of the negative and positive alleles among the parents. The fact that the [F] value has a positive sign leads to the conclusion that there was an excess of dominant alleles in the background of the parents affecting this character. The ratio $\frac{1}{2}F/\sqrt{D/H_1 - H_2/} = 0.89$ is greater than zero and suggests that the ratio of h to d is relatively consistent over all loci. Hence, the overall picture of incomplete dominance is probably the result of incomplete dominance at all loci, rather than complete dominance at some loci and no dominance at others. The values of narrow and broad heritability are 81.10% and 97.55%, respectively.

Experiment II

The mean rating for plants at a freezing temperature of $-14°$ C reveals a significant difference between the varieties 'Chinese Spring' and 'Arthur' (Table 7). The frost resistance of the monosomic F_2 hybrids is compared to that of the 'Chinese Spring' × 'Arthur' F_2 disomic. In terms of regrowth of plants on the 0 to 5 scale, none of the monosomic hybrids exhibited frost resistance significantly superior to that of the F_2 disomic. In this experiment seven monosomics (1A, 2A, 3A, 3B, 5B, 6D and 7D) were significantly (P = 0.05 and P = 0.01) frost sensitive, while monosomic hybrids 5A, 1B, 2B and 4B proved to be relatively frost resistant, but the differences between the latter and the disomics were non-significant. The average frost resistance of all 21 monosomics was lower than that of the disomic.

Figure 2 shows the percentage survival of monosomic F_2 hybrids. Monosomic hybrids 2B, 4B and 5D were significantly more frost resistant than the disomics, while the evaluation of the 3A, 3B and 6D monosomics in terms of percentage survival confirms that they were frost sensitive.

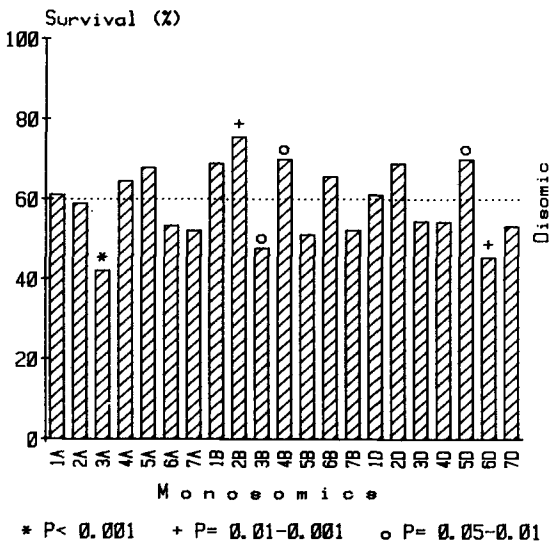

Fig. 2. Survival (%) of 'Chinese Spring' monosomics × 'Arthur' F_2 hybrids at a freezing temperature of $-14°$ C

Experiment III

The evaluation of regrowth on a 0-5 scale after freezing at both $-9°$ C and $-11°$ C shows that there is a significant difference between the recipient ('Chinese Spring') and donor ('Cheyenne') varieties (Table 8). Since the effect of the individual 'Cheyenne' chromosomes is examined in a 'Chinese Spring' genetic background, the frost resistance of 'Cheyenne' substitution lines is compared to that of the 'Chinese Spring' variety. A significant difference between 'Chinese Spring' and 'Cheyenne' can also be demonstrated after freezing at $-9°$ C, though this difference is much less

Table 7. Average rating for plants at a freezing temperature of $-14°$C in the F_2 generation of 'Chinese Spring' monosomics × 'Arthur'

Hybrids and parents	Average rating	Difference from disomics
1A	1.16	−0.46*
2A	1.17	−0.44*
3A	0.91	−0.70**
4A	1.59	−0.02
5A	1.87	0.26
6A	1.36	−0.26
7A	1.34	−0.27
1B	1.72	0.11
2B	1.82	0.21
3B	1.06	−0.56*
4B	1.80	0.19
5B	0.99	−0.62**
6B	1.60	−0.01
7B	1.29	−0.32
1D	1.60	−0.01
2D	1.61	0.00
3D	1.32	−0.29
4D	1.34	−0.27
5D	1.54	−0.07
6D	0.96	−0.66**
7D	1.12	−0.49*
Disomics	1.61	0.00
'Chinese Spring'	0.03	−1.58***
'Arthur'	4.01	2.40***

*, **, ***P = 0.05, P = 0.01, P = 0.001, respectively.

Table 8. Average rating for plants with chromosomes of Cheyenne substituted into Chinese Spring at a freezing temperature of −9°C or −11°C

Chromosome substituted	Freezing temperature			
	−9°C		−11°C	
	Average rating	Difference from Chinese Spring	Average rating	Difference from Chinese Spring
1A	3.09	−0.24	1.00	0.22
2A	3.13	−0.20	0.71	−0.07
3A	3.42	0.09	0.51	−0.27
4A	3.67	0.33	0.78	0.00
5A	4.02	0.69**	2.42	1.64***
6A	3.60	0.27	0.44	−0.33
7A	3.38	0.04	1.44	0.67**
1B	3.96	0.62*	1.04	0.27
3B	3.24	−0.09	1.04	0.27
4B	3.00	−0.33	1.36	0.58**
5B	3.44	0.11	1.29	0.51*
6B	3.49	0.16	1.00	0.22
7B	3.49	0.16	0.64	−0.13
1D	3.29	−0.04	1.09	0.31
2D	2.62	−0.71**	0.87	0.09
3D	3.11	−0.22	0.44	−0.33
4D	3.73	0.40	1.24	0.47*
5D	4.11	0.78**	1.91	1.13***
6D	3.96	0.62*	1.22	0.44
7D	3.07	−0.27	0.36	−0.42
'Chinese Spring'	3.33	0.00	0.78	0.00
'Cheyenne'	4.82	1.49***	4.02	3.24***

*, **, ***P = 0.05, P = 0.01, P = 0.001, respectively.

than that observed after freezing at −11° C. This suggests that freezing at −11° C gives a more reliable indication of the effect of the individual substitutions. It should be noted that the frost resistance of two substitution lines (5A, 5D) was significantly different from that of 'Chinese Spring' at both freezing temperatures, though these differences were far greater at −11° C. After freezing at −9° C two substitution lines (1B, 6D) were more frost resistant at the P = 0.05 level of significance than 'Chinese Spring', but the fact that these chromosomes carry genes for frost resistance was not exhibited at −11° C. Freezing at lower temperatures shows that in 'Cheyenne' not only chromosomes 5A and 5D, but also 7A, 4B, 5B and 4D carry one or more genes for frost resistance, though the gene effects to be found in the latter chromosomes are far less significant than those in chromosomes 5A and 5D. The same tendency was apparent if the frost resistance of 'Cheyenne' substitution lines into 'Chinese Spring' is expressed as percentage survival (Fig. 3). 'Cheyenne' chromosomes 3A,

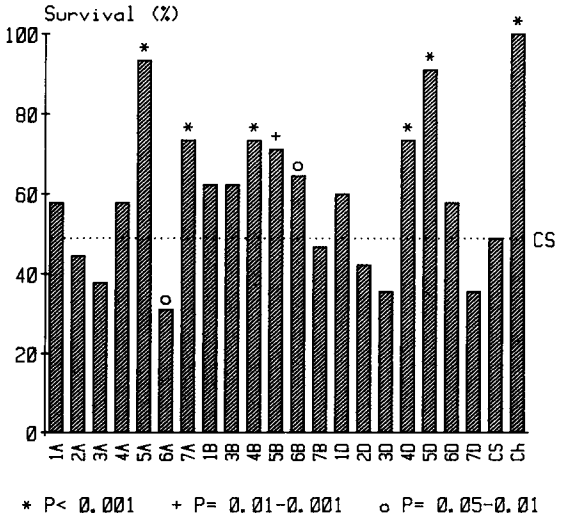

Fig. 3. Survival (%) of plants with chromosomes of 'Cheyenne' (Ch) substituted into 'Chinese Spring' (CS) at a freezing temperature of −11° C

6A, 3D and 7D in a 'Chinese Spring' genetic background reduced the frost resistance slightly, but only in the case of 6A did this reach the P = 0.05 level of significance. A similar, non-significant negative effect was induced by substituting chromosomes 3A, 6A and 7D of 'Cappelle Desprez' into 'Chinese Spring' (Law and Jenkins 1970).

Discussion

In Europe winter wheat is grown predominantly, and gives yields 30-40% higher than spring wheat, provided frosts in snowless winters or early spring do not damage the crop. Levitt (1956) reported that winters when the survival of the plants is severely reduced, resulting in a decrease in yield, occur about once every 10 years under field conditions. This fact obliges wheat breeders to include selection for winter and frost hardiness among their breeding aims, and to create the conditions necessary for artificial frost resistance testing.

Winter hardiness is a complex, quantitative, genetically determined physiological trait, an important limiting element of which is frost resistance. Over the last 50 years a large number of different methods have been devised for studying frost resistance, depending on the facilities available to the researchers (Dexter 1956; Steponkus 1978). The various research results can only be compared with certain reservations, since the material used in the experiments, the raising, hardening and freezing conditions and the direct and indirect methods used after freezing to evaluate survival differ considerably from one research group to the other.

Previously the genetics of frost resistance was mainly studied under natural field conditions. Since survival is determined not only by frost damage to the tillering node of the plant, but also by other factors, e.g. disease, pushing out, water insufficiency, etc., or by interactions between these factors, it is unlikely that a simple genetic system will be responsible for frost damage. Even resistance to artificial freezing is almost certain to be a complex character (Olien 1967; Rajki 1980).

Both previous data on the genetics of frost resistance and the results of our own diallel, monosomic and substitution analyses indicate that the genetic control of frost resistance is extremely complex and implies the effect of several genes. The results of diallel analysis confirm earlier work (Gullord 1975; Puchkov and Zhirov 1978), which indicates that frost resistance is determined by an additive-dominant genetic system. In the present study it was demonstrated that the variance component due to GCA was higher than that due to SCA, indicating a preponderance of the additive type of gene action. Since the contribution of the additive gene actions to the genetic variance was relatively higher than the contribution of dominance, this may support the possibility of selecting for frost resistance.

Under the experimental conditions used in this study, with freezing at -14° C, the frost resistant varieties examined contained recessive genes and the frost sensitive varieties contained dominant genes. Results on the direction of dominance agree with those of Puchkov and Zhirov (1978), who used a severe freezing test similar to that developed at Martonvásár. Gullord et al. (1975) postulate that there are different sets of genes acting under high and low intensity freezing. Analysis of 'Chinese Spring'/'Cheyenne' substitutions and 'Rannyaya 12' F_2 monosomics (Sutka and Rajki 1979) seems to justify this hypothesis.

The published data and the results presented here suggest that a number of genes control frost resistance. The results of the monosomic and chromosome substitution analyses suggest that considerable variation occurs between the effects of these genes. In the case of monosomic analysis some of these effects could be due to chromosome dosage rather than allelic variation, whereas different chromosome transmission rates may contribute to the lack of agreement between different monosomic analyses. The study of chromosome substitution lines overcomes these disadvantages. It does appear however that the results of F_2 monosomic analysis on 'Mironovskaya 808', 'Rannyaya 12' and 'Arthur' show that large effects on frost resistance can definitely be associated with chromosomes 5A, 2B, 4B, 6B and 5D. Except for chromosome 2B where the line is not available, these results were confirmed by the study of the 'Chinese Spring'/'Cheyenne' substitution lines.

An important aspect of further detailed studies on the genetics and cytogenetics of frost resistance is likely to be research on how the chromosomes and genes so far associated with frost resistance relate to the chromosomes and genes which determine the response to cold, illumination and daylength, regeneration ability, certain physiological and biochemical processes, etc. It is not clear, for instance, whether the genes controlling frost resistance and vernalisation response on chromosomes 5A and 5D (Law et al. 1976) are the same or are different. According to the most recent reports by Cahalan and Law (1979), it is unlikely that the same genetic factors are involved in the control of cold resistance and vernalisation response, and this opens up the possibility of selecting independently for the two characters.

Both frost resistance and regeneration and tillering ability can be associated with chromosomes 4B and 4D (Sutka and Rajki 1978), but it is not clear even in this case whether the same or different genes are involved on the same chromosomes. With respect to the chromosomes in homoeologous group 2, there must certainly be some relation between frost resistance and response to daylength. Illumination, and consequently daylength, promotes the accumu-

lation of sugars, leading to the hardening of the plants, which in its turn increases the frost resistance. According to data published by Welsh et al. (1973) and Law et al. (1978) response to daylength is associated with chromosomes 2B and 2D.

Acknowledgements

The author wishes to express his sincere gratitude to Dr. Erna Rajki for her critical reading of the manuscript. Thanks are also due to Andor Ábrányi for his help in carrying out the biometrical analysis and to Barbara Harasztos for revising the manuscript linguistically.

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Received July 11, 1980
Communicated by R. Riley

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