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EFFECT OF VERNALIZATION ON GRAIN FILL DURATION AND GRAIN WEIGHT IN SPRING WHEAT

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Abstract

Vernalization response genes are known to contribute indirectly to grain yield by influencing flowering time, number of tillers and spikelets in sensitive wheat genotypes. There has been no report of the effect of vernalization on grain fill duration and grain weight in wheat. The objective of this study was to investigate the effect of vernalization on grain fill duration and grain weight in a set of 5 high latitude spring wheat, differing in vernalization response, and their 10 F_1 hybrids obtained from a one-way diallel cross. The 15 genotypes were grown with and without 42d-vernalization treatment. Vernalization altered grain fill duration and grain weight in both sensitive and in-sensitive genotypes and no clear pattern was observed in terms of the vernalization responsiveness of the genotypes. No correlation was found between grain fill duration and grain weight in vernalized and non-vernalized treatment, indicating that the increase in grain fill duration of some of the genotypes with vernalization did not have an effect on grain weight. In order to harvest the full yield potential, vernalization sensitive genotypes may be grown in those eco-regions of high northern latitudes where growing season is relatively long and where temperatures are usually above the vernalization range.

Introduction

Vernalization response, or high temperature inhibition of reproductive development, is widespread in temperate plant species (Flood & Halloran, 1986). Winter wheat requires exposure to a continuous cold treatment (vernalization) prior to reproductive initiation. Spring wheat generally does not have such a requirement, but some cultivars do respond to cold by flowering early (Levy & Peterson, 1972; Jedel *et al*., 1986; Iqbal *et al*., 2006). Vernalization sensitivity/insensitivity in hexaploid wheat is controlled by alleles at the major vernalization loci, *Vrn-A1*, *Vrn-B1*, *Vrn-D1* and *Vrn-D5* (Pugsley, 1972). Winter wheat possesses recessive alleles at all these loci while spring wheats have dominant alleles at one or more of them. The dominant allele of *Vrn-A1* confers complete insensitivity to vernalization and is epistatic to dominant alleles of *Vrn-B1*, *Vrn-D1* and *Vrn-D5*, which confer low sensitivity to vernalization (Pugsley, 1971, 1972).

Vernalization affects floral initiation time, leaf number, timing of other growth stages up to emergence of the flag leaf, tiller number (Levy & Peterson, 1972; Iqbal *et al*., 2006) and spikelet number (Gororo *et al*., 2001; Whitechurch & Snape, 2003; Iqbal *et al*., 2006) in sensitive genotypes. Due to inconsistent vernalization conditions in high northern latitudes, vernalization responsive spring wheat genotypes tend to exhibit variable days to maturity and yield potential (Jedel, 1994).

Vernalization response genes are known to contribute indirectly to grain yield by influencing flowering time, number of tillers and spikelets in sensitive genotypes. To date, there has been no report of the effect of vernalization on grain fill duration and grain weight in wheat. The objective of this study was to investigate the effect of vernalization on grain fill duration and grain weight in high northern latitude spring wheats.

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Materials and Methods

Five Canadian spring wheat cultivars differing in vernalization response were selected for this study. The cultivars included ‘AC Taber’ (sensitive), ‘AC Foremost’ (sensitive), ‘AC Barrie’ (insensitive), ‘AC Intrepid’ (insensitive) and ‘Cutler’ (insensitive) (Iqbal *et al*., 2006).

The five cultivars were crossed in a one-way diallel mating design to obtain a total of 10 [(5(5-1)/2] cross combinations. One set of the ten F_1 hybrids and five parents (30 seeds per genotype) were vernalized for six weeks as sprouted seeds at 1^oC in the dark. To provide control plants at the same growth stage, un-vernalized seeds (30 per genotype) were germinated a week before the end of the vernalization treatment at room temperature. Two seedlings for each set (vernalized and un-vernalized) were then transplanted into 12.5cm diameter pots (thinned to one plant pot^{-1}) containing *Meteromix*. The transplants were arranged as a factorial combination of vernalization and genotype treatments (2×15) in a RCB with five blocks (each having two pots per treatment; a total of 10 plants per treatment) in a walk-in chamber maintained at 16 hours photoperiod and a 21 ± 2^oC constant temperature. A light intensity of about 300 µmol m^{-2} s^{-1} at plant level was supplied through a combination of fluorescent tubes and incandescent lamps. Plants were watered when the surface of the pot was dry and fertilized weekly with a water soluble commercial fertilizer (20-20-20: N-P_2O_5-K_2O). Observations were made on the main culm for number of days from transplanting to anthesis and maturity and grain weight. Grain fill duration was estimated as number of days from anthesis to physiological maturity.

To test the significance of vernalization and genotypic effects, three sets of analyses were conducted in the MIXED procedure of SAS (Anon., 2003). For the purposes of estimating genotypic performances under vernalized and un-vernalized conditions, best linear unbiased predictors (BLUPs) were obtained. The genotype effect was further partitioned into parents and hybrids (using BY GENOTYPE statement) and parents versus hybrids (using the ESTIMATE statement). Likelihood ratio testing was used to test if individual variance components were zero. Likelihood ratios were constructed as differences between the -2 Residual Log Likelihood values of the reduced covariance model (without the effect being tested) and the full covariance model (with the effect being tested) (Yang, 2002).

Diallel analyses were performed on the mean values of parents and F_1 crosses, employing an Additive-Dominance (AD) genetic model (Zhu, 2003). The genetic variance components were estimated based on an AD model using a mixed linear model approach, minimum norm quadratic unbiased estimation (MINQUE) (Rao, 1971). The genetic effects were predicted using the Adjusted Unbiased Prediction (AUP) method (Zhu & Weir, 1996). Jackknifing over genotype (4 reps for each genotype) was used to estimate standard errors of variances and the predicted genetic effects (J. Zhu, personal communication). Narrow-sense heritability across environments was estimated as $h_N^2 = (V_A + V_{AA})/V_P$, and broad-sense heritability across environments as $h_B^2 = (V_A + V_{AA} + V_D)/V_P$. The significances of variance components were tested using one-tailed *t*-tests, whereas those of genetic effects were tested using two-tailed *t*-tests. All genetic analyses were performed in the software ‘QGAStation 1.0’ (Chen & Zhu, 2003).

Table 1. Analyses of variance for effect of vernalization on grain fill duration and grain weight in a one-way diallel cross among five spring wheat cultivars differing in maturity.

Source	Variance components	
	Grain fill duration	**Grain weight**
a. Combined		
Block	0.55 ^{ns}	6.14**
Vernalization (V)^{z}	**	*
Genotype (G)	1.1 ^{ns}	1.81 ^{ns}
Parents (P)	2.89 ^{ns}	2.49 ^{ns}
Crosses (C)	1.33 ^{ns}	1.44 ^{ns}
P vs C^{y}	ns	ns
V × G	3.12**	3.19 ^{ns}
V × P	0.54 ^{ns}	4.14 ^{ns}
V × C	2.7 ^{ns}	4.10 ^{ns}
Residual	9.4	14.24
b. Vernalized treatment		
Block	0^{ns}	12.5**
Genotype	4.89 **	5.4*
Parents	2.89 ^{ns}	6.42 ^{ns}
P vs C^{y}	*	ns
Crosses	4.74*	5.96 ^{ns}
Residual	11.1	14.03
c. Un-vernalized treatment		
Block	1.05 ^{ns}	1.48 ^{ns}
Genotype	3.52 **	4.98*
Parents	4.39 ^{ns}	6.32 ^{ns}
P vs C^{y}	ns	ns
Crosses	3.3*	5.55**
Residual	7.68	12.61

**,* Significant at $p<0.01$, and $p<0.05$, respectively, ns indicates non-significant effect ($p\geq0.05$)

^{z}Fixed effect

^{y}Estimates of parents versus crosses

Results and Discussion

Combined analysis of variance revealed significant ($p<0.05$) variation due to vernalization for both grain fill duration and grain weight (Table 1). The effect of genotype was not significant for any of the traits studied. However, the interaction effect of vernalization and genotype was significant for grain fill duration. None of the three components of genotypic variance (parents (P), hybrids (H) and P vs. H) was significant for the traits studied

Significant ($p<0.05$) genotypic variation existed for both traits when vernalized (Table 1). Among genotypic components, variance due to hybrids was significant ($p<0.05$) for grain fill duration, but not for grain weight. Estimate of parents vs. hybrids was also significant ($p<0.05$) for grain fill duration only. Genotypic effects were also significant for both grain fill duration and grain weight for un-vernalized treatment (Table 1).

Vernalization significantly affected grain fill duration of ‘Taber’ and ‘Barrie’ (Table 2). Grain fill duration of these genotypes increased with vernalization. Grain fill duration also increased for all hybrids involving ‘Taber’, and for ‘Cutler × Foremost’ and ‘Foremost×Barrie’ when vernalized. Grain weight decreased with vernalization, although the decrease was not significant for most of the genotypes. Among parents, grain weight significantly decreased for ‘Foremost’ only. Among the crosses, grain weight significantly decreased for ‘Taber × Foremost’, ‘Taber × Intrepid’ and ‘Cutler × Intrepid’. No correlation between grain fill duration and grain weight was observed for un-vernalized or vernalized treatment.

Significant ($p<0.01$) additive genetic effects were observed for grain fill duration in both un-vernalized and vernalized treatment (Table 3). However, dominance effect was significant for grain fill duration only in vernalized treatment. Variances due to errors were high for both traits under vernalized and un-vernalized treatments. Additive genetic effect was significant for grain weight in un-vernalized treatment only. However, dominance effects were significant for grain weight in both treatments. As a result of high error variances, narrow-sense heritabilities were low for grain fill duration and grain weight in both treatments.

The present study demonstrated that vernalization did alter grain fill duration in some of the genotypes studied, but no clear pattern was observed in terms of the vernalization responsiveness of the genotypes. Our previous studies showed that ‘Taber’ and ‘Foremost’ were vernalization responsive and that ‘Cutler’, ‘Barrie’, and ‘Intrepid’ were vernalization non-responsive (Iqbal *et al*., 2006). In the present study, vernalization altered grain fill duration of ‘Taber’ and all the hybrids involving ‘Taber’. Similarly, vernalization altered grain fill duration in two of the hybrids involving ‘Foremost’ but not in ‘Foremost’. However, vernalization also altered grain fill duration in one of the three vernalization non-responsive genotypes ‘Barrie’. This indicates that the change in grain fill duration of ‘Taber’ and hybrids involving ‘Taber’ in response to vernalization may or may not be due to its vernalization responsiveness.

Vernalization altered grain weight of ‘Foremost’ but not of ‘Taber’, suggesting that the change may or may not have been due to vernalization responsiveness of these genotypes. No correlation was found between grain fill duration and grain weight in vernalized and non-vernalized treatment, indicating that the increase in grain fill duration of some of the genotypes with vernalization did not have an effect on grain weight. Longer grain fill duration has not been consistently found having close association with a high grain weight (Frederick & Bauer, 1999). This suggests that during vernalization, grain fill duration is increased but due to limited sink during this period, grain weight is not affected despite the fact that source is in excess with increased grain fill duration.

Results of the present study have implications for wheat production in high northern latitudes, where vernalization conditions do not occur consistently (Jedel, 1994). Under such conditions, the non-fulfillment of vernalization requirement would be advantageous as this will result in increased sink (number of spikelets per spike) strength of the vernalization sensitive genotypes, thereby conferring higher grain yield. Vernalizing temperatures, on the other hand, would fulfill the vernalization requirement of sensitive genotypes, resulting in limited sink (fewer spikelets per spike). This re-enforces the idea that vernalization sensitive wheat genotypes may be grown in those ecoregions of high northern latitudes, where growing season is relatively long and where vernalizing temperatures do not occur. This may help in exploiting the full yield potential of such genotypes.

Table 2. Best linear unbiased predictors (BLUPs) of genotypes for grain fill duration and grain weight under vernalized (V) and un-vernalized (UV) treatments in a one-way diallel among five spring wheat cultivars differing in maturity.

Genotype	Grain fill duration (Days)		Grain weight (mg)	
Parents	**UV**	**V**	**UV**	**V**
Taber	44.0	48.1	44.1	41.4
Cutler	45.4	46.2	44.0	41.2
Foremost	46.6	48.7	42.8	37.2
Barrie	42.0	45.9	42.8	40.3
Intrepid	44.1	45.2	39.6	39.9
Crosses				
Taber x Cutler	44.0	50.6	43.7	42.8
Taber x Foremost	43.1	49.3	48.1	40.8
Taber x Barrie	39.9	47.6	42.3	40.8
Taber x Intrepid	43.8	49.2	43.1	38.3
Cutler x Foremost	45.2	51.3	43.5	42.0
Cutler x Barrie	44.7	46.6	41.7	40.5
Cutler x Intrepid	44.7	47.3	42.2	36.1
Foremost x Barrie	43.3	49.1	43.1	41.1
Foremost x Intrepid	44.8	48.0	42.1	41.2
Barrie x Intrepid	43.1	45.4	42.3	41.4
Standard error [y]	**2.48**	**1.46**	**2.00**	**1.83**
Standard error [z]	**1.71**		**1.91**	

[y] Standard error of the difference between BLUPs within columns

[z] Standard error of the difference between un-vernalized and vernalized treatments

Table 3. Proportions (%) of variance components to phenotypic variance for grain fill duration and grain weight in a one-way diallel cross among 5 spring wheats.

Parameter [y]	Grain fill duration		Grain weight	
	Un-vernalized	**Vernalized**	**Un-vernalized**	**Vernalized**
V_A/V_P	25.9**	16.5**	16.8**	0^{ns}
V_D/V_P	3.4^{ns}	19.5**	13.9**	31.8**
V_e/V_P	70.7	64.0	69.3	68.2
h^2_N	25.9**	16.5**	16.8**	0^{ns}
h^2_B	29.3**	36.0**	30.7**	31.8**

** Significantly different from zero at $p<0.01$; ^{ns} Not significant ($p\geq0.05$)

[y] V= Variance, P= Phenotypic, A= Additive, D= Dominance, e= Residual

h^2_N and h^2_B are narrow and broad-sense heritabilities

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