GENETICS OF FREEZING HARDINESS IN WINTER WHEAT (*Triticum aestivum* L.)

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ABSTRACT

GENETICS OF FREEZING HARDINESS IN WINTER WHEAT (*Triticum aestivum* L.)

By

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The inheritance of freezing hardiness was studied in (1) the winter tender variety Genesee, the hardy variety Winoka and the populations derived from the cross between them, and (2) in two complete diallels, one with six and one with four parental genotypes. The plant material was tested in an artificial freezing procedure under both high and low intensity freezing conditions. Moisture content in young leaf sections close to the crown was studied in nine wheat varieties and in genotypes from the four parental diallel.

Freezing hardiness was found to be a quantitative character. The genetic variation found in F_2 and backcross populations appeared to be only additive. Interaction between F_2 lines and the level of freezing intensity suggests that genes controlling freezing hardiness under high intensity freezing is different from the genes controlling freezing hardiness under low intensity.

Magne Gullord

Analysis of both diallels showed that freezing hardiness is controlled by partially dominant genes which are mostly additive in their effect.

No reciprocal differences with respect to freezing hardiness were identified in any of the diallels.

Moisture content in leaf segments close to the crown was negative correlated with freezing hardiness. Moisture explained about 70 percent of the variation in freezing hardiness in nine winter wheat varieties. If kinetic inhibitor ratings was included as an additional independent variable, about 80 percent of the variation in freezing hardiness was explained.

Low moisture content was found to be controlled by partially dominant genes mostly additive in their effect.

GENETICS OF FREEZING HARDINESS IN WINTER WHEAT (*Triticum aestivum* L.)

By

Magne Gullord

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INTRODUCTION

Yield of winter wheat is 30-50 percent higher than that of spring wheat, when winter kill is not a factor. Winter wheat also has the advantage of aiding in the distribution of farm labor.

The level of freezing hardiness in soft winter wheat compared to hard red winter is low (10). According to Everson et al. (7) 20 percent of the soft winter wheat in the state of Michigan suffers some winter injury every year. Injury varies from slight damage to occasional total loss in individual fields.

A joint effort was initiated by the Agricultural Research Service, USDA and Michigan Agricultural Experiment Station in 1960 to increase freezing hardiness in soft winter wheat. An artificial freezing technique has been developed for efficient screening of breeding materials both under high and low intensity freezing. This study utilizes this freezing procedure, and the theoretical work of Dr. C. R. Olien on the relationships between water content in the cereal crown and the intensity of the freezing process.

Nine winter wheat cultivars varying in freezing hardiness were selected for a genetic study. The objectives were to: (1) study the inheritance of freezing hardiness under high and low intensity freezing and (2) study the relationship between leaf moisture content and freezing hardiness, and the inheritance of moisture content.

REVIEW OF LITERATURE

Winter survival of cereals depends mainly on three factors: (1) winter habit, (2) disease and insect resistance, and (3) resistance to freezing. Other factors and interactions may also influence survival (32).

Winter habit is a necessary character for fall sown cereals. With winter habit, plants remain in a vegetative growth stage during cold weather and resist freezing damage to varying degrees. Length of the vernalization process varies with variety and is not correlated with winter hardiness.* In crosses between spring and winter wheat, the spring habit is generally dominant over winter habit, and depending on the parents involved in the cross, one, two, or three independently inherited genes were found to control these characters (2, 16, 36, 50).

In areas where the field is covered with snow during the winter, snowmolds (*Fusarium nivale* Fr.), Cesati, *Typhula idahoensis* (Remsberg) and *T. incarnata* often damage winter cereals. Attacks by diseases and insects usually make the plants less resistant to freezing.

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*E. H. Everson. Unpublished data.

The most important and frequent cause of damage in winter cereals is freezing. Because of the erratic nature of winter killing and high experimental error in field testing, breeders must usually depend on average performance of lines over a wide range of locations and years to determine freezing hardiness. Development of rapid and more efficient laboratory methods for testing winter cereals has therefore been the object of much investigation (5, 10, 11, 17, 20, 23, 48, 49). In earlier studies, plants were test-frozen in pots or flats (5, 11), but moisture content was difficult to control. Olien (27) identified the crown as the critical region for damage to winter cereals. Severe destruction of these tissues result in death of the plant. A crown freezing technique was developed by Kretschmer (17, 18) and modified by Marshall (20) for evaluation of winter oats. Warnes and Johnson (48) modified Marshall's freezing procedure for evaluation of winter barley. Metcalf _et al_. (23) developed a crown freezing technique where the moisture content in the crown could be controlled. The method was later modified by Gullord _et al_. (10).

High correlations were found between percent survival of winter cereals under controlled freezing conditions and under field conditions when the latter were means of several years' testing over many locations (20, 37, 42).

Several attempts have been made to find simple chemical or physical measurements of winter cereals which could give an indication of resistance to freezing. Moisture content in leaves of winter wheat was reported to be negatively correlated with winter hardiness (1, 21, 25). Shutt (46) found a similar relation in apple twigs. In an attempt to understand the nature of winter hardiness, Olien (28) studied the different types of stresses associated with different types of water redistribution in barley. He identified two main types of freezing processes in hardy cereal crowns: (1) equilibrium or low intensity freezing, and (2) non-equilibrium or high intensity freezing.

Equilibrium freezing occurs when the liquid between protoplasts is closely associated with cell walls and protoplasts, and heat is slowly removed from tissues containing ice crystals. The kill temperature in equilibrium freezing for wheat varies between -15 and 20C (10), but is not low enough to provide sufficient free energy to kill by frost desiccation (31). The free energy of freezing is dissipated by a shift in activation energies of water transition as adhesion and more complex bonding interactions develop between ice and plant components, whereas the free energy of desiccation is dissipated by a shift in vapor pressure as water evaporates (33, 34).

The injury under equilibrium freezing is cytological, centered around ice crystals and involves most of the tissues in the crown (35).

A non-equilibrium freezing occurs when moisture content in the crown is high (>70%) and heat is rapidly removed. Freezing occurs so rapidly that water molecules do not have time to diffuse to areas where crystal growth is unrestricted. A large amount of free energy is dissipated by formation of ice structures and disruption of tissues. Wheat is killed at higher temperatures 0 to 15C (10), depending on free energy of freezing, which is a function of crown moisture in a standard freezing test (23). The injury under high intensity freezing is histological and takes place in specific tissues and plant regions (35). Toxication of adjacent tissues occur during degeneration of injured tissues.

Different gene systems are very likely to operate in cereal genotypes under two such different stresses as those described. Evidence to support this hypothesis comes from Gullord *et al*. (10) and Metcalf *et al*. (23) who showed significant interactions between wheat genotypes and level of intensity under which the genotypes were frozen. Interaction in percent survival of F_2 and F_3 barley lines and field locations shown by Eunus *et al*. (6) may also support this hypothesis, though different

levels of disease or insect attacks in the various locations also could create the reported genotype x location interaction.

The structure of ice crystals influences survival under high intensity freezing. Olien (29) identified cell wall carbohydrates that modified ice crystal structure in rye (kinetic inhibitors). The polymers had little effect on the freezing temperature, but interfered with liquid $\rightleftarrows$ solid reaction as a competitive inhibitor. Shearman *et al*. (45) reported correlation between kinetic inhibitor ratings and survival of winter wheat under high intensity freezing.

Stability of membranes under different types of freezing stresses is very likely to influence freezing hardiness in plants. Schmuetz (44) showed high correlation (r = .85) between freezing hardiness and the content of membrane stabilizing sulfhydryl groups (SH) in six day old unhardened seedlings of 87 wheat varieties differing in winter hardiness.

Most genetic studies of freezing hardiness have been conducted under natural field conditions. Since survival is not only determined by freezing stresses, but also by disease and insect attacks, heaving, etc. and interactions of these, no simple genetic system can be expected to control freezing hardiness when studied in the field. Even resistance to artificial freezing may be complex according to Olien (30).

Inheritance of freezing resistance was studied in winter cereals early in this century. Nilsson-Ehle (26) crossed two winter wheat varieties intermediate in winter hardiness and found transgressive segregation for the character. He concluded that winter hardiness behaved as other quantitative characters controlled by many genes. Similar results were later reported in winter wheat (12, 19, 21, 38, 42, 43, 49), in winter oats (3, 14, 24) and in winter barley (6, 39, 40, 41).

An eighteen parental diallel in barley was tested for winter hardiness in six field locations and under controlled conditions and analyzed by Rhode and Pulham (40, 41) and reanalyzed by Eunus et al. (6). Dominant and recessive genes both additive and non-additive in their effect controlled winter hardiness. Jenkins (14) tested a five parental oat diallel for freezing hardiness under controlled freezing conditions. In one severe freezing test, freezing resistance was largely determined by recessive genes, essentially additive in their effect. Under less severe conditions his data indicates that freezing hardiness was controlled by dominant genes. Muehlbauer et al. (24), Quisenberry (37), and Worzella (49) similarly reported that dominant genes controlled winter hardiness under mild winter conditions while lack of dominance was found under more severe conditions. Schafer (43) reported that winter hardiness was probably controlled by recessive genes, since a majority of the F_3 rows from a cross between Turkey and Jenkin showed severe winter injury.

Significant reciprocal differences in winter hardiness were reported by Muehlbauer et al. (24). The differences were inconsistent over locations indicating that the cytoplasmic factors were influenced by environment.

Heritability studies of winter hardiness in cereals indicate that heritability estimates (broad sense) are proportional to the range in winter hardiness between the parents. Rhode and Pulham (40) calculated 20 heritability estimates on the average survival of bulk F_2 and bulk F_3 progenies from 18 winter barley varieties crossed in a diallel series. The values ranged from 36 to 74 percent. When progenies from crosses involving the five most tender varieties were eliminated, the heritability estimates ranged from 0 to 48 percent. Amirshahi and Patterson (3) similarly found that the heritability was lower in crosses with related than with unrelated varieties.

Cytogenetic studies in barley showed that winter hardiness was associated with V and B loci on chromosomes 2 and 5 respectively (41). Law and Jenkins (19) test froze 21 possible substitution lines between the tender wheat variety Chinese Spring and the hardier variety Cappelle Desprez. They found that only the 4D, 5D and 7A chromosomes were involved in freezing resistance and that their effect was additive. It is reasonable that the D genome accounts for the major portion of freezing hardiness, since it enables the original hexaploid wheats to expand and colonize more northern latitudes than tetraploids.

Simple inheritance of freezing hardiness has been reported in crosses between broccoli and kale x cabbage (4). Two dominant genes with epistatic effect were found to control freezing hardiness.

MATERIALS AND METHODS

Generation Materials

A cross between Genesee and Winoka was made in the greenhouse during the winter of 1971. F_1 and F_2 seeds were space planted in the field in the fall of 1971 and 1972 respectively. A segregation for seed coat color not significantly different from 15:1 (red to white) in F_3 seeds confirmed that we had a segregating population. 1597 F_2 lines were classified in four classes according to morphological characters: (1) breadless - red chaff, (2) beardless - white chaff, (3) bearded - red chaff and (4) bearded - white chaff. A segregation not significantly different from 9:3:3:1 indicated that beardlessness and red chaff were controlled by two dominant independent genes.

Backcrosses to both parents were made in the winter of 1972 and F_1 plants were grown in the greenhouse in the spring of the same year. Ninety-six F_2 lines, forty-six backcross lines, F_1 of the Genesee-Winoka cross and Genesee were freeze tested in a 12 by 12 partially balanced lattice design. Each incomplete block consisted of two pots containing twelve test plants and two plants each of Genesee and Winoka. Each line was replicated four times per test in each of eight high intensity freezing tests and five low intensity tests. Genesee and Winoka were replicated twenty-four times in each arrangement. The test temperature under high intensity freezing varied between -14.4 and -13.3C and between -17.8 and -16.9C for low intensity freezing.

Diallels

One four and one six complete parental diallel were made in the greenhouse in the winter of 1973. The winter wheat varieties used as parents had been tested for freezing hardiness (10) and are within diallels ranked in the order of increasing freezing hardiness (Table 1).

Table 1. Winter wheat varieties used as parents in two complete diallels.

Diallel I		Diallel II	
CI or PI no.	Common Name	CI or PI no.	Common Name
15079	Arrow	13278	Monon
12653	Genessee	13083	Dual
326310	Mironovskaja 808	8033	Yogo
13083	Dual	6155	Minturki
14000	Winoka		
6938	Kharkov 22 MC		

Both diallels were tested by using the high and low intensity freezing methods described by Gullord et al. (10). A six by seven partially balanced lattice with three arrangements was used to test diallel I. The parents were repeated two times within each arrangement, to achieve the required 42 treatment number. Each culture represented one incomplete block containing six test plants and two Winoka checks. The parents and the F_1's were replicated fifteen times in each of six freezing tests, three under high intensity conditions and three under low. The test temperature under high intensity freezing was -13.6C in all three tests whereas the temperatures were -18.2, -17.5 and -16.7C in the low intensity tests.

Diallel II was tested in a 4 by 4 square balanced lattice. Each culture contained four test plants in addition to two Winoka checks. The parents and the F_1's were replicated twenty-five times in each of the three freezing tests, one under high and two under low intensity freezing. The test temperatures were -13.5C under high intensity freezing and -18.3 and 18.1C under low.

Leaf Moisture Content

Moisture content was determined in the nine varieties used as parents in the diallels and in the genotypes of diallel II, the reciprocal crosses not included. The plants were randomized within pots and grown in growth chambers for five weeks at 15.5C and then hardened at 2C for three weeks. Tillers and older leaves were removed before a 2.5cm cylindric part of the young leaf tissue closest to the crown was cut off and put in a small air-tight drying vial. The samples were then weighed and dried at 70C for 24 hours before being weighed again. Moisture content was calculated by dividing the amount of water removed while drying, by the fresh weight of the leaf sample multiplied by one hundred.

Genetic Variance Components

The F_2 and backcross variances were calculated on means of four observations in each of eight and five tests under high and low intensity freezing respectively. Twenty-four means of four observations were created for each of Genesee and Winoka in each test. The average variance of Winoka and Genesee was used as an estimate of error. Variances of F_2, backcrosses and parents, were partitioned into additive and non-additive, and environmental variances according to Mather and Jinks (22). The formulas used are shown below.

$$F_2 = 1/2D + 1/4H + E$$

$$BC_1 + BC_2 = 1/2D + 1/2H + 2E$$

$$\text{Narrow heritability} = \frac{1/2D}{1/2D + 1/4H + E}$$

$$\text{Broad heritability} = \frac{1/2D + 1/4H}{1/2D + 1/4H + E}$$

D = additive variance

H = dominance variance

E = error variance

Diallel Analysis

Average crown meristem ratings over fifteen and twenty-five replications respectively for diallel I and II were used in the analysis of variance of the two diallels. Diallel I tested under low intensity freezing was also analyzed by using percent survival (log transformed).

Hayman's (13) approach was applied to test the diallels for additivity, non-additivity and reciprocal differences by using tests as replication, in the cases where the freezing tests were repeated more than once. In diallel I under low intensity freezing and freezing hardiness evaluated as meristem rating, each test was analyzed for general and specific combining ability and reciprocal differences by using Griffing's (9) method I (parents, one set of F_1's and their reciprocals are included) and model I (fixed model-selected parent lines). The same procedure was also used when analyzing the one test of diallel II under high intensity freezing.

If no reciprocal differences were found the W_r/V_r approach described by Jinks (15) and Hayman (13) was applied to the diallels after averaging over reciprocal crosses in each test. V_r is the variance within arrays and W_r is the covariance of the r^{th} array with the non-recurring parents.

Two methods described by Mather and Jinks (22) were used to test the adequacy of the simple additive-dominance model. Gene action and heritability were calculated when the model was satisfactory. The formulas used are shown below (22).

$$V_p = D + E$$

$$\bar{V}_r = 1/4D + 1/4H_1 - 1/4F + \frac{N+1}{2N} E$$

$$\bar{W}_r = 1/2D - 1/4F + 1/N\ E$$

$$V_{\bar{r}} = 1/4D + 1/4H_1 - 1/4H_2 - 1/4F + \frac{N+1}{2N^2} E$$

$$\text{Narrow heritability} = \frac{1/2D + 1/2H_1 - 1/2H_2 - 1/2F}{1/2D + 1/2H_1 - 1/4H_2 - 1/2F + E}$$

$$\text{Broad heritability} = \frac{1/2D + 1/2H_1 - 1/4H_2 - 1/2F}{1/2D + 1/2H_1 - 1/4F_2 - 1/2F + E}$$

N = number of parents in the diallel

V_p = parental variance

$\bar{V}_r$ = mean variance of r arrays

$\bar{W}_r$ = mean covariance of r arrays

$V_{\bar{r}}$ = variance of the array means

E = pooled error variance

D = fixable additive variance

H_1 = dominance variance

H_2 = dominance variance

F = non-fixable additive variance

u = frequency of dominant genes

v = frequency of recessive genes

When the ranking of the array variances and the array covariances were consistent over the appropriate tests, W_r/V_r graphs were calculated after averaging over tests within diallel and test intensity. Points coordinated on the plane made by W_r and V_r axis were confined by a limiting parabola

$$W_r = (V_r \cdot V_p)^{1/2}.$$

RESULTS AND DISCUSSION

Generation Material

The frequency distribution of meristem ratings under high and low intensity freezing are shown in Tables 2 and 3 respectively. Freezing hardiness was quantitatively inherited both under high and low intensity freezing. Under low intensity freezing Genesee was killed in most cases, the variation of Winoka was therefore used as the only estimate of error. The additive and non-additive genetic components and heritability for freezing hardiness are shown in Table 4. The non-additive component is much higher under low intensity freezing than under high intensity freezing. This could very likely be caused by deviation from normality of the BC_1 population under low intensity freezing (Table 3). The heritability found under high intensity freezing (57.7%) is therefore more reliable than the heritability found under low intensity freezing (2.2%). The relationship between meristem ratings under high and low intensity freezing for F_2 and the backcross populations are shown in Figures 1-3. Low correlation coefficients between meristem ratings under high and low intensity freezing may be due to: (1) large standard error (range .23-.31) on the means and/or (2) different genes controlling resistance to freezing under high

TABLE 2.--Frequency distributions of lower peripheral crown meristem ratings for F_2, backcross and parental populations from the cross Genesee x Winoka, tested under high intensity freezing conditions.

	Crown Meristem Rating														
Upper Class Limit	.25	.50	.75	1.00	1.25	1.50	1.75	2.00	2.25	2.50	2.75	3.00	3.25	3.50	Total
Lower Class Limit	0	.26	.51	.76	1.01	1.26	1.51	1.76	2.01	2.26	2.51	2.76	3.01	3.26	
Genesee			2*	5	5	10	2								24
BC_1				1	4	8	3	4	2	1					23
F_2				1	6	8	20	24	19	11	7	2			96
BC_2							2	5	6	5	3	2			23
Winoka										7	9	5	3		24

*Each unit of the frequency distribution is a mean of 32 observations (4 reps x 8 tests).

TABLE 3.--Frequency distribution of lower peripheral crown meristem ratings for F_2, backcross and parental populations from the cross Genesee x Winoka, tested under low intensity freezing conditions.

	Crown Meristem Rating														
Upper Class Limit	.25	.50	.75	1.00	1.25	1.50	1.75	2.00	2.25	2.50	2.75	3.00	3.25	3.50	Total
Lower Class Limit	0	.26	.51	.76	1.01	1.26	1.51	1.76	2.01	2.26	2.51	2.76	3.01	3.26	
Genesee	22*	2													24
BC_1		3	4	5	4	1	1	1	3	1					23
F_2		3	9	11	17	17	15	11	9	3	2				96
BC_2					1	1	3	6	6	4	1		1		23
Winoka									2	5	7	4	4	2	24

*Each unit of the frequency distribution is a mean of 20 observations (4 reps x 5 tests).

TABLE 4.--Means and variances of lower peripheral crown meristem ratings for Genesee, Winoka and populations derived from the cross between them, tested under both high and low intensity freezing.

Population	N	Low Intensity Freezing		High Intensity Freezing	
		Means	Variances	Means	Variances
Genesee	24	.09	-	1.21	.63
BC_1	23	1.14	1.81	1.57	.87
F_2	96	1.42	1.34	1.92	1.37
BC_2	23	2.03	.84	2.21	1.03
Winoka	24	2.74	.57	2.67	.53
D			.06		1.58
H			2.96		0
Narrow heritability			2.2%		57.7
Broad heritability			57.5%		57.7%

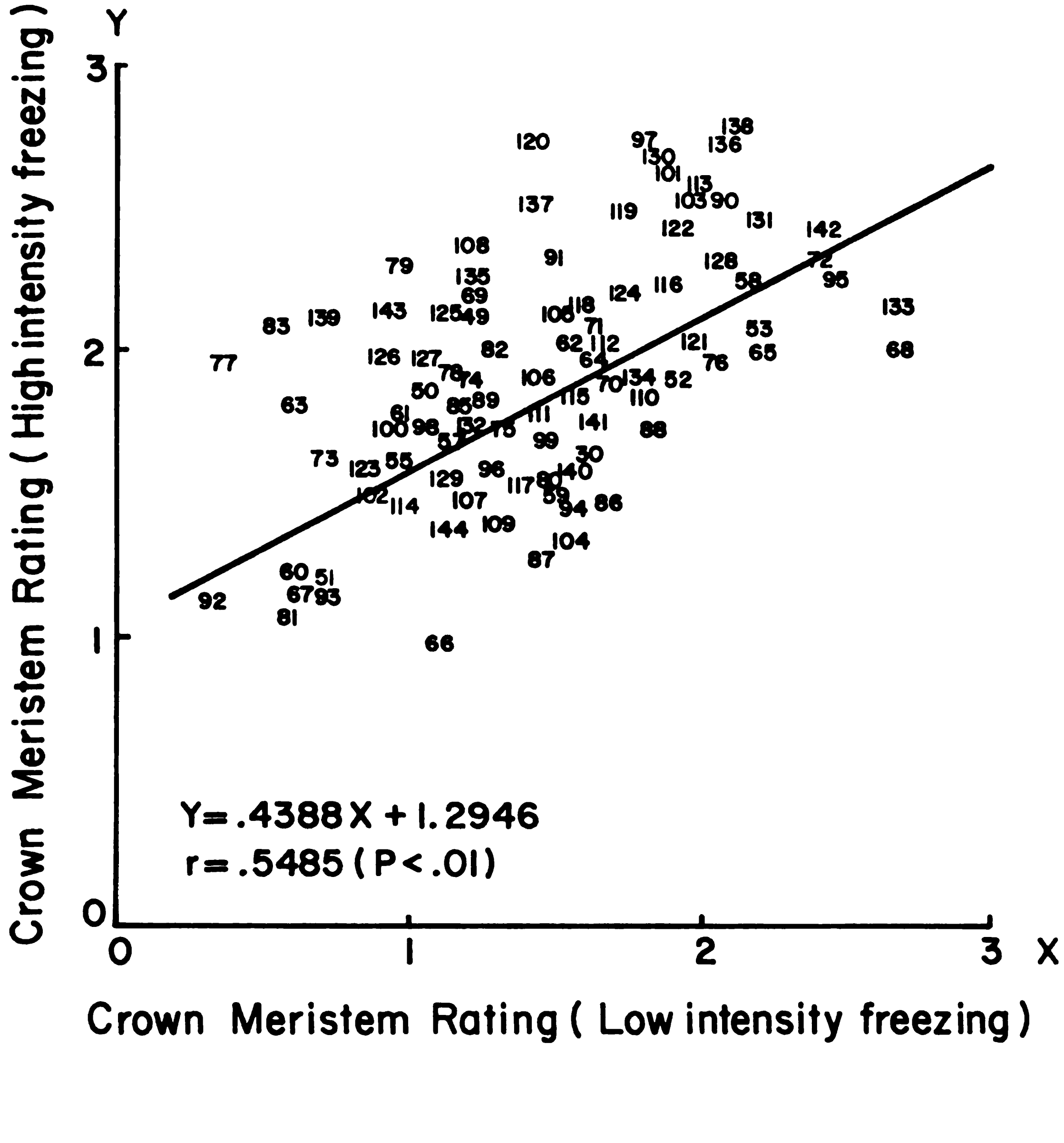

Figure 1.--Relationship between lower peripheral crown meristem ratings under high and low intensity freezing for 96 F_2 families originating from a cross between Genesee and Winoka, averages over 8 and 5 freezing tests respectively.

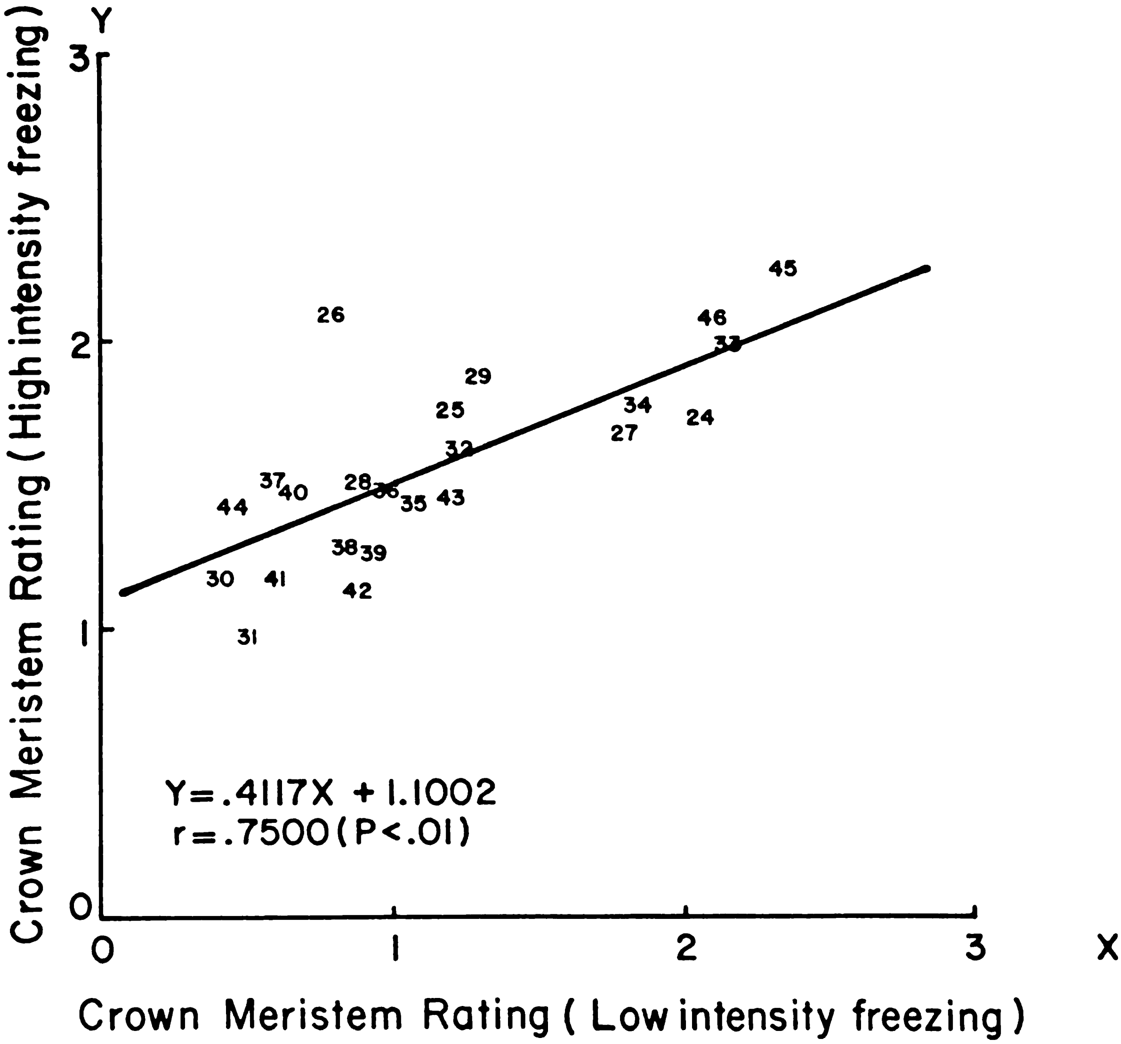

Figure 2.--Relationship between lower peripheral crown meristem ratings under high and low intensity freezing for 23 BC_1 families originating from a cross between Genesee and Winoka, averages over 8 and 5 freezing tests respectively.

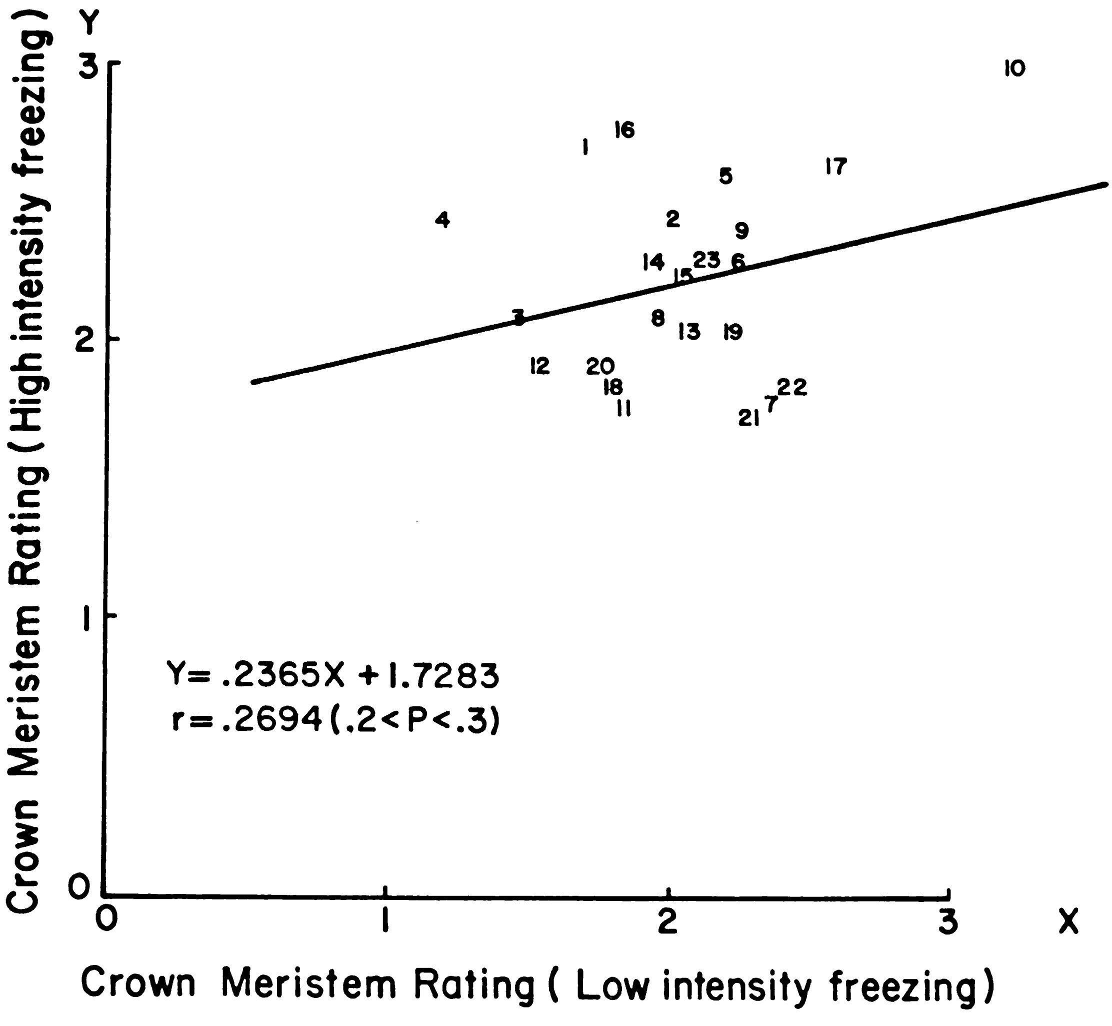

Figure 3.--Relationship between lower peripheral crown meristem ratings under high and low intensity freezing for 23 BC_2 families originating from a cross between Genesee and Winoka, averages over 8 and 5 freezing tests respectively.

and low intensity freezing. Analysis of variance showed significant ($P < .001$) interaction between F_2 families and freezing conditions. For the two backcross populations the interaction was slightly significant ($.05 < P < .1$). Significance implies that the deviation from the regression is partially explained by different sets of genes acting under high and low intensity freezing. The F_2 Family Number 77 (Figure 1) very likely has genes that protect against high intensity freezing, but has a low level of protection against low intensity freezing. Family Number 68 has the same amount of protection against high intensity freezing as Number 77, but has in addition a very high level of protection against low intensity freezing. Similar results have been reported in some advanced winter wheat selections (10) and in F_2 and F_3 populations of barley (6).

Significant ($P < .05$) higher meristem ratings were found for bearded than for beardless F_2 families with red chaff tested under high intensity freezing. The trend was the same under low intensity freezing, but the difference was not significant. The relationship between freezing hardiness and beardedness is likely to be due to linkage between genes controlling freezing hardiness and the gene determining beardedness, and not to a gene with pleiotropic effect, since beards were found to be controlled by one recessive gene, and freezing hardiness by dominant genes.

Diallels--High Intensity Freezing

Inheritance of winter hardiness as measured by lower peripheral crown meristem damage tested under high intensity freezing is studied both in diallel I and diallel II. The results of diallel I will be presented and discussed first. Table 5 shows that the error variances are homogeneous and are therefore pooled to give a test interaction mean square as a common error variance. There is a significant additive (a) and dominant (b) effect. The mean deviation of the F_1's from their midparental values (b_1) is significant, and indicates that the dominance deviations of the genes are predominantly in one direction. The mean dominance deviation of the F_1's from their mid-parental values within each array does not differ significantly over arrays (b_2). There is, however, a significant dominance deviation that is unique to each F_1(b_3), also called specific combining ability. No significant average maternal differences (c) or other reciprocal differences not ascribed to c(d) is found between reciprocal crosses (Table 5).

V_r and W_r were calculated for each test after averaging over reciprocal crosses. Highly significant ($P < .01$) differences in the magnitude of ($W_r + V_r$) over arrays shows that there is non-additive genetic variation for freezing resistance. No significant ($.50 < P < .75$) differences in the magnitude of ($W_r - V_r$) over arrays indicate that the

TABLE 5.--The analysis of variance of freezing hardiness measured as lower peripheral crown meristem ratings of a six parental diallel tested under high intensity freezing.

Source of Variation	df	MS	F*	P	F†	P
a	9.8811	5	95.0106	<.001	88.4611	<.001
b	.4329	15	4.9588	<.001	3.8756	<.001
b_1	3.7367	1	132.9786	.01-.001	33.4530	<.001
b_2	.0974	5	3.2113	.1-.05	.8325	.75-.50
b_3	.2522	9	2.0096	.1-.05	2.2578	.05-.01
c	.1403	5	.6794	.75-.50	1.2560	.25-.10
d	.1371	10	1.3060	>.75	1.2265	.50-.25
Tests	7.4490	2			66.6876	<.001
Pooled error	.1117	70				
Total	.7541	107				

*Each component of variation tested against its own test interaction.

†All components of variation tested against pooled test interaction mean square.

additive-dominance model with genes independently distributed among the parents is adequate to describe the variation in freezing hardiness. The non-additive genetic variance can, therefore, be ascribed to the dominance effects of genes only. The joint regression analysis of W_r on V_r for the three tests are highly significant ($P < .001$) and the regression coefficient ($.9914 \pm .0883$) is significantly different from 0 but not different from unity. This also indicates that non-additive genetic variation is present as dominance only.

The relative order of W_r and V_r values are nearly consistent over tests, and a W_r/V_r graph calculated by using the mean meristem ratings over tests shows that Kharkov 22 MC has the lowest W_r and V_r values and contains the most dominant genes, while Genesee and Arrow have the highest values and hence the highest proportion of recessive genes (Figure 4). Table 6 shows that Winoka is the hardiest cultivar but not significantly better than Kharkov 22 MC, and Arrow the most tender cultivar with the other varieties in between.

The gene actions and heritability estimates are shown in Table 7. H_1 is smaller than D indicating incomplete dominance, the same conclusion can be drawn from the W_r/V_r graph intercepting W_r axis significantly ($P < .01$) above origin. The mean value of uv over all loci, estimated from the ratio $1/4\ H_2/H_1$, is not significantly greater than the

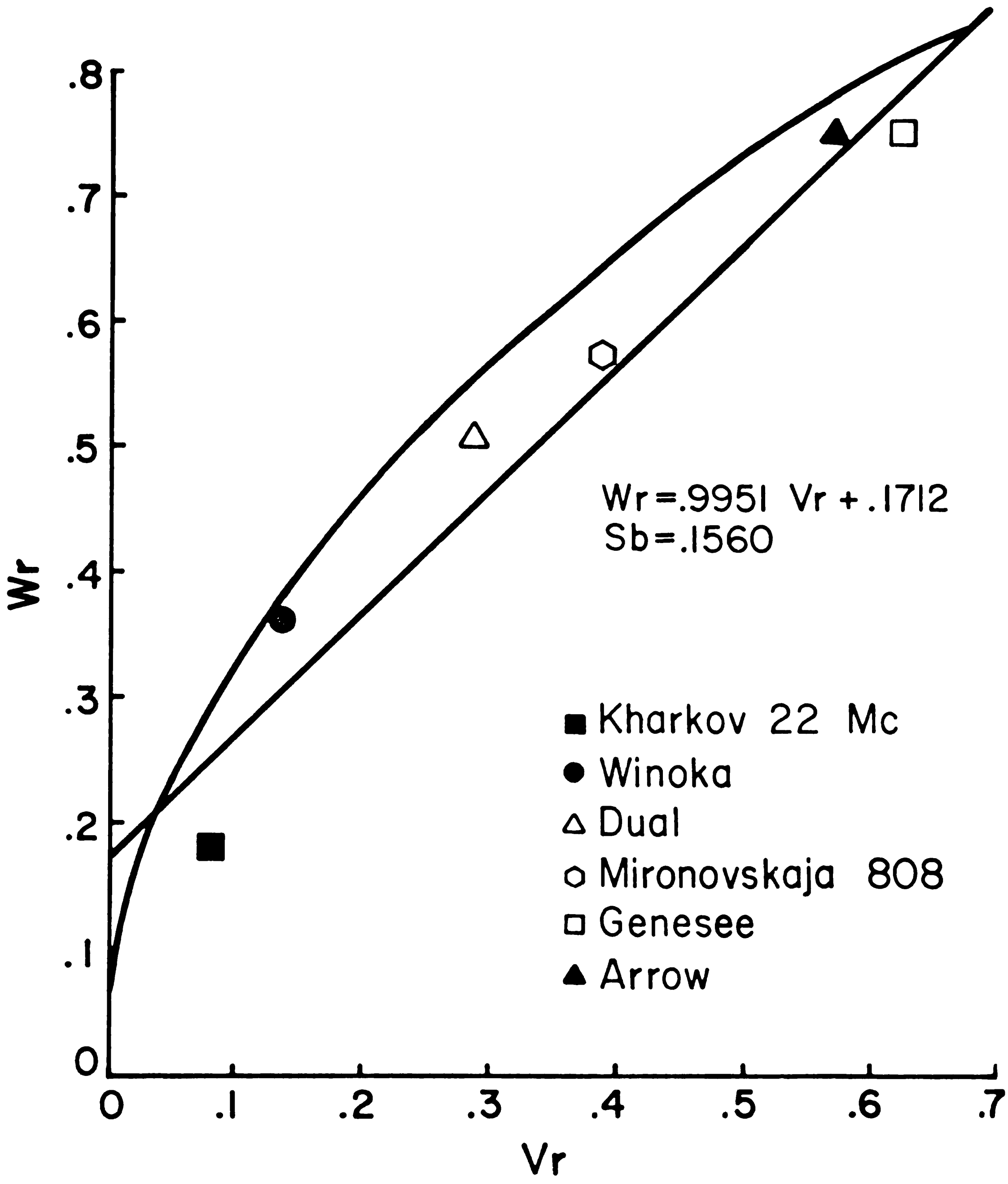

Figure 4.--The regression of W_r on V_r for freezing hardiness in terms of lower peripheral crown meristem ratings of a six parental diallel tested under high intensity freezing.

TABLE 6.--Lower peripheral crown meristem ratings of parents and F_1's from a six parental diallel tested under high intensity freezing, totals of three freezing tests after averaging over reciprocal crosses.

Parental Number	Parent	1	2	3	4	5	6	V_r	W_r
1	Genesee	3.99	6.65	4.42	8.55	10.02	7.11	.6242	.7527
2	Dual		7.26	6.06	9.18	10.07	9.21	.2943	.5023
3	Arrow			2.10	7.37	8.45	5.90	.5704	.7476
4	Winoka				9.96	10.43	9.71	.1360	.3637
5	Kharkov 22 MC					9.33	10.98	.0870	.1710
6	Mironovskaja 808						7.65	.3889	.5731
	SUM	40.54	48.43	34.10	55.20	59.28	50.56	2.1008	3.1104

TABLE 7.--Components of variation of freezing hardiness under high intensity freezing in a six parental diallel.

Components of Variation	Estimated Values
D	.9819 ± .0735
H_1	.1421 ± .1673
H_2	.1876 ± .1567
F	-.1413 ± .1258
E	.1117
$\sqrt{H_1/D}$	.3803
uv	.3301
Narrow Heritability	77.26%
Broad Heritability	83.99%

maximum value of .25 which arises when u = v = .5. Narrow and broad heritability for the freezing hardiness under high intensity freezing is 77.26 and 83.99 percent respectively (Table 7).

In this selected set of wheat genotypes freezing hardiness measured under high intensity freezing is on the average controlled by partially dominant genes mostly additive in their effect. The position of Winoka in relation to Kharkov 22 MC in the W_r/V_r graph (Figure 4) indicates that the dominance is less complete in Winoka than in Kharkov 22 MC. This is in agreement with the lack of dominance found for freezing hardiness in the generation material (Table 4) originating from the cross between Genesee and Winoka.

Only results from one freezing test under high intensity conditions is available for diallel II. Table 8 shows that genotypic differences exist for freezing hardiness. The combining ability analysis of variance according to Griffing (9) are shown in Table 9, in which both general and specific combining ability are significant. After averaging over reciprocal crosses, since there were no significant reciprocal differences, the W_r and V_r values and the regression line between the values were calculated. The regression coefficient is significantly ($.01 < P < .05$) different from zero but not ($P < .75$) from unity, indicating that non-allelic interaction is present as dominance only.

TABLE 8.--Analysis of variance of the lower peripheral crown meristem ratings of parents and F_1's from a four parental diallel tested under high intensity freezing.

Source of Variation	df	MS	F	P
Total				
Replication	24	1.9340	2.4175	<.001
Genotypes (adj.)	15	5.2985	6.6232	<.001
Effective error	285	.8000		

TABLE 9.--Analysis of variance of the lower peripheral crown meristem ratings for combining ability and reciprocal differences of parents and F_1's of a four parental diallel tested under high intensity freezing.

Source of Variation	df	MS	F	P
General combining ability	3	.8680	26.7901	<.001
Specific combining ability	6	.0771	2.3796	.05-.025
Reciprocal differences	6	.0187	.5772	.75-.500
Error	285	.0324		

The regression line intercepts the W_r axis a significant ($P < .01$) distance above origin which implies that dominant gene action under high intensity freezing is incomplete. Yogo has the lowest W_r and V_r values and Monon the highest (Figure 5). According to Table 10 Minturki is the most hardy variety and Monon the most tender. Freezing hardiness seems to be controlled by partially dominant genes mostly additive in their effect also in this set of genotypes.

Diallels--Low Intensity Freezing

Inheritance of winter hardiness as measured by lower peripheral crown meristem ratings tested under low intensity freezing was studied in both diallel I and diallel II. The calculations in diallel I were based on percent survival transformed to logarithms to achieve normality and these results are presented first.

The error variances are homogenous except for b_1, which is significant only against the pooled error variance (Table 11). This discrepancy for b_1 is a result of its own test interaction being based on only two degrees of freedom. The error variances are pooled to give a test interaction mean square as a common error variance. As for the high intensity freezing, the material shows significant additive (a) and dominant (b) effects. The mean freezing hardiness of the F_1's is significantly higher than the mid-parental value (b_1) and a significant dominance deviation that is

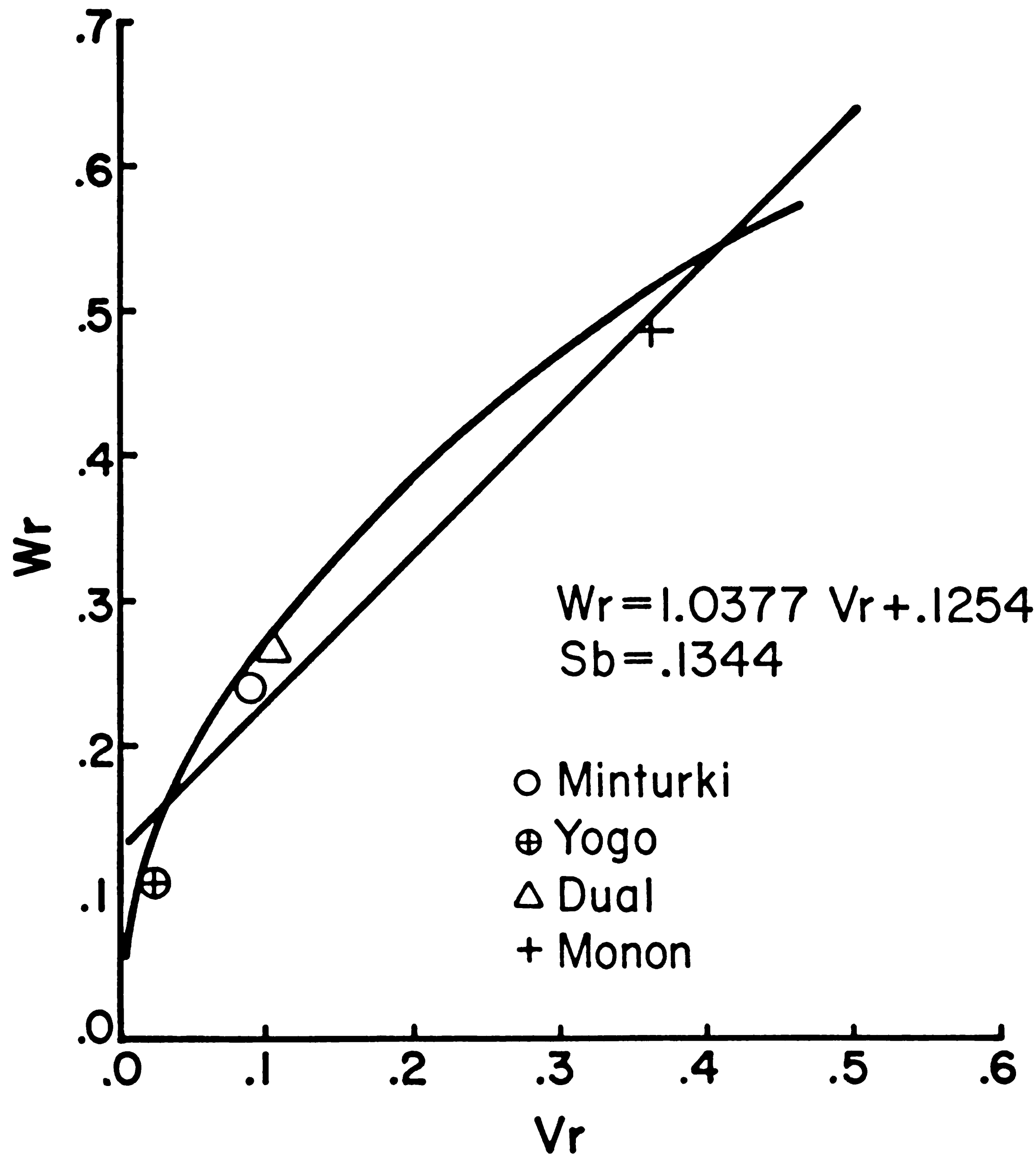

Figure 5.--The regression of W_r on V_r for freezing hardiness in terms of lower peripheral crown meristem ratings of a four parental diallel tested under high intensity freezing.

TABLE 10.--Lower peripheral crown meristem ratings of parents and F_1's from a four parental diallel tested under high intensity freezing, means of 25 replications and reciprocal crosses.

Parental Number	Parent	1	2	3	4	V_r	W_r
1	Dual	3.27	3.69	3.80	3.10	.1093	.2657
2	Yogo		3.71	3.91	3.58	.0189	.1101
3	Minturki			4.36	3.64	.0954	.2440
4	Monon				2.33	.3646	.4925
Sum		13.86	14.89	15.71	12.65	.5882	1.1123

TABLE 11.--The analysis of variance of freezing hardiness measured as percent survival (transformed to logarithms) of a six parental diallel tested under low intensity freezing.

Source of Variation	df	MS	F*	P	F†	P
a	5	4.1139	25.4030	<.001	68.2239	<.001
b	15	.2434	4.3464	<.001	4.0365	<.001
b_1	1	1.0383	17.1620	.25-.10	17.2189	<.001
b_2	5	.1926	5.4887	.05-.01	3.1940	.05-.01
b_3	9	.1832	2.7303	.05-.01	3.0381	.01-.001
c	5	.0498	1.5911	.50-.25	.8259	.75-.50
d	10	.0623	2.0393	.10-.05	1.0315	.50-.25
Tests	2	.5307			8.8010	<.001
Pooled error	70	.0603				
Total	107	.2839				

*Each component of variation tested against its own test interaction.

†All components of variation tested against pooled test interaction mean square.

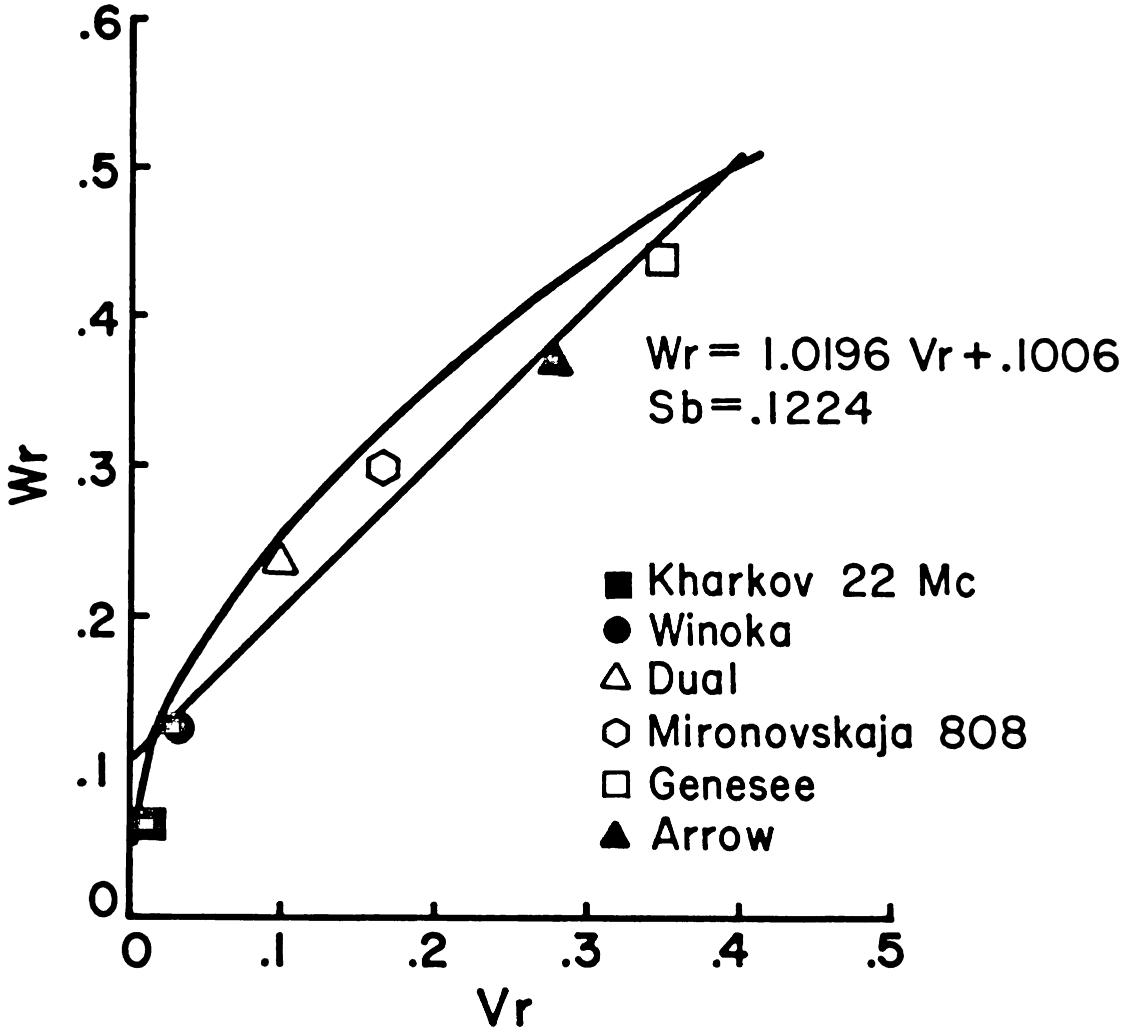

Figure 6.--The regression of W_r on V_r for freezing hardiness in terms of percent survival (transformed to logarithms) of a six parental diallel tested under low intensity freezing.

unique to each F_1 (b_3) is found. The mean dominance deviation of the F_1's from their mid-parental values within each array differ significantly over arrays (b_2). No average maternal differences (c) or other reciprocal differences not ascribed to c (d) were identified between reciprocal crosses.

With no reciprocal differences, V_r and W_r were calculated for each array and freezing test after averaging over reciprocal crosses. Highly significant ($.01 < P < .05$) differences in the magnitude of ($W_r + V_r$), and no significant ($.25 < P < .5$) differences in the magnitude of ($W_r - V_r$), indicate that the additive dominance model is adequate for the variation in freezing hardiness. A highly significant ($P < .001$) joint regression of W_r on V_r for the three tests, and the linear regression coefficient ($1.0547 \pm .0779$) which is significantly ($P < .01$) different from 0 but not ($.5 < P < .4$) from unity, confirm the adequacy of the additive dominance model.

The relative values of W_r and V_r are nearly consistent over tests, and a W_r/V_r graph was calculated for the diallel after averaging over the three freezing tests (Figure 6). Kharkov 22 MC has the lowest W_r and V_r values and, therefore, contains the most dominant genes. Genesee, however, has the highest values and the greatest number of recessive genes. The other cultivars in order of decreasing number of dominant genes for freezing hardiness are:

Winoka, Dual, Mironovskaja 808 and Arrow. Table 12 shows that Kharkov 22 MC is the most hardy cultivar, and Genesee the most tender.

Components of variation and heritability estimates are shown in Table 13. H_1 is smaller than D, indicating that dominance is incomplete, the same conclusion is drawn from the W_r/V_r graph, since the line intercepts the W_r axis at a point significantly ($.01 < P < .025$) above origin. The mean value of uv over all loci, estimated from the ratio $1/4\ H_2/H_1$ is not significantly different from the maximum value of .25 indicating that recessive and dominant genes are in the same proportion. Narrow and broad heritability are 68.57 and 76.12 percent respectively (Table 13).

Freezing hardiness measured under low intensity freezing is apparently controlled by partially dominant genes mostly additive in their effect. The relative order of the W_r and V_r values for the six genotypes are identical under high and low intensity freezing (Figures 4 and 5). This suggests that the same sets of genes may control freezing hardiness under both levels of freezing intensity. This conclusion disagrees with results from the segregating population presented earlier. The varieties used in this study have probably been selected under natural conditions over long periods of time and they may have adapted in a similar degree to both high and low intensity freezing.

TABLE 12.--Percent survival (transformed to logarithms) of parents and F_1's from a six parental diallel tested under low intensity freezing, totals of three freezing tests after averaging over reciprocal crosses.

Parental Number	Parent	1	2	3	4	5	6	V_r	W_r
1	Genesee	.6021	3.7875	1.9833	4.7559	5.3748	3.3099	.3483	.4428
2	Dual		4.9104	3.3429	5.5080	5.6574	5.0241	.0977	.2394
3	Arrow			.8451	4.4289	5.1255	2.4492	.2812	.3695
4	Winoka				5.6748	5.7261	5.2584	.0308	.1339
5	Kharkov 22 MC					5.7879	5.5425	.0069	.0606
6	Mironovskaja 808						4.3437	.1643	.3056
Sum		19.8135	28.2393	18.1749	31.3521	33.2142	25.9278	.9292	1.5518

TABLE 13.--Components of variation for freezing hardiness in a six parental diallel under low intensity freezing.

Components of Variation	Estimated Values
D	.5866 ± .2086
H_1	.1369 ± .1423
H_2	.1196 ± .1098
F	.1507 ± .1976
E	.0603
$\sqrt{H_1/D}$	.4831
uv	.2708
Narrow heritability	68.57%
Broad heritability	76.12%

If that is the case different gene systems controlling freezing hardiness under high and low intensity freezing can therefore be identified only in a segregating population.

The error variances for diallel II under low intensity freezing are homogeneous and are, therefore, pooled to give a test interaction mean square as a common error variance (Table 14). Table 14 shows that there is a significant additive (a) and dominant (b) effect. The mean deviation of the F_1's from their midparental value (b_1) is also significant. Neither the mean dominance deviation of the F_1's from their midparental values within each array (b_2) nor the dominance deviation unique to each $F_1(b_3)$, specific combining ability, is significant. No average maternal differences (c) or other reciprocal differences not ascribed to c (d) between reciprocal crosses were found to be significant (Table 14).

Slightly significant ($.05 < P < .1$) differences in the magnitude of ($W_r + V_r$) over arrays and lack of significant differences in the magnitude of ($W_r - V_r$) over arrays indicate that the additive dominance model is adequate for describing the variation in freezing hardiness. The adequacy of the model is confirmed by a highly significant ($P < .01$) joint regression of W_r on V_r, with a regression coefficient ($.9271 \pm .0586$) significantly different from zero but not from unity.

TABLE 14.--The analysis of variance of freezing hardiness measured as lower peripheral crown meristem ratings of a four parental diallel tested under low intensity freezing.

Source of Variation	df	MS	F*	P	F†	P
a	3	4.3228	11.1470	.05-.01	22.7636	<.001
b	6	.6620	5.1199	.05-.01	3.4860	.05-.01
b_1	1	3.0317	60.1528	.10-.05	15.9647	.01-.001
b_2	3	.0767	.3639	>.75	.4039	>.75
b_3	2	.3552	7.6387	.25-.10	1.8705	.25-.10
c	3	.0341	.1635	>.75	.1796	>.75
d	3	.0099	.1045	>.75	.0521	>.75
Tests	1	11.0921			58.4102	<.001
Pooled error	15	.1899				
Total	31	1.0004				

*Each component of variation tested against own test interaction.

†All components of variation tested against pooled test interaction mean square.

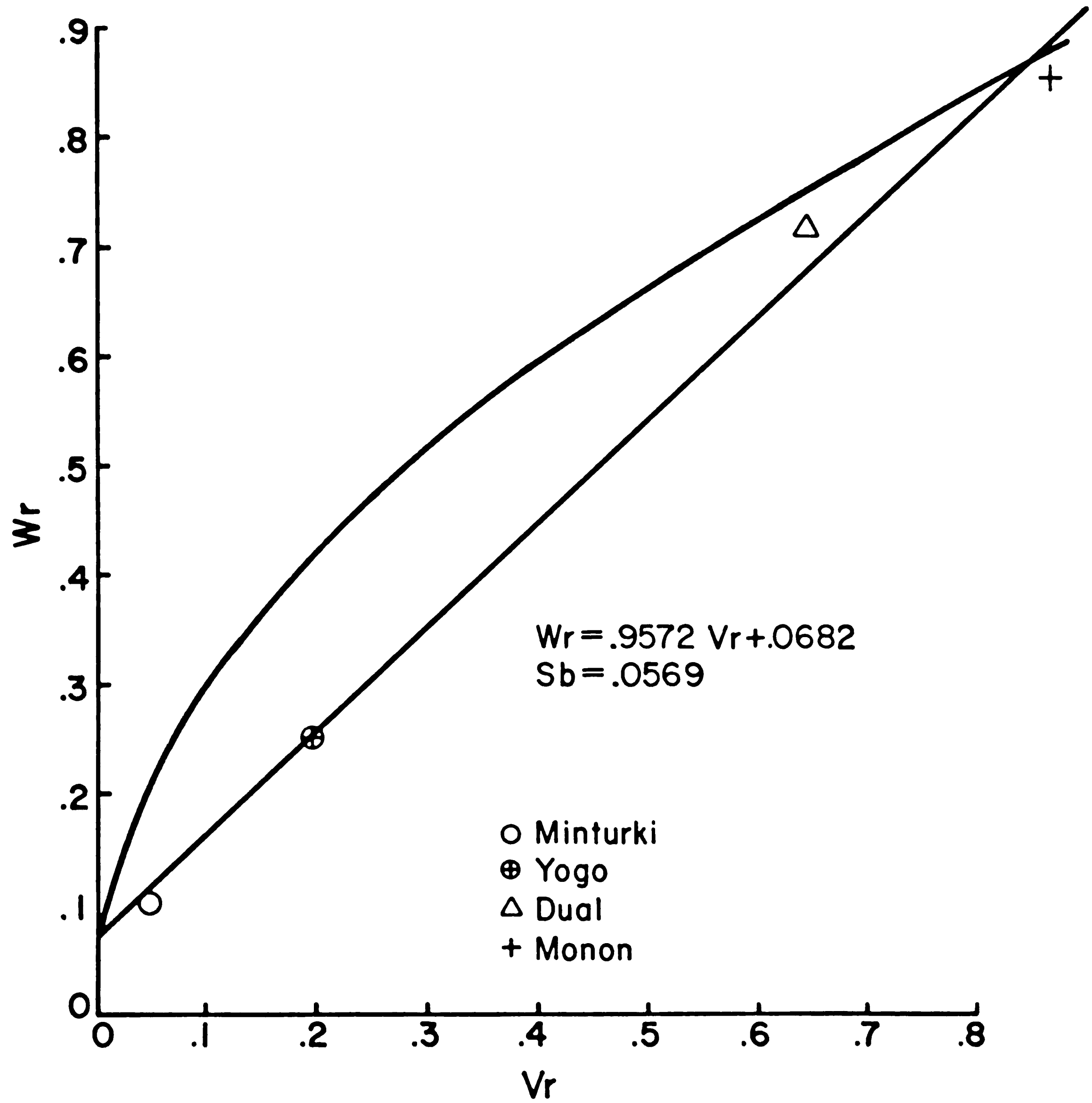

Figure 7.--The regression of W_r on V_r for freezing hardiness in terms of lower peripheral crown meristem ratings of a four parental diallel tested under low intensity freezing.

The relative order of the W_r and V_r values are almost consistent over the two tests. The W_r/V_r graph calculated after averaging over tests shows that Minturki has the lowest W_r and V_r values and contains the most dominant genes while Monon has the highest value and hence the highest proportion of recessive genes (Figure 7). The meristem ratings in Table 15, shows that Minturki is the most hardy and Monon the most tender.

The gene action of freezing hardiness is shown in Table 16. The term $\sqrt{H_1/D}$ is smaller than one, indicating that the dominance is incomplete. The W_r/V_r graph intercepting the W_r axis, significant ($P < .01$) above origin also suggests partial dominance. The mean uv value over all loci is not significantly different from .25 indicating that the proportion of dominant and recessive genes is equal to .5. The average narrow and broad heritability for freezing hardiness is 63.90 and 77.09 percent respectively (Table 16).

Freezing hardiness evaluated under low intensity freezing in diallel II is also controlled by partially dominant genes mostly additive in their effect. The relative order of the W_r and V_r values are not consistent for high and low intensity freezing (Figures 5 and 7), Yogo and Minturki have changed position. Two explanations are possible: (1) different gene systems are controlling freezing hardiness under the two levels of freezing inten-

TABLE 15.--Lower peripheral crown meristem ratings of parents and F_1's from a four parental diallel tested under low intensity freezing, totals of two freezing tests after averaging over reciprocal crosses.

Parental Number	Parent	1	2	3	4	V_r	W_r
1	Dual	3.56	6.12	6.64	3.70	.6423	.7251
2	Yogo		5.50	7.56	5.96	.1979	.2518
3	Minturki			6.92	6.70	.0443	.1050
4	Monon				2.76	.8605	.8630
Sum		20.02	25.14	27.82	19.12	1.7450	1.9449

TABLE 16.--Components of variation for freezing hardiness in a four parental diallel under low intensity freezing.

Components of Variation	Estimated Values
D	.8309 ± .0170
H_1	.3896 ± .1794
H_2	.4369 ± .1610
F	-.2755 ± .4945
E	.1899
$\sqrt{H_1/D}$	.6847
uv	.2804
Narrow heritability	63.90%
Broad heritability	77.09%

sity, (2) because the freezing temperature under the high intensity was too high the frequency distributions of the meristem ratings of the hardiest genotypes are skewed toward the upper end of the scale. This explains the low W_r and V_r values for the hardiest varieties (Yogo, Minturki and Dual). A lower freezing temperature would be necessary to separate the three genotypes with respect to W_r and V_r values.

Influence of the Severity of the Freezing Test on Gene Action

Diallel I tested under low intensity freezing at three different temperatures, is used to show changes in gene action with the severity of freezing conditions. Significant ($P < .001$) genotypic differences in freezing hardiness evaluated as meristem ratings were found for all tests. Genotypic variation was separated into general and specific combining ability in addition to reciprocal differences according to Griffing (9). The two former components were significant in all three tests whereas the latter was not significant in any tests (Tables 17, 19, and 21). W_r/V_r graphs were calculated after averaging over reciprocal crosses. The slopes of the graphs were all significantly different from zero but not from unity (Figures 8, 9 and 10) indicating the adequacy of the additive-dominance model. The graphs intercept the W_r axis significantly above the origin which is an indication of

TABLE 17.--Analysis of variance of the lower peripheral crown meristem ratings for combining ability and reciprocal differences of parents and F_1's of a six parental diallel tested under low intensity freezing at a temperature of -18.2 C.

Source of Variance	df	MS	F	P
General combining ability	5	7.1212	90.9476	<.001
Specific combining ability	15	.2600	3.3206	<.001
Reciprocal differences	15	.6337	.0422	>.750
Error	484		.0783	

TABLE 18.--Lower peripheral crown meristem ratings of parents and F_1's from a six parental diallel tested under low intensity freezing at a temperature of -18.2 C, averages over replications and reciprocal crosses.

Parental Number	Parent	1	2	3	4	5	6	V_r	W_r
1	Genesee	.13	.13	.06	1.35	1.41	.16	.4248	.8083
2	Dual		1.13	.41	2.75	2.41	1.44	1.1015	1.2939
3	Arrow			.06	.44	1.50	.32	.2828	.5209
4	Winoka				2.94	3.32	1.97	1.1893	1.2270
5	Kharkov 22 MC					2.81	2.28	.5489	.8939
6	Mironovskaja 808						.63	.7942	1.1072
Sum		3.24	8.27	2.79	12.77	13.73	6.88	4.3435	5.8512

TABLE 19.--Analysis of variance of the lower peripheral crown meristem ratings for combining ability and reciprocal differences of parents and F_1's of a six parental diallel tested under low intensity freezing at a temperature of -17.5 C.

Source of Variance	df	MS	F	P
General combining ability	5	6.2688	64.4938	<.001
Specific combining ability	15	.1910	1.9650	.025-.01
Reciprocal differences	15	.1547	1.5920	.100-.05
Error	484	.0972		

TABLE 20.--Lower peripheral crown meristem ratings of parents and F_1's from a six parental diallel tested under low intensity freezing at a temperature of -17.5 C, averages over replications and reciprocal crosses.

Parental Number	Parent	1	2	3	4	5	6	V_r	W_r
1	Genesee	.14	.91	.41	1.20	2.37	.88	.6065	.9600
2	Dual		1.67	.56	2.93	3.28	1.49	1.1796	1.4475
3	Arrow			.10	1.63	1.75	.45	.4825	.8830
4	Winoka				2.88	2.88	2.04	.5573	.8935
5	Kharkov 22 MC					3.33	2.38	.3738	.6705
6	Mironovskaja 808						1.32	.5078	.9445
Sum		5.91	10.84	4.90	13.56	15.99	8.56	3.7075	5.7990

TABLE 21.--Analysis of variance of the lower peripheral crown meristem ratings for combining ability and reciprocal differences of parents and F_1's of a six parental diallel tested under low intensity freezing at a temperature of -16.7 C.

Source of Variation	df	MS	F	P
General combining ability	5	4.9985	51.2667	< .001
Specific combining ability	15	.2594	2.6605	< .001
Reciprocal differences	15	.1503	1.5415	.10-.05
Error	484		.0975	

TABLE 22.--Lower peripheral crown meristem ratings of parents and F_1's from a six parental diallel tested under low intensity freezing at a temperature of -16.7 C, averages over replications and reciprocal crosses.

Parental Number	Parent	1	2	3	4	5	6	V_r	W_r
1	Genesee	.12	.94	.24	1.38	2.39	.35	.7578	.9969
2	Dual		1.55	.98	1.82	2.72	2.08	.4623	.6706
3	Arrow			.17	1.34	2.18	.21	.6553	.9253
4	Winoka				2.69	2.36	1.93	.2842	.6090
5	Kharkov 22 MC					2.93	2.70	.0789	.1896
6	Mironovskja 808						.90	1.0391	1.1652
Sum		5.42	10.09	5.12	11.52	15.28	8.17	3.2776	4.5566

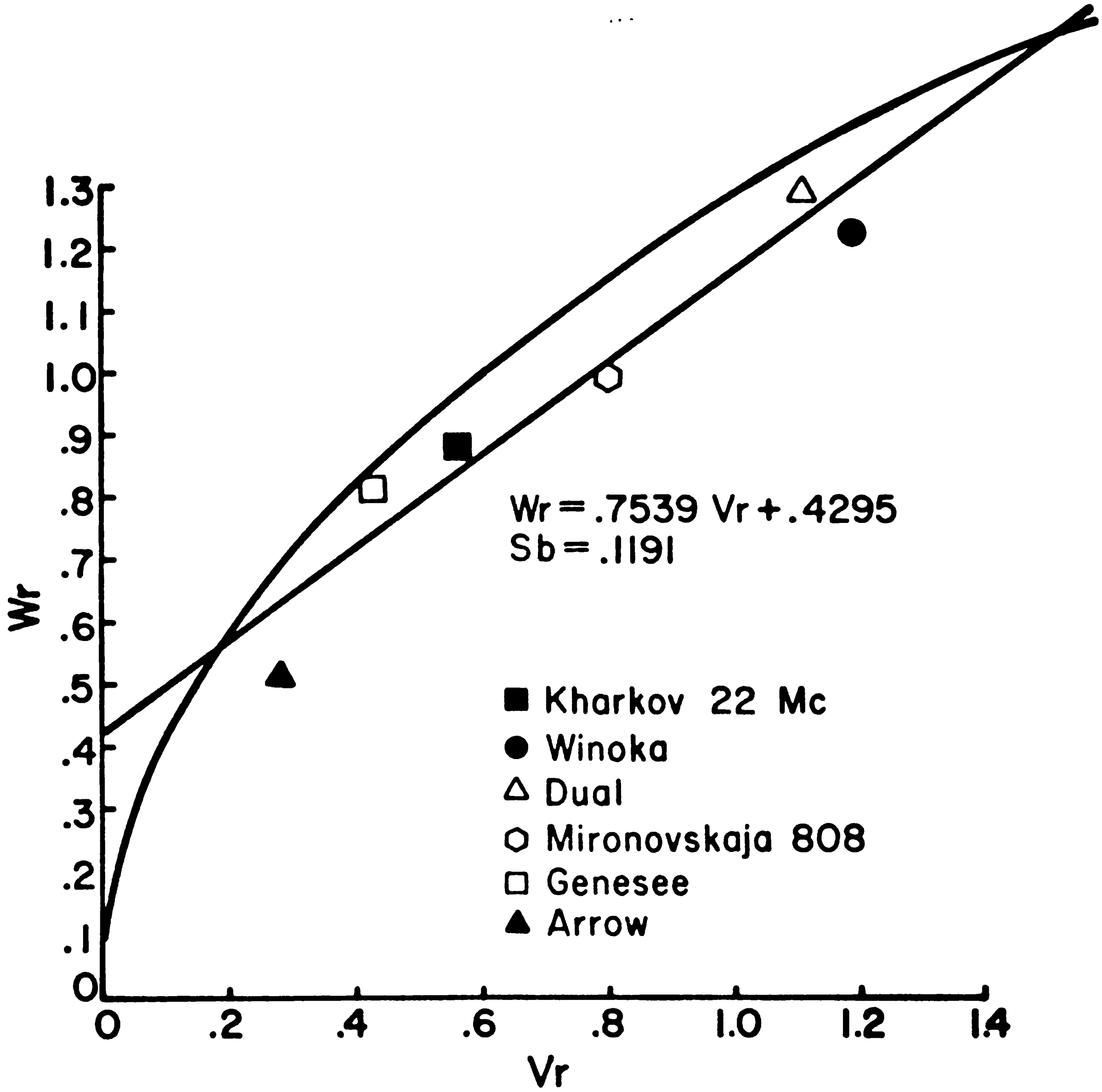

Figure 8.--The regression of W_r on V_r for freezing hardiness in terms of lower peripheral crown meristem ratings of a six parental diallel tested under low intensity freezing at -18.2C.

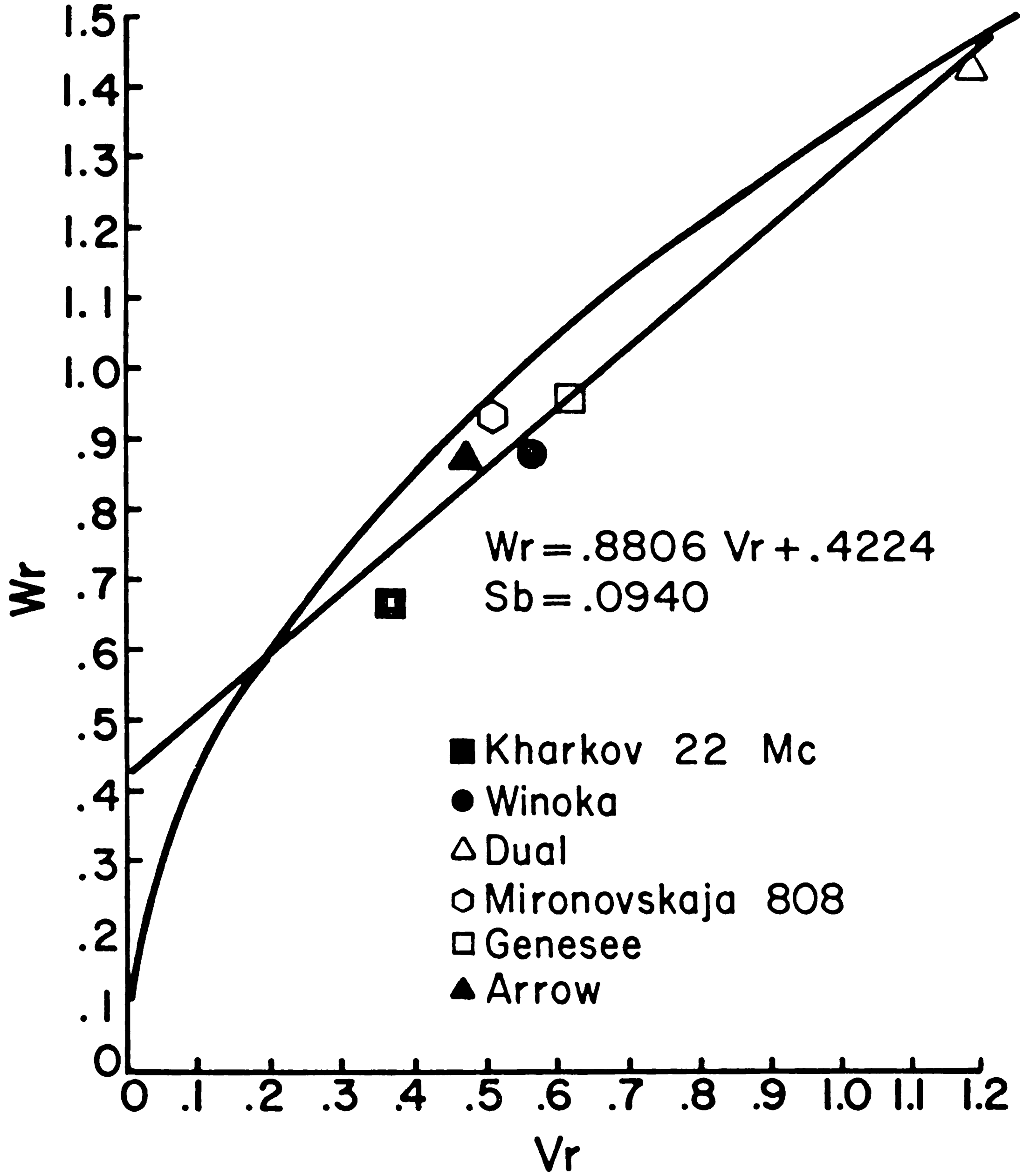

Figure 9.--The regression of W_r on V_r for freezing hardiness in terms of lower peripheral crown meristem ratings of a six parental diallel tested under low intensity freezing at -17.5C.

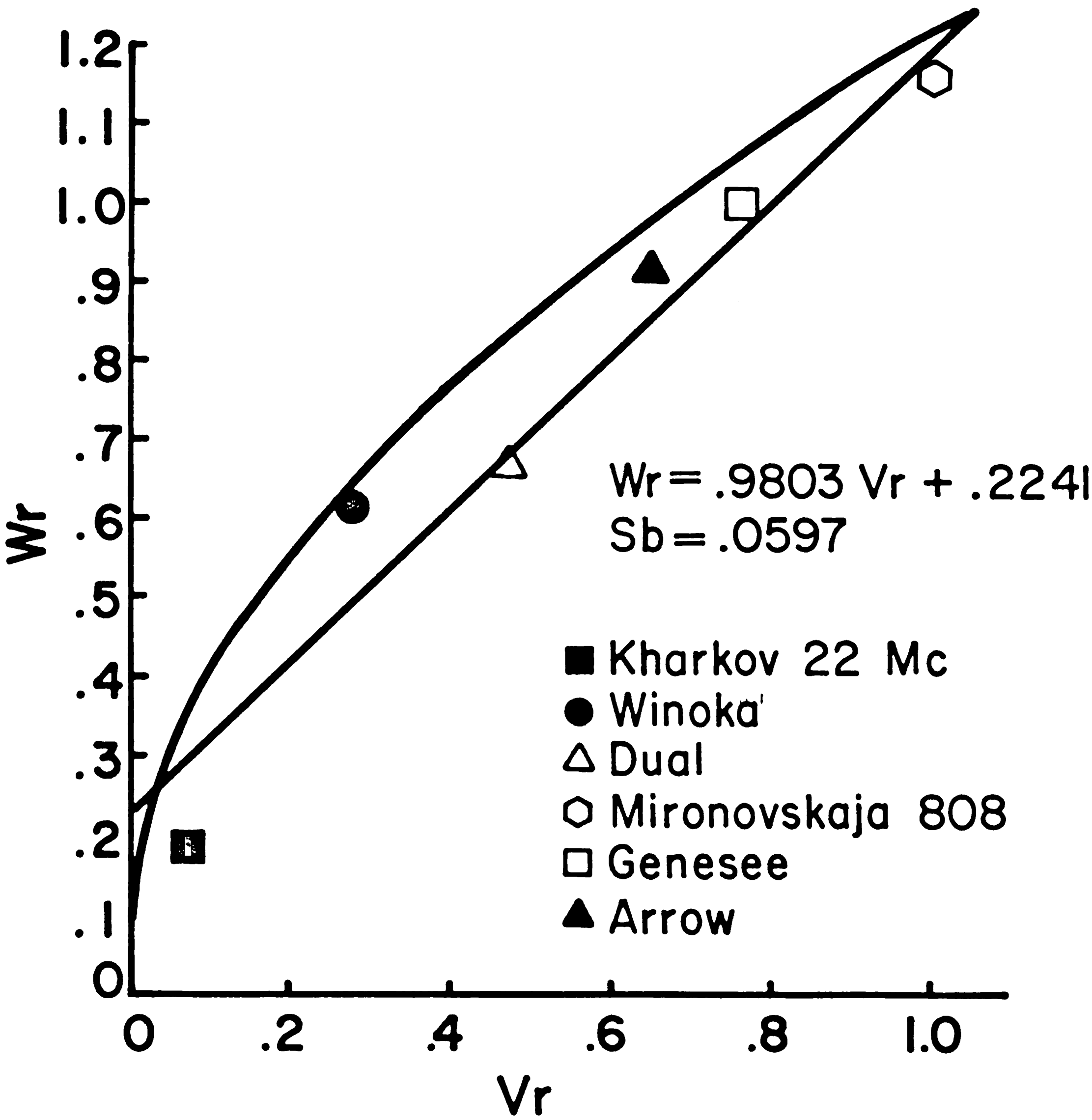

Figure 10.--The regression of W_r on V_r for freezing hardiness in terms of lower peripheral crown meristem ratings of a six parental diallel tested under low intensity freezing at -16.7C.

incomplete dominance. The dominance seems to be less complete under the two most severe freezing conditions (Figures 8 and 9) than under the mildest freezing condition. This is in agreement with results reported by Eunus et al. (6). Arrow has the lowest W_r and V_r values and Winoka and Dual the highest values in the test with the lowest test temperature (Figure 8). Under the mildest freezing condition of the three, Kharkov 22 MC has the lowest W_r and V_r values whereas Mironovskaja 808, Genesee and Arrow have the highest (Figure 10). The ranking of the cultivars according to the W_r and V_r values under intermediate freezing temperatures is intermediate to the extreme tests. Tables 18, 20, and 22 show that Kharkov 22 MC and Winoka are the most hardy cultivars in all tests, whereas Arrow and Genesee are the most tender and Dual and Mironovskaja 808 intermediate. This data indicates that freezing hardiness is controlled by the most dominant genes at the highest freezing temperature, the most recessive genes at the lowest freezing temperature and dominant and recessive genes in the same proportion at the intermediate freezing temperature. This is in agreement with results obtained in winter oats (14, 24) and winter wheat (43).

The meristem rating scale used in this study to evaluate freezing hardiness, varies between 1 and 4, 0 (dead) and 5 (undamaged) being off the scale. Under severe freezing conditions the frequency distribution of the meristem ratings of the tender genotypes are skewed toward the lower limit of the scale, and the mean meristem rating will accordingly be overestimated. Assuming the range in freezing hardiness within an array is less than the scale range, overestimated means will result in reduced array variances and covariances. The low W_r and V_r values shown for Arrow and Genesee at the lowest freezing temperatures in Tables 18 and 20 are due to the reduced range in freezing hardiness for the arrays and not to recessive genes controlling the character.

A freezing test is difficult to monitor so that a normal or close to normal frequency distribution for meristem ratings is achieved for all genotypes tested simultaneously. The interpretation of a diallel will, however, not be wrong, if the freezing temperature is adjusted so the frequency distributions for the hardy genotypes are skewed a little toward the upper limit of the scale. Too mild conditions may prevent separation of the most hardy genotypes when freezing hardiness is controlled by dominant genes.

Relationship Between Freezing Hardiness and Leaf Moisture Content

Moisture content was measured in young leaf tissue of nine winter wheat cultivars. Table 23 shows that there are significant differences between varieties for the character.

TABLE 23.--Moisture content of young leaves for nine winter wheat cultivars, averages over 14 replications.

Genotype	Moisture Content in Percent
Minturki	73.33 a*
Yogo	73.74 ab
Winoka	74.22 ab
Kharkov 22 MC	74.48 bc
Mironovskaja 808	75.36 cd
Genesee	75.99 de
Monon	76.40 e
Arrow	76.88 e
Dual	76.92 e

*Duncans Multiple Range test after Steel and Torri (47).

A regression analysis between the mean moisture content and freezing hardiness under high and low intensity freezing evaluated as meristem ratings, showed a significant negative correlation in both cases, and that moisture content explained 68.9 and 72.3 percent, respectively of the variation in freezing hardiness (Figures 11 and 12). These results are in agreement with the higher kill temperatures reported in wheat genotypes (10, 23) as a result of environmental induced higher crown moisture. Higher moisture content in crown tissues results in more free energy of ice crystal growth available for disrupting crown tissues (28). According to presented materials valid predictions

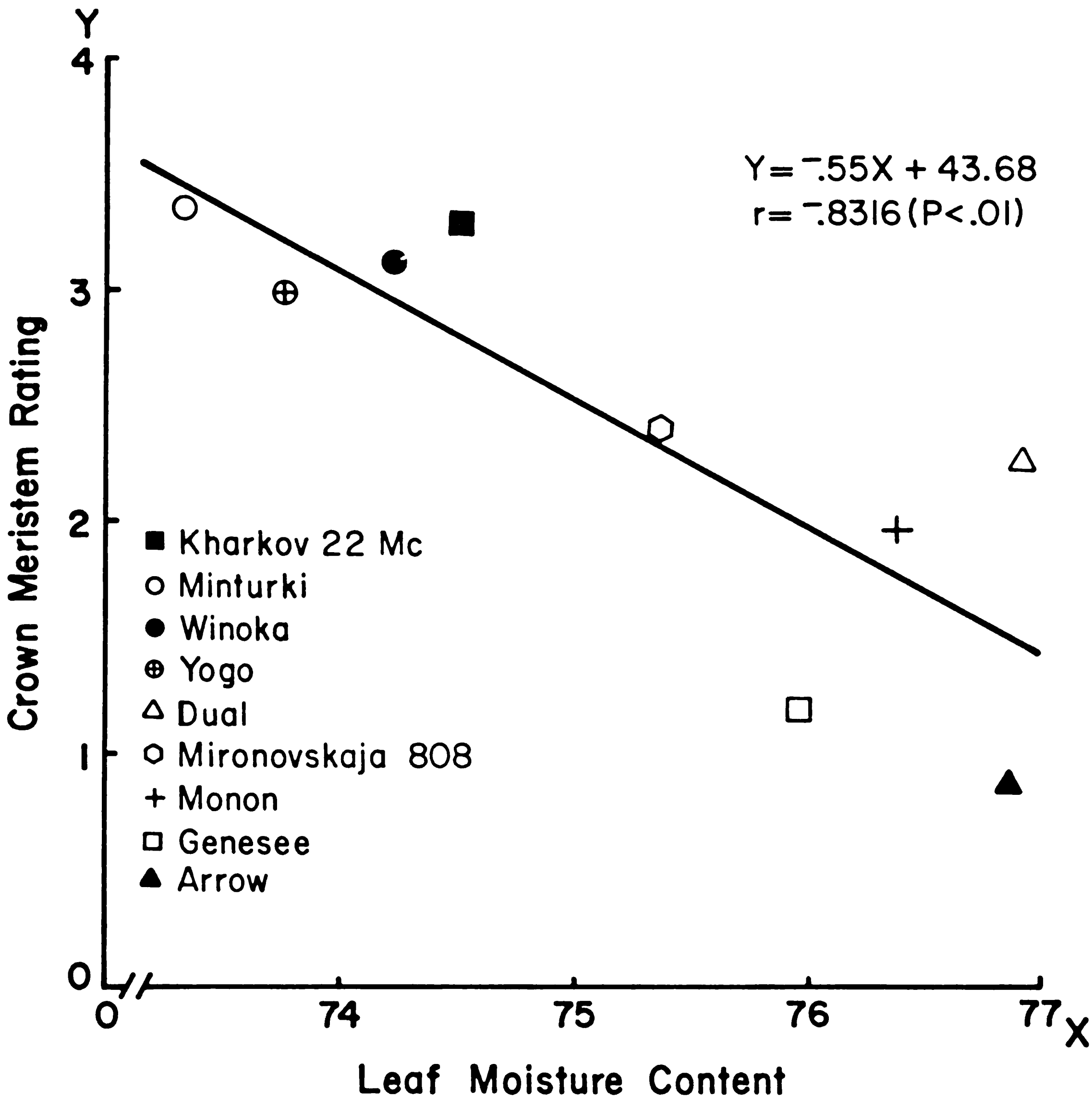

Figure 11.--Relationship between freezing hardiness in terms of lower peripheral crown meristem ratings tested under high intensity freezing and leaf moisture content for nine winter wheat cultivars.

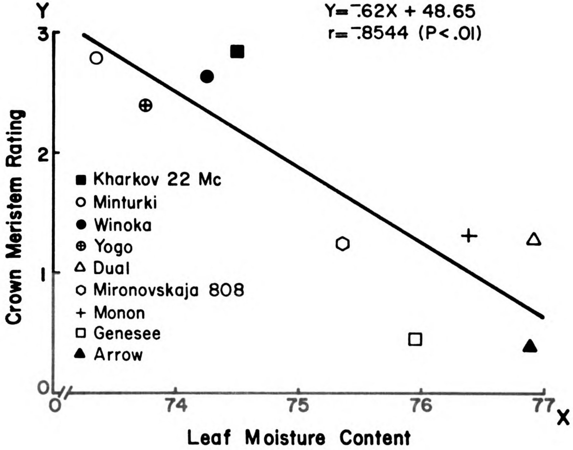

Figure 12.--Relationship between freezing hardiness in terms of lower peripheral crown meristem ratings tested under low intensity freezing and leaf moisture content for nine winter wheat cultivars.

of the freezing hardiness of genotypes could be made by knowing the moisture content of the leaf tissue close to the crown. To make sure one is not working with linkage between moisture and freezing hardiness this relationship should first be confirmed in a segregating population.

As can be seen in Figures 11 and 12, factors other than moisture content must account for the relatively high freezing resistance of Dual, or low freezing resistance of Genesee. Shearman et al. (45) showed a good relationship between freezing hardiness and kinetic inhibitor ratings in winter wheat. If kinetic inhibitor ratings (data provided by Dr. Olien) were included as an independent variable in addition to moisture content, 79.5 and 83.0 percent of the variation in freezing hardiness were explained under high and low intensity freezing respectively.

The inheritance of moisture content was studied in diallel II. Significant differences were found between genotypes (Table 24).

TABLE 24.--Analysis of variance of moisture content of young leaves near the crown of parents and F_1's of a four parental diallel.

Source of Variation	df	MS	F	P
Replication	4	19.2483	16.2983	<.001
Genotypes	9	10.4349	8.8356	<.001
Error	36	1.1810		

The regression coefficient of the W_r/V_r graph is significantly different from zero, but not from unity (Figure 13), indicating that non-allelic interaction is present as dominance only. The graph intercepts the W_r axis significantly ($P < .001$) above origin, suggesting that the dominance is only partial. Minturki and Yogo have the lowest W_r and V_r values and the most dominant genes whereas Monon has the highest W_r and V_r values and the highest proportion of recessive genes. According to Table 25, Yogo and Minturki have the lowest moisture whereas Monon has the highest. Low moisture appears to be controlled by partially dominant genes mostly additive in their effect.

TABLE 25.--Moisture content of young leaves close to the crown of F_1's and parent plants from a four parental diallel, averages of five replications.

Parental Number	Parent	1	2	3	4	V_r	W_r
1	Dual	75.62				1.1740	2.0983
2	Yogo	73.79	72.19			.8181	1.7095
3	Minturki	73.81	72.05	72.69		.6891	1.5609
4	Monon	75.73	73.56	73.65	75.95	1.6745	2.5116
Sum		298.95	291.59	292.20	298.89	4.3557	7.8803

Measurements of cross sections of leaf and root tissues close to the crown was made of Winoka, Kharkov 22 MC and Arrow. Moisture content seemed to be positively correlated with cell size.

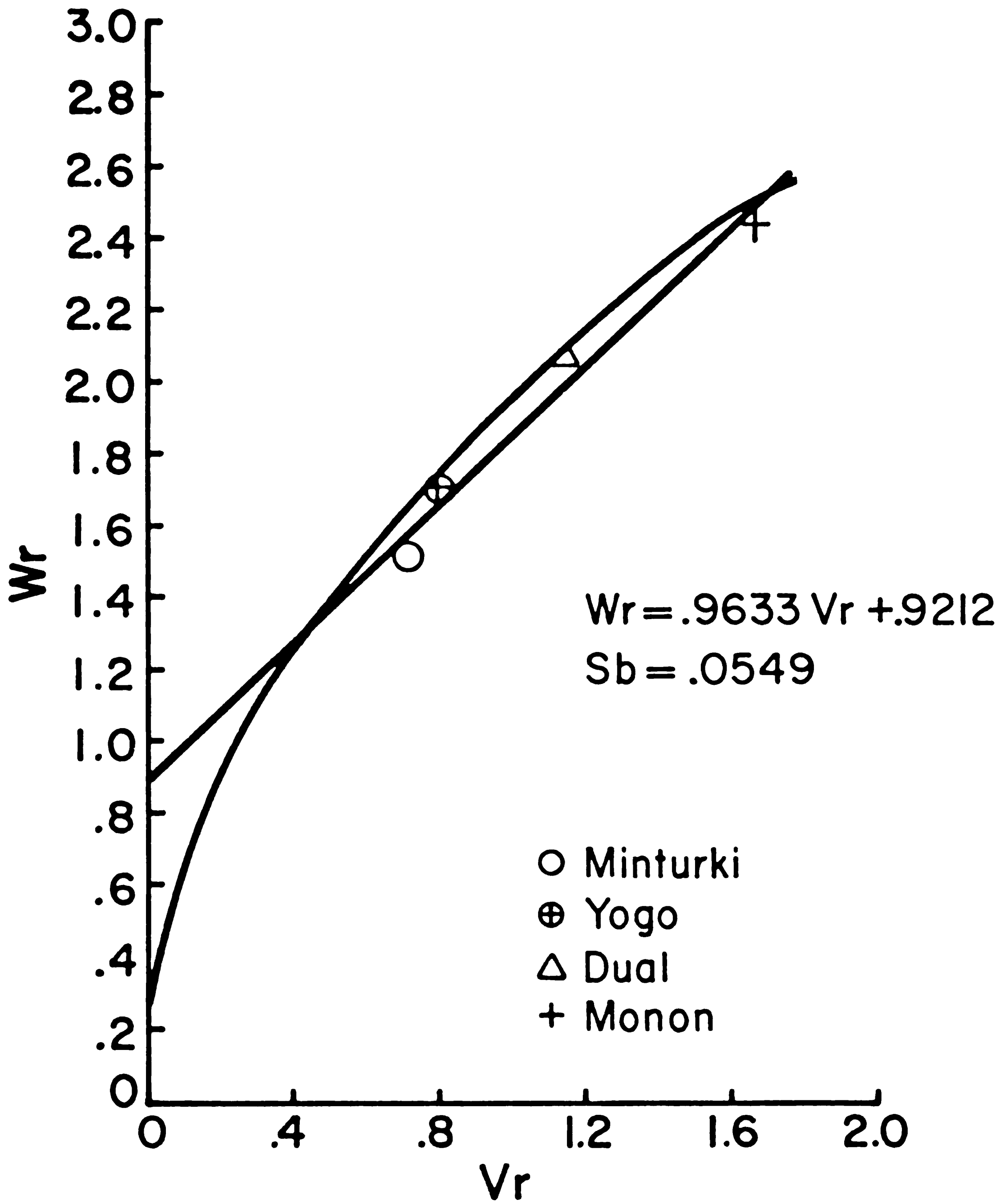

Figure 1?.--The regression of W_r on V_r for leaf moisture content of a four parental diallel.

SUMMARY AND CONCLUSIONS

Inheritance of freezing hardiness was studied in (1) F_2 and backcross populations originating from a cross between Genesee and Winoka and (2) in two complete diallels, one six and one four parental diallel. The material was tested under both high and low intensity freezing according to a procedure described by Gullord et al. (10). Moisture content in young leaves close to the crown was studied in nine winter wheat genotypes varying in freezing hardiness, and in a four parental diallel.

1. Freezing hardiness was found to be a quantitative character controlled by many genes.

2. Significant interaction between F_2 lines and the level of freezing intensity suggests that genes controlling freezing hardiness under low intensity freezing is different from the genes controlling freezing hardiness under high intensity.

3. The simple additive-dominance model with independent gene distribution described by Hyman (13) adequately describes the variation in freezing hardiness in both diallels under both levels of freezing intensity.

4. Analysis of both diallels showed that freezing hardiness is controlled by partially dominant genes which are mostly additive in their effect. Some or all of the genes found to control freezing hardiness under low intensity freezing may very likely be different from the dominant genes found to control freezing hardiness under high intensity freezing.

5. No reciprocal differences were found in either of the diallels tested under any level of freezing intensity.

6. Very severe freezing conditions resulted in lower array variances and covariances than expected for the tender varieties. The reason is not that recessive genes control freezing hardiness at severe freezing conditions, but that the frequency distributions of the crown meristem ratings were skewed toward the lower limit of the scale, resulting in overestimated crown meristem rating means and reduced array variances and covariances for the tender genotypes.

7. Highly significant negative correlation was found between moisture content in young wheat leaves and freezing hardiness evaluated under both high and low intensity freezing in nine winter wheat genotypes.

8. About seventy percent of the variation in freezing hardiness was explained by moisture content in the young wheat leaves.

9. If kinetic inhibitor ratings were included as an independent variable in addition to moisture content, about eighty percent of the variation in freezing hardiness was explained both under high and low intensity freezing.

10. Low moisture content was found to be controlled by partially dominant genes mostly additive in their effect.

11. Some or all of the partially dominant genes controlling low moisture content in wheat leaves may be identical to the partially dominant genes found to control freezing hardiness. Some of the genes controlling the kinetic inhibitors in wheat are also very likely among the genes found to control freezing hardiness.

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