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Inheritance of Cold Tolerance in Common Wheat (*Triticum aestivum* L.)

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Abstract: Low temperature is one of the most severe abiotic stresses limiting wheat growth, productivity, and distribution. Understanding the genetic nature of cold and frost tolerance is regarded as the primary step in wheat breeding programs. This study used a winter wheat cultivar, Norstar, which has a high level of cold tolerance (LT_{50} = –22.3 °C), and a highly cold-susceptible Iranian spring wheat variety, Zagros (LT_{50} = –3.5 °C), as parental lines to develop different generations. Seven generations, P_1, P_2, F_1, F_2, $F_{2:3}$, BC_1, and BC_2, were used for generation mean and generation variance analysis for estimating genetic effects and variances, and also for determining the number of genes governing cold tolerance in wheat. LT_{50}, the temperature at which 50% of the plants were killed, was used as a measure of cold tolerance. Broad-sense and narrow-sense heritabilities were 80.1% and 65.98%, respectively. Estimating gene number by different formulae showed that several genes or QTL were involved in the genetic control of LT_{50}. Additive, dominance, additive x additive, additive x dominance, and dominance x dominance effects were significant, indicating that all modes of gene action were involved in governing cold tolerance in this type of wheat cross.

Key Words: Frost tolerance, gene action, gene number, generation mean analysis, generation variance analysis, heritability, LT_{50}, wheat

Introduction

Freezing temperature is an important abiotic stress, which causes significant losses in crop production and limits the distribution of agronomic species throughout the world (Thomashow, 1998). Frost-tolerant plants can survive exposure to low temperature and are less susceptible to serious damage from freezing temperatures (Limin and Fowler, 1993; Sutka, 2001). Therefore, one of the major objectives in breeding programs of cool-season cereals is to select or develop lines that minimize frost damage during the vegetative phase (Fowler et al., 1981).

Cold hardiness is a quantitative, complex trait (Sutka, 2001; Thomashow, 2001). Nearly all wheat chromosomes (Galiba et al., 1995), or at least 10 chromosomes of 21 chromosome pairs are important in winter hardiness (Sutka, 2001). Sutka (1981, 2001), using monosomic and line substitution analysis, emphasized the important role of 5A, 7A, 4A, and 5D chromosomes. Although a large number of studies have been carried out to understand the genetic control of cold tolerance in wheat, different modes of gene action have been reported to control this trait. Additive, recessive, incomplete dominance, and overdominance gene action have been implicated in cold tolerance (Brule-Babel and Fowler, 1988; Limin and Fowler, 1993; Sutka, 2001). Thomashow (1998, 2001) contends that, although there are some reports of non-additive gene action, cold and frost tolerance are mainly controlled by several genes with additive effects. Sutka (1981), based on a diallel analysis, reported that the effect of additive genetic variance in controlling cold tolerance is higher than non-additive genetic variance. Nouraein (2006) also indicated the prominence of additive effects of genes in governing cold tolerance in a diallel analysis of 7 wheat genotypes, including spring and winter varieties. However, Sutka et al. (1999) reported that a gene with dominant effect, Fr_1, is involved in the control of wheat frost tolerance. This gene was linked to the Vrn_1 gene responsible for vernalization and rosette growth type. These genes are

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located on the distal part of the 5A chromosome of wheat (Sarma et al., 1998; Sutka et al., 1999; Vagujfavli et al., 2000). The importance of this region in the abiotic stress resistance of wheat is now well understood (Galiba, 2002). Kobayashi et al. (2005) outlined that the Vrn-Fr1 region consists of main QTL (Quantitative trait loci) and these QTL control both frost tolerance and vernalization requirement. Sutka (2001) reported that frost-sensitive wheat varieties have the largest number of dominant genes, while frost-resistant varieties have the highest proportion of recessive genes. One possible reason for the discrepancies about the mode of gene action is partly related to the freezing assay methods. Use of LT_{50} (the temperature at which 50% of plants are killed in a controlled-freeze test) as a measure of cold tolerance in different wheat varieties provides more accurate results (Fowler et al., 1996; Limin and Fowler, 2000). Fowler et al. (1981, 1999) evaluated the relationship of LT_{50} to several characters as a measure of cold and frost tolerance in wheat. They stated that the LT_{50} measurement is the most heritable and accurate measure of cold tolerance related to the field survival index.

The research program presented herein was conducted to study the inheritance of frost tolerance in a wheat cross of Norstar x Zagros.

Materials and Methods

Plant materials and freezing test

To study the genetic control of cold tolerance in wheat, 2 cultivars, Norstar and Zagros, were crossed to develop different generations used in the present study. Norstar is a standard, highly cold-resistant winter wheat cultivar (LT_{50} = –22.3 °C) and Zagros is an Iranian, highly cold-susceptible spring cultivar (LT_{50} = –3.5 °C). The produced generations, P_1, P_2, F_1, F_2, F_3, BC_1, and BC_2, were used for the freezing test. The 6 basic generations were evaluated in 2 replications, with 60 individuals in each experimental unit. For the F_3 generation, 350 families, each consisting of 60 individuals, were assessed without replication. Cold tolerance was assessed according to Fowler et al. (1981) and Mahfoozi et al. (2001b). A set of 12 test temperatures ranging from –3 °C to –25 °C, with increments of 2 °C was used. Seeds were first imbibed in filter paper-lined petri dishes at 4 °C to ensure uniform germination. Germinated seeds were transplanted in a controlled greenhouse under 20 °C and a 14/10 h (D:N) photoperiod. When the growing seedlings reached the 3-4-leaf stage (Zadoks et al., 1974), the plants were transferred to a growth chamber at 2 °C with a 14/10 h (D:N) photoperiod for cold acclimation. After 35 days of acclimation, the crowns were detached from the plants and covered with moist sand in aluminum cans and placed in a programmable freezer and kept at –3 °C for 12 h. After this period, they were cooled at a rate of 2 °C/h to –17 °C and then cooled at a rate of 8 °C/h to a minimum of –30 °C (Mahfoozi et al., 2001b). Five crowns were removed for each of the tested temperatures in each generation. Samples were thawed overnight at 4 °C and replanted in controlled chambers at 20 °C with a 14/10 h (D:N) photoperiod. Plant recovery was rated after 3 weeks of regrowth and LT_{50} was calculated for each generation.

Statistical analyses

The means and variances of parental, F_1, F_2, F_3, BC_1, and BC_2 generations were used to estimate the components of gene action by the weighted least squares method (Mather and Jinks, 1982). The accuracy of the additive-dominance model was tested using the following equations:

$$A = 2\overline{BC_1} - \overline{P_1} - \overline{F_1}$$

$$B = 2\overline{BC_2} - \overline{P_2} - \overline{F_1}$$

$$C = 4\overline{F_2} - 2\overline{F_1} - \overline{P_2} - \overline{P_2}$$

Additionally, a joint scaling test was performed for verifying the adequacy of all the models studied. The epistatic model describing non-allelic interactions between pairs of loci was tested by following the statistical model described by Mather and Jinks (1982):

$$Y = m + \alpha\,[d] + \beta\,[h] + \alpha^2\,[i] + 2\alpha\beta[j] + \beta^2[l]$$

where Y = generation mean, m = mean of all possible homozygous lines deriving from the cross, [d], [h], [i], [j], and [l] = net directional effects of loci contributing to additive, dominance, additive x additive , additive x dominance, and dominance x dominance components, respectively, and α and β = coefficient of genetic parameters. Due to the different sizes and variances of generations, the weighted least square method was used to predict the genetic parameters (Steel and Toorie,

1981; Kearsey and Pooni, 1996). The genetic model that best fit the data was found by the mean of joint scaling test (Mather and Jinks, 1982), and the accuracy of the models was verified by chi-square test. Components within each model were evaluated for significance by t-test.

Estimates of dominance ratio, broad-sense heritability (h^2_B) (Kearsey and Pooni, 1996), narrow-sense heritability (h^2_N) (Warner, 1952), standard errors of h^2_B (Ehdaie and Weines, 1994), and h^2_N (Ketata et al., 1976) for LT_{50} were obtained using the following equations:

Dominance ratio = $(4\sigma^2_D/2\sigma^2_A)^{1/2}$

$h^2_B = (V_{F2} - V_E)/V_{F2}$

$h^2_N = [2\ V_{F2} - (V_{BC1} + V_{BC2})]/V_{F2}$

$SE(h^2_B) = \{1/V^2_{F2}[V^2_{P1}/df_{p1} + V^2_{P2}/df_{p2} + V^2_{F1}/df_{F1} + (V^2_{P1} + V^2_{P2} + V^2_{F1})/df_{F2}]\}^{1/2})/V_{F2}$

$SE(h^2_N) = \{2\{[(V_{B1}+V_{B2})^2/\ df_{F2}] + (V^2_{B1}/df_{B1}) + (V^2_{B2}/df_{B2})\}\}^{1/2}$

Dominance variance: $\sigma^2_D = V_{BC1} + V_{BC2} - V_{F2} - V_E$

Additive variance: $\sigma^2_A = 2V_{F2} - (V_{BC1} + V_{BC2})$

$V_E = (V_{P1} + V_{P2} + 2V_{F1})/4$

Gene number was estimated by the formulae listed in Table 1 (Chen and Line, 1995). Although each formula has its restrictions and assumptions, all assume equal gene effects (Dehghani et al., 2002).

Results and Discussion

The least square means of LT_{50} for the parental lines (Norstar, P_1) and (Zagros, P_2), their progeny (F_1, F_2, $F_{2:3}$, BC_1, and BC_2), and several contrasts among generations are presented in Tables 2 and 3, respectively. The cold tolerance levels of F_1, F_2, and BC_1 were not significantly different from the parental midpoint. $F_{2:3}$ and BC_2 generations were significantly less tolerant as compared to the mid-parent value. Although all generations had cold tolerance levels that were significantly different from the susceptible parent, Zagros, none of the generations were more tolerant than the resistant parent, Norstar (Table

Table 1. The different formulae used to estimate the number of genes controlling LT_{50} measurement in wheat.

Formula number[a]	Formulae[b]
1	$n^c = (\bar{P}_1 - \bar{P}_2)^2/[8(V_{F2} - V_{F1})]$
2	$n = (\bar{P}_1 - \bar{P}_2)^2/[8(V_{F2} - V_{F1})]$ $\quad V_E = (V_{P1} + V_{P2} + 2V_{F1})/4$
3	$n = (\bar{P}_1 - \bar{P}_2)^2/[8(V_{BC1} - V_{BC2} - V_E)]$
4	$n = (\bar{P}_1 - \bar{P}_2)^2/[8(V_{F2} - V_{BC1} - V_{BC2})]$
5	$n = (\bar{P}_1 - \bar{P}_2)^2/[1.5 - 2h^e\ (1 - h)]/8(V_{F2} - V_E)]$
6	$n = (GR^f)^2/5.33[V_{F3} - (V_{P1} - V_{P2})/2]$
7	$S^c_1 = (\bar{F}_1 - \bar{P}_1)^2/4(V_{BC1} - V_E)]$
8	$S_1 = (\bar{F}_1 - \bar{P}_2)^2/4(V_{BC2} - V_E)]$

a: Formulae 1-3 from Lande (1981), 4-5 from Wright (1968), 6 from Bjarko and Line (1988) and 7-8 from Milus and Line (1986).

b: In each formula, $\bar{P}_1$, $\bar{P}_2$, $\bar{F}_1$ and so on represent mean of respective generations.

c: n and s_1 represents the number of genes in formulae 1-6 and 7-8, respectively.

e: $(\bar{F}_1 - \bar{P}_1)/(\bar{P}_2 - \bar{P}_1)$

f: GR = (max-min) F_3 family means

Table 2. Mean LT_{50} of 7 generations of Norstar x Zagros wheat cross.

Cross	Generations						
	P_1	P_2	F_1	F_2	F_3	BC_1	BC_2
Norstar x Zagros P_1 P_2	–22.25(0.53)[a]	–3.5(0.43)	–10.5(0.38)	–9.5(1.06)	–8.5(0.12)	–14.25(0.56)	–9.4(0.8)

[a] The values in parentheses represent the standard errors of the generation mean

Table 3. Parental LT_{50} mean (XP) and planned contrasts between parental, F_1, F_2, BC_1, BC_2, and F_2-derived F_3 populations of Norstar x Zagros wheat cross.

LT_{50} Cross	Mean Differences						
	XP	F_1-XP	F_2-XP	F_3-XP	BC_1-XP	BC_2-XP	P_1-P_2
Norstar x Zagros P_1 P_2	–12.87	2.37	3.37	4.37*	–1.38	3.47*	–18.75

*Significant at the 0.05 probability level ($LSD_{0.05}$ = 3.4)

3). Since Norstar is highly cold-tolerant and Zagros is highly cold-susceptible, transgressive segregation toward the tolerant parent was not obtained. However, the cold hardiness (LT_{50}) frequency distribution of $F_{2:3}$ lines tended to be skewed toward the cold-susceptible parent. This may be evidence of the existence of some dominance in controlling frost tolerance in this wheat cross (Table 2). Limin and Fowler (1993), in crosses of Norstar with 4 wheat cultivars and 5 synthetically produced hexaploid lines, observed a high level of cold hardiness in some F_1 progenies compared to their parental mean; however, the tolerance levels of F_1s were less than those of Norstar. They indicated that some degree of dominance gene action was involved in the cold tolerance of those crosses.

The estimated numbers of genes controlling LT_{50} using different formulae are presented in Table 4. The formulae 1, 2, 5, 6, and 7 gave similar estimates of the number of genes controlling cold hardiness in the wheat crosses. Formulae 4 and 8 provided the maximum and minimum estimates of gene number, respectively (11.9 and 3.02) (Table 4). Although the estimates of different formulae may be subjected to their inherent assumptions, it is seen that estimated numbers, except in formulae 4, were close to each other. Based on these formulae, it appears that 3 to 6 genes are segregating in the Norstar x Zagros crosses. These types of analyses estimate the maximum number of genes; however, the genes controlling quantitative traits could be linked and could, therefore, segregate as a group or effective factor (Milus and Line, 1986). If this were true for the present study, the formulae would have estimated the number of effective factors, and the number of individual genes would have been greater.

Table 4. Estimated number of segregating genes for LT_{50} of the Norstar x Zagros wheat cross, based on formulae in Table 1.

Cross	Formulae number							
	1	2	3	4	5	6	7	8
Norstar x Zagros	5.9	6.3	4.3	11.9	6.5	5	5.55	3.02

Estimated average degree of dominance for LT_{50} was 1.25 (Table 5), which indicated the importance of dominance gene action in the inheritance of LT_{50} in this wheat cross. However, epistatic effects and linkage may upwardly bias the dominance, and even partial dominance may become pseudo-overdominance (Hayman, 1954). Parodi et al. (1983) also showed that in a diallel cross the major portion of genetic

Table 5. Estimation of variance components, dominance ratio, and heritabilities of LT_{50} in Norstar x Zagros wheat cross.

Variance components				Heritability		
V_E	$V_{[d]}$	$V_{[h]}$	$V_{[dh]}$	h^2_b	h^2_n	Dominance Ratio
1.39	3.69[a]	2.91[a]	–1.03[a]	0.80(0.09)[b]	0.66(0.25)[b]	1.25

[a] $P \leq 0.01$

[b] The value in parentheses represent standard errors

variability of cold tolerance was associated with dominance and was additive by additive effects.

After scaling tests, of which the results were not significant (data not shown), the joint scaling tests for 8 models were also performed. Only 4 models had non-significant χ^2, but the χ^2 value in the full model was less than one (Table 6). Therefore, this model was selected to estimate genetic parameters. All additive, dominance, additive x additive, additive x dominance, and dominance x dominance effects were significant, at least at the 5% probability level (Table 7), which indicated the importance of the additive, dominance, and epistatic modes of gene action in controlling cold tolerance in wheat. Brule-Bable and Fowler (1988) also emphasized that both additive and dominance gene action are important for frost tolerance in the spring in winter type wheat crosses. Fowler and Limin (2001) stated that cold tolerance within a species is mainly controlled by additive gene action, and that the discovery of a dominant gene on the 5A chromosome that affects cold tolerance (Storlie et al., 1998; Sutka, 2001) was one important exception. Limin and Fowler (1993) reported that the majority of F_1 progenies from a diallel cross of winter varieties were not significantly different from the midparents, but in some cases the differences were significant, indicating dominance gene action. It seems that the result of each study depends on the particular type of plant material and hardening and freezing conditions (Fowler and Limin, 2004). Chen et al. (1983) and Mahfoozi et al. (2001a) reported that the acclimation duration and condition are important factors involved in a plant's ability to reach its maximum cold or frost tolerance capacity.

Table 6. Chi-square goodness-of-fit test of 7 genetic models for LT_{50} of Norstar x Zagros wheat cross.

Cross	Model[a]	χ^2 Value[b]	P value
Norstar x Zagros	m [d] [h]	2.3	ns
m [d] [h] [i]	6.5	ns	
m [d] [h] [j]	31.2	< 0.01	
m [d] [h] [l]	29.0	< 0.01	
m [d] [h] [i] [j]	6.55	< 0.05	
m [d] [h] [i] [l]	1.9	ns	
m [d] [h] [j] [l]	23.0	< 0.01	
m [d] [h][i] [j] [l]	< 1	ns	

[a] m = mean, [d] = additive component, [h] = dominance component, [i] = additive x additive epistatic component, [j] = additive x dominance epistatic component, [l] = dominance x dominance epistatic component.

[b] Degree of freedom for the test is equal to 7 minus the number of components in the model.

ns = not significant

Broad- and narrow-sense heritability estimates based on variance of different generations were 80.1% and 65.98%, respectively (Table 5). The high heritability estimates indicated that cold tolerance is a heritable character. High heritability estimates for cold tolerance have been reported in wheat (Sutka 1981; Brule-Bable and Fowler, 1988; Sutka, 2001). Brule-Bable and Fowler (1988) stated that low heritability estimates are generally associated with large experimental errors and narrow crosses, while intermediate to high heritability estimates are associated with wider crosses. This idea corresponds with the results of our study, because the parents, Norstar and Zagros, were quite different in responding to cold stress (LT_{50} for Norstar = –22.3 °C and LT_{50} for Zagros = –3.5 °C). On the other hand, the estimated heritability values may have been upwardly biased by the epistatic gene action present in this study.

Table 7. Estimation of the genetic components from the generation mean analysis obtained for LT_{50} using the six-parametric model.

Cross	Componenta						
	m	[d]	[h]	[i]	[j]	[l]	χ^2
Norstar x Zagros	–3.68b	–9.37c	–16.64b	–9.83c	4.07c	9.19b	< 1d

a m = mean, [d] = additive component, [h] = dominance component, [i] = additive x additive epistatic component, [j] = additive x dominance epistatic component, [l] = dominance x dominance epistatic component.

b $P \leq 0.05$

c $P \leq 0.01$

d not significant

Conclusion

Based on the results, it could be stated that all modes of gene action, i.e. additive, dominance, and epistasis, are responsible for the inheritance of frost tolerance in this wheat cross, and because of high narrow- and broad-sense heritabilities, selection for cold and frost tolerance should be effectively practiced in breeding programs using this cross. In addition, since low temperature tolerance is a genetically complex character, the use of marker-assisted selection may facilitate genetic improvement of cold tolerance in these programs.

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