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Genetic effects of *Vrn* genes on heading date and agronomic traits in bread wheat

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Summary

The *Vrn*1, *Vrn*2 and *Vrn*3 genes have different values of effects on heading date and related yield components. The genetic background and environment do not affect the ranking of *Vrn* genotypes according to earliness within near-isogenic line sets; however, they do influence the level of differences between heading dates of particular genotypes and between effect values, respectively. The frequencies of defined *Vrn* genotypes in the global set of spring bread wheat cultivars are associated with grain weight per plant predicted on the basis of *Vrn* gene effects averaged over backgrounds and over environments. Peculiarities of backgrounds and environments alter the grain yield ranges of *Vrn* genotypes. For early photoperiod-insensitive wheats, planted in stress conditions at grain filling, the highest yield was predicted for double dominant *Vrn* genotypes with *Vrn*3. This gene is rarely used by the breeders in middle latitudes and its wider adoption is encouraged.

Introduction

During the last two decades the wheat genetics laboratory of this Institute has been involved in studies of the genetics of wheat growth habit. Starting with the set of near-isogenic lines carrying different alleles of *Vrn* loci in a Triple Dirk background (Pugsley, 1971, 1972), we completed the set by adding double dominant and triple dominant genotypes such as *Vrn*1 *vrn*2 *Vrn*3, *vrn*1 *Vrn*2 *Vrn*3 and *Vrn*1 *Vrn*2 *Vrn*3. Using Pugsley's lines as donors of dominant *Vrn* alleles, similar sets were produced in the backgrounds of other winter wheat cultivars (Stelmakh & Avsenin, 1983) that differed in their level of photoperiod-sensitivity. For example, Triple Dirk appeared to be completely insensitive, Skorospelka 3b was slightly sensitive and Mironovskaya 808 was highly sensitive and late. The presumed *Ppd* genotypes of those wheats were: *Ppd*1 *ppd*2 *ppd*3 – Skorospelka 3b; *ppd*1 *Ppd*2 *Ppd*3 – Triple Dirk and *ppd*1 *ppd*2 *ppd*3 – Mironovskaya 808 (Stelmakh & Kuczerov, 1984).

The genetic analysis of various spring cultivars was carried out using recessive and monogenic dominant genotypes as testers of *Vrn* genes. More than one thousand spring wheat stocks were analyzed and part of the results was included in the catalogue of Stelmakh et al. (1987). Segregating populations were planted in long-day conditions to avoid, to some extent, the effects of differences in photoperiodic sensitivity.

The geographic distribution of *Vrn* genes in landraces and improved wheats was discussed by Stelmakh (1990). Significant differences in *Vrn* genotype frequencies were discovered in the global set of spring cultivars, and there were evident zonal differences in the percentage of particular genotypes and of certain dominant genes. The majority of stocks carried *Vrn*1 and/or *Vrn*2. This fact will be important for the discussion of the results presented here. The observed genotype frequencies differed significantly from the expected ones calculated on the basis of mean *Vrn* allele frequencies. This showed some breeding preferences for certain genotypes.

To understand the nature of their breeding value we have investigated the genetic effects of different *Vrn* genes on heading date, as the main character affected by them, and on different agronomic traits. The value of genetic effects for six different background and for various environments have been widely reported and discussed in the Russian literature (for example, Stelmakh, 1987a, b; Voronin, 1988). The subject of this paper is to discuss in broad terms the influence of *Vrn* alleles on variation of particular characters irrespective of environmental and/or background peculiarities.

Material and methods

Three sets of near-isogenic lines (in the backgrounds of Triple Dirk, Skorospelka 3b and Mironovskaya 808), their F_1 and several F_2 and BC generations were planted in sequential randomized blocks. The genotypes of the parental lines and generations are set out in Table 1. Unvernalized seeds were sown in late spring for two seasons in a natural field environment (near Odessa) and in the controlled environments of a phytotron, differing in day-length (12, 18, 24 hours) and temperature (22/17° C and 26/21° C at day/night, respectively, for two seasons).

Heading dates (DH), calculated as number of days from sowing for asynchronously germinating genotypes and from emergence or any other date for synchronous genotypes, were recorded. After harvesting, several agronomic traits were recorded (30 plants for non-segregating generations and 60–150 plants for segregating ones). The characters included plant height (PH – cm), tiller number (TN), spikelet number (SN), grain number and grain weight per ear and per plant (GN/E, GW/E – g, GN/P, GW/P – g, respectively).

Character means were used for the calculation of *Vrn* gene effects according to the genetic model of Mather & Jinks (1971). In all cases scaling tests showed significant deviations from zero indicating

Table 1. *Vrn*[1] genotypes tested within the sets of near-isogenic lines in the backgrounds of three varieties

Lines, generations	Mironovskaya 808		Triple Dirk, Skorospelka 3b	
	Number	Genotype	Number	Genotype
P	7	except triple dominant	8	all possible
F_1	16	except a – *V*1 *V*1 *V*2 *V*2 *V*3 *v*3 b – *V*1 *V*1 *V*2 *v*2 *V*3 *V*3 c – *V*1 *v*1 *V*2 *V*2 *V*3 *V*3	19	all possible
F_2	4	selfed d – *V*1 *v*1 *V*2 *v*2 *V*3 *v*3 e – *V*1 *V*1 *V*2 *v*2 *V*3 *v*3 f – *V*1 *v*1 *V*2 *V*2 *V*3 *v*3 g – *V*1 *v*1 *V*2 *v*2 *V*3 *V*3	3	selfed a, b, c
crosses	6	(e, f, g) × d e × *v*1 *v*1 *V*2 *V*2 *V*3 *V*3 f × *V*1 *V*1 *v*2 *v*2 *V*3 *V*3 g × *V*1 *V*1 *V*2 *V*2 *v*3 *v*3	3	(a, b, c) × d
Total	33		33	

[1] *Vrn* symbol is abbreviated as *V*.

inadequacy of the additive-dominance model. In the joint scaling tests, using the least square technique (means and expectations were weighted since some segregating generations were used), it was shown that only the model including all possible genetic effects was adequate for describing variation within the sets studied. A total of 27 parameters were computed for three genes with two alleles from the means of 33 generations in each set (23 common and 10 unequal generations, see Table 1). Most parameters were significant for each trait.

In a parallel experiment all genotypes were prevernalized as green seedlings held at 2° C for 50 days and provided with continuous light. This equated both DH and the other trait means for all genotypes and generations within defined sets, that resulted in insignificance of genetic effects on all characters (Voronin, 1988). Thus almost all the variation within the unvernalized sets could be attributed to the differences in *Vrn* genotypes.

An analysis of variance of genetic parameters in different backgrounds and environments was carried out to investigate general trends and limits of the models. Under certain limitations the parameter values and the expected character means were analyzed.

Out of the possible 27 parameters for each trait 8 parameters were chosen to describe the genetic variation within the subsets of homozygous (parental) lines only. These parameters included the effects of d_1, d_2, d_3, i_{12}, i_{13}, i_{23}, i_{123} and m. This simplified the discussion and it seemed to be enough at the present status of wheat breeding when only cultivars of homozygous genotypes have practical use.

Results and discussions

If the magnitudes of genetic parameters depend on background and/or environmental variation, discussion of their means is possible since they do describe the genetic variation of character values (within the sets) averaged over defined factors. The variance analysis of genetic effects on DH is set out in Table 2. Similar to the mean of DH, the parameter m exhibited dependence on background and environmental differences and on background × environment interaction. Interactions were not obtained for the effects of d_1, d_2, i_{12} and i_{123}. The presence of interaction for d_3 might be explained by specific action of the dominant *Vrn*3 allele at high temperature affecting later growth stages prior to heading (Stelmakh, 1987b) while *Vrn*1 and *Vrn*2 mainly influenced the duration of the initial stages of plant development. Background dependence was exposed for all parameters, which showed the interaction of effects with background specificity. The same was typical in different environments for many effects averaged over backgrounds. So we can speculate what are the general trends for *Vrn* effects, by using their average values, only within certain limitation.

Separate analyses of variance of genetic effects for particular backgrounds (variability of environ-

Table 2. Analysis of variance of *Vrn* gene effects on DH

Item	df[1]	MS							
		m	d_1	d_2	d_3	i_{12}	i_{13}	i_{23}	i_{123}
Background	2	1071.6***	47.60***	64.60***	89.01***	111.47***	46.96*	71.43**	57.65***
Environments	7	585.4*	2.87*	16.54***	26.16**	18.80***	10.16	11.99	4.77*
Interactions	14	144.8***	0.27	1.99	4.78**	4.11	7.78**	10.81***	2.59
Residual	$lm(n-1)$	16.6	1.39	1.93	2.17	2.62	2.95	3.18	2.46

[1] $lm(n-1)$ is equal to 768 for m; 512 for d_1, d_2, d_3; 448 for i_{12}, i_{13}, i_{23}; 360 for i_{123}.

* Significant at $P < 0.05$.

** Significant at $P < 0.01$.

*** Significant at $P < 0.001$.

ments) and for the defined environments (variability of backgrounds) showed specific peculiarities (Stelmakh, 1987). The earlier and photoinsensitive background of Triple Dirk resulted in the absence of environmental dependence of all effect values. By comparison, the dependence was distinct in the late, highly photosensitive genotype, Mironovskaya 808 only, resulting in an increase of *d* magnitudes and in decreased *i* magnitudes when tested in later environments (i.e. at lower temperature and/or in shorter day-lengths). That led to a more obvious manifestation of differences between character values for certain genotypes. In other words later backgrounds and/or environments promoting lateness provided larger differences between effect values as well as between means of particular *Vrn* genotypes within a near-isogenic set. By comparison, earlier backgrounds, similar to long day and high temperature environments, led to decreases in such differences. Correlations between differences of effects and of means were high and negative (from − 0.89 to − 0.94) and regressions were close to linear (Stelmakh, unpublished). Such relationships partly explain the results of variance analysis and at the same time they make possible a discussion of the average values of effects.

Table 3 shows the mean effects (averaged over environments) on DH for particular genetic backgrounds. The additive effects of all three genes were negative resulting in faster heading of carriers of dominant alleles. Their values were different, *Vrn*1 had the greatest effect and *Vrn*2 had the least one. The effects of digenic interactions were positive leading to the inhibition of additive effects. But their magnitudes pointed out the greater earliness of double dominant homozygotes compared to the respective monogenic dominant lines. The negative effects of trigenic interaction contributed to additional earliness of triple dominant homozygotes.

The relationship of signs and magnitudes of genetic parameters illustrated that *Vrn* genes appeared to act as non-complementary (duplicate but with different effects) genes with classical (for *Vrn*1) or incomplete (for *Vrn*3) dominant epistasis. Despite the significant influence of background or environmental factors (Table 2), the model of averaged effects had to be judged adequate for the description of variation of the respective character means (Table 3). That reflected the close interdependence in variation of genetic effects and character values. When the effects were computed from the character values averaged over environments and/or over backgrounds, the differences between

Table 3. Genetic effects of *Vrn* genes on DH (number of days) averaged over environments

Parameters	$LSD_{0.05}$*	Background			
		Triple Dirk	Skorospelka 3b	Mironovskaya 808	Mean
m	1.14	54.5	55.3	66.8	61.1
d_1	1.92	−12.8	−10.4	−11.7	−11.6
d_2	1.87	−10.2	−4.5	−5.3	−6.5
d_3	2.03	−12.2	−5.8	−7.9	−8.7
i_{12}	2.18	+10.2	+12.3	+16.6	+13.1
i_{13}	2.06	+11.5	+14.2	+18.3	+14.6
i_{23}	1.93	+8.5	+12.0	+17.0	+12.5
i_{123}	2.23	−9.1	−5.0	−4.7	−6.3
$LSD_{0.05}$**		1.52	1.70	1.86	1.59
$\chi^2_{(6)}$***		6.39	6.92	8.14	10.03

m = mean DH in the set of all possible lines homozygous for three *Vrn* genes.

d_1, d_2, d_3 = additive effects of each *Vrn* gene, respectively.

i_{12}, i_{13}, i_{23}, i_{123} = effects of digenic and trigenic non-allelic interactions.

* Between backgrounds for defined parameter. ** Between effects for particular background. *** For mean DH in the total set of 33 lines and generations.

them and respective means of genetic effects were negligible. The values of effects computed by both procedures correlated very positively (r = 0.88–0.96).

The magnitudes of effects and their signs resulted in constant ranking of homozygous *Vrn* genotypes for DH within defined backgrounds and environments (Table 4). The ranges of genotypes were similar either when predicted by means of genetic effect or when observed by average values of the character. The triple dominant genotype was the earliest and the fully recessive one (winter type) was the latest. Within these limits the other 6 genotypes were arranged in sequence of *Vrn*1 *vrn*2 *Vrn*3 ... *vrn*1 *Vrn*2 *vrn*3. The features of backgrounds and environments, mentioned above, altered the level of differences between genotypes but the ranking remained the same. A carrier of the single dominant *Vrn*2 illustrates an example of *Vrn* gene × *Ppd* background interaction. In the highly photosensitive background it represents alternative (transitory or intermediate) wheat (Stelmakh, 1986). The same genotype in a photoinsensitive background has a late, but typical spring, phenotype. For that background, which displayed the absence of an environmental dependence of genetic effects, the prediction of DH was possible by previously calculated parameters when the values of *m* (depending on particular environment) could be determined. Such a prediction was valid (Stelmakh, 1987a) and the differences between predicted and observed DH were ± (0.5–0.7) days only.

The effects of *Vrn* genes on agronomic traits are summarized in Table 5. Even their averaged values for different backgrounds, tested in various environments, were not the same for defined parameters. The most evident differences were noticed for GW/P and GN/P. However, for GN/P the model of parameter means had to be judged inadequate for the analysis of variation of character means. Possibly it reflected similar inadequacy on TN. The model was perfectly valid for the other traits except GW/E. Trait values for defined genotypes in the average background and environment were predicted (Table 6) to speculate how *Vrn* genes might affect the final yield through their effects on DH. TN, GW/E and GN/P were included in this prediction despite the inadequacy of the model because the observed rankings of line means for these characters were similar to those predicted. The highest GW/P was characteristic for the carriers of *Vrn*1 and/or *Vrn*2, whereas the triple dominant genotype had the lowest. Such ratios were in close accordance with the frequencies of *Vrn* genotypes in the global set of cultivars (Stelmakh, 1990). They

Table 4. Earliness of *Vrn* genotypes within the background types

Groups	Range of mean DH	*Vrn* genotypes in background	
		Photoinsensitive	Photosensitive
Early	37–39	*Vrn*1 *vrn*2 *Vrn*3	–
		*Vrn*1 *Vrn*2 *vrn*3	–
		*Vrn*1 *vrn*2 *vrn*3	–
Medium early	42–45	–	*Vrn*1 *vrn*2 *Vrn*3
		–	*Vrn*1 *Vrn*2 *vrn*3
		–	*Vrn*1 *vrn*2 *vrn*3
Medium	46–47	*vrn*1 *Vrn*2 *Vrn*3	–
		*vrn*1 *vrn*2 *Vrn*3	–
Late	52–53	–	*vrn*1 *Vrn*2 *Vrn*3
		–	*vrn*1 *vrn*2 *Vrn*3
		*vrn*1 *Vrn*2 *vrn*3	–
Very late*	61–65	–	*vrn*1 *Vrn*2 *vrn*3

DH = number of days to heading calculated by genetic effects.

* Transitory (= alternative or intermediate).

Table 5. The effects of *Vrn* genes on different traits averaged over backgrounds and environments

Parameters	Characters							
	DH	PH	TN	SN	GN/E	GW/E	GN/P	GW/P
m	61.1*	79.7*	2.9*	16.1*	31.6*	1.03*	76.5*	2.14*
d_1	−11.1*	−3.4*	−0.2	−0.9*	+0.1	+0.03	−9.0	−0.05
d_2	−4.9*	−0.0	−0.3*	−0.2	+1.4*	+0.03	−2.6	−0.13*
d_3	−6.9*	−2.0*	−0.3	−0.6*	+0.8*	+0.00	−5.5	−0.22*
i_{12}	+14.5*	−0.9*	−0.2	−0.7*	−3.0*	−0.15*	−13.8*	−0.55*
i_{13}	+16.2*	−1.2*	−0.1	−0.6*	−1.8*	−0.13*	−9.9	−0.44*
i_{23}	+14.5*	−0.6	−0.3*	−0.0	−0.2	−0.03	−10.8*	−0.37*
i^{123}	−4.2*	+0.1	−0.3	−0.1	+0.6*	+0.00	−4.6	−0.24*
$\chi^2_{(6)}$**	10.03	8.17	15.36*	9.42	8.70	12.91*	23.86*	10.73

* Significant at $P < 0.05$.

** For the character means of 23 common and 10 unequal (in each of two types of sets) lines and generations – 43 totally. Means of missing generations were computed from the available data, thus decreasing *df*.

reflected some breeding preferences for certain genotypes owing to the mean advantages or disadvantages in the average potential of GW/P.

The data in Table 6 help also to reveal the general ways of yield formation for certain *Vrn* genotypes with similar background. The triple dominant genotype is usually so early that it decreases all components and final GW/P. The double dominant *Vrn*1 *Vrn*2 *vrn*3 genotype has good tillering and its earliness provides, on average, good potential for grain filling. The *vrn*1 *Vrn*2 *vrn*3 and *vrn*1 *Vrn*2 *Vrn*3 genotypes have high SN and GN/P but their comparative lateness prevents the realization, on average, of this potential because of poor grain filling. Genotype *Vrn*1 *vrn*2 *vrn*3 has close to middle values for all yield components and excellent grain filling because of earliness, so all these result in maximal GW/P. Because carriers of dominant *Vrn*3 do not surpass these lines in the average background and environment, they are not represented so frequently in the global set.

Analyzing the advantages of *Vrn* genotypes on GW/P separately for defined backgrounds or environments some specificity was revealed (Table 7). For the highly photosensitive background of Mironovskaya 808, tested in the favourable environment of a phytotron, the three highest GW/P values came from carriers of *Vrn*1 and/or *Vrn*2. But in field conditions (high temperature and drought during grain filling) the double dominant genotypes had superiority. For the early and photoinsensitive background of Skorospelka 3b, even in

Table 6. Character means for different *Vrn* genotypes computed by the averaged effects (for effect values and χ^2, see Table 5)

Genotypes	Characters							
	DH	PH	TN	SN	GN/E	GW/E	GN/P	GW/P
*Vrn*1 *vrn*2 *vrn*3	43.7	78.5	3.0	16.7	32.3	1.28	77.2	2.93
*vrn*1 *Vrn*2 *vrn*3	57.9	86.2	3.2	17.6	31.0	1.07	98.5	2.63
*vrn*1 *vrn*2 *Vrn*3	50.8	82.5	3.0	17.1	33.5	0.98	84.9	2.24
*Vrn*1 *Vrn*2 *vrn*3	43.2	79.6	3.4	15.0	33.2	1.09	81.8	2.81
*Vrn*1 *vrn*2 *Vrn*3	42.2	75.3	3.3	14.8	29.5	1.10	83.9	2.57
*vrn*1 *Vrn*2 *Vrn*3	48.1	81.8	2.8	17.9	34.5	1.27	95.1	2.58
*Vrn*1 *Vrn*2 *Vrn*3	41.5	70.9	1.3	12.5	31.9	0.79	20.3	0.24
$LSD_{0.05}$	4.3	6.1	0.87	1.43	2.47	0.35	21.9	0.43

Table 7. Best genotype ranges for grain yield per plant (GW/P) expected by *Vrn* genes effects

Background	Environment	Range of *Vrn* genotype		
		1	2	3
Average	Average	*Vrn*1 *vrn*2 *vrn*3	*Vrn*1 *Vrn*2 *vrn*3	*vrn*1 *Vrn*2 *vrn*3
Average	Greenhouse	*Vrn*1 *vrn*2 *vrn*3	*vrn*1 *Vrn*2 *vrn*3	*Vrn*1 *vrn*2 *Vrn*3
	Field	*vrn*1 *Vrn*2 *Vrn*3	*Vrn*1 *vrn*2 *Vrn*3	*Vrn*1 *Vrn*2 *vrn*3
Mironovskaya 808	Greenhouse	*Vrn*1 *vrn*2 *vrn*3	*vrn*1 *Vrn*2 *vrn*3	*Vrn*1 *Vrn*2 *vrn*3
	Field	*Vrn*1 *Vrn*2 *vrn*3	*Vrn*1 *vrn*2 *Vrn*3	*vrn*1 *Vrn*2 *Vrn*3
Skorospelka 3b	Greenhouse	*Vrn*1 *vrn*2 *vrn*3	*vrn*1 *Vrn*2 *vrn*3	*vrn*1 *Vrn*2 *Vrn*3
	Field	*vrn*1 *Vrn*2 *Vrn*3	*Vrn*1 *vrn*2 *Vrn*3	*vrn*1 *Vrn*2 *vrn*3

favourable conditions, *vrn*1 *Vrn*2 *Vrn*3 ranked the third for GW/P, and in a natural stress environment, the advantage of dominant *Vrn*3 (combined with *Vrn*2 or with *Vrn*1) was obvious.

Thus there are compelling reasons to recommend breeders for the wider involvement of *Vrn*3 donors in their programmes. These were seldomly used in the states of the former USSR, but N. Borlaug unconsciously promoted the spreading of *Vrn*3 from the early 1950's. It has been reported already that within this century the dominant *Vrn*3 was introgressed into many modern cultivars of countries close to equator (Stelmakh, 1987b). The main direction of introgression was from the Japanese landrace, Akakomugi, to Italian wheats. Later it moved from Italy through Mentana to Mexican semidwarf wheats, and then via cultivars such as Sonora 64 and Lerma Rojo 64 to a wider range of wheats world-wide.

The results presented here concern only three well known *Vrn* genes with two distinct, extreme alleles. If there is unambiguous evidence for the existance of allelic series, with individual alleles differing in impact on the rate of development, similar studies of genetic effects will need to be carried out for each pair of alleles. However, such studies of presumble alleles must take into account the possible dependence of *Vrn* effects on background peculiarities as mentioned above, in order not to be misled in exposure of new alleles.

Now that variation associated with *Vrn* genes is well understood, studies of variation associated with similar loci derived from related species would seem appropriate. There is a possibility that alien genes will have effects of different magnitude and for some geographic areas they may offer advantages over the genes currently available. The introgression of alien genes has already occurred with the introduction of both alleles of the *Vrn*1, *Vrn*2, *Vrn*3 genes and of non-allelic variation (Stelmakh, 1992).

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