Influence of genetic systems of *VRN*- and *PPD* genes on the ecological adaptation of wheat and *Triticale*

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The productivity of wheat and *Triticale* plants and their adaptation to climatic conditions are associated with their growth habits and heading rate, which are controlled to a great extent by the systems of *Vrn* (requirements in vernalization) and *Ppd* (sensitivity to photoperiod) genes. There is evidence for the influence of these genes on frost resistance. In this connection, a comparative study on the influence of *Vrn* and *Ppd* genes on the heading rate and frost resistance of wheat and *Triticale* plants under Belarussian conditions is important. Sets of common wheat lines (*T. aestivum* L.), nearly isogenic in the *Vrn* system, differing in also their sensitivity to the photoperiod, as well as hexaploid *Triticale* lines (*X Triticosecale* Wittmack) carrying the same genes were used in this study. The number of days from emergence to heading (NDH) at spring sowing and the overwintering level at autumn sowing were determined under field conditions over the period 1995–2000. The genetic effects of *Vrn* genes responsible for heading rate are modified to a great extent for the system of *Ppd* genes depending on the genetic background. Frost resistance in the wheat and *Triticale* lines studied depends on the interaction between *Vrn* and *Ppd* genes, availability and specificity of rye chromosomes and environmental conditions.

Key words: isogenic lines of common wheat, *Vrn* and *Ppd* genes, hexaploid *Triticale*, gene expression

INTRODUCTION

The productivity of wheat and *Triticale* plants and their adaptability to climatic conditions are associated with their growth habits and heading rate, which are controlled to a great extent by the systems of *Vrn* genes (requirements to vernalization) and *Ppd* genes (sensitivity to photoperiod). Adaptation of the new grain crop, *Triticale,* to climatic conditions remains to be one of the most important problems of plant genetics and breeding. Late ripeness typical of most of the spring forms of *Triticale* is one of the weak points limiting their large-scale production under Belarussian conditions. One may try to overcome this drawback by both developing *Triticale* forms with early heading and ripening dates and by growing late ripe forms at underwinter sowings in regions with relatively mild overwintering conditions. Some authors note a close relation between frost resistance and the systems of *Vrn* and *Ppd* genes [1–5].

In this connection it is important to study the influence of *Vrn* and *Ppd* genes on the heading rate and winter resistance of *Triticale* plants in comparison with wheat under Belarussian conditions.

MATERIALS AND METHODS

Sets of common wheat lines (*T. aestivum* L.), nearly isogenic in the *Vrn* system, differing also in the sensitivity to the photoperiod, as well as hexaploid *Triticale* lines (X *Triticosecale* Wittmack) carrying the same genes were used in the study. The wheat lines under investigation were developed based on the genetic backgrounds of two cultivars and differed in the sensitivity to photoperiod: cv. 'Triple Dirk' (TD) is neutral to the photoperiod, its genotype has the formula *ppd1 Ppd2 Ppd3* in the given gene system; cv. 'Mironovskaya 808' (M808) is sensitive to the photoperiod, its genotype is recessive for *ppd* genes. The *Triticale* lines were selected from the advanced F4–F5 generations of wheat-rye amphiploids synthesized by us on the basis of the above-mentioned wheat lines and forms of winter (cv. 'Voskhod') and spring alloplasmic rye (AR). The samples were studied under field conditions over 1995–2000 at spring and underwinter sowings. Comparable lines were planted on experimental plots 1 m^2 in size (5 rows 1 m long, each containing 20 plants, supply area 20×5 cm per plant). As a criterion for determining the phenotypic expression of *Vrn* genes at spring sowing, the number of days from emergence to heading (NDH) was used. The NDH was controlled mainly by the *Vrn* genes, because we tried to exclude the direct effect of the *Ppd* system on the heading date by conducting the experiment under a long light day (14–16 h) in May–June. At autumn sowing, not only the *Vrn* genes but also the gene system of photoperiodic reaction had an effect on plant development, since the light day lasts 11–9 h in October–November. Seeds obtained from isolated spikes were used for sowing. The degree of overwintering was determined by the ratio of the number of plants that remained after winter to the number of plants that germinated in autumn.

RESULTS AND DISCUSSION

Considerable differences (Table 1) in NDH were observed among both wheat and *Triticale* lines ($P < 0.01$). The system of the *Vrn* genes had a major effect on NDH in wheat and *Triticale* at spring sowing. However, the effect of dominant *Vrn* genes in the genetic background of various cultivars was somewhat modified: the wheat lines of cv. TD headed earlier in all experimental years than spring analogs of cv. M 808. Here, most likely the effect of interaction between two genetic systems (*Vrn* and *Ppd* genes) manifested itself. Genotype ranking for NDH remained in both sets of wheat lines during all experimental years depending on the availability of certain *Vrn* genes.

When analyzing NDH in *Triticale* lines, variability in the expression of dominant *Vrn* genes was revealed. It depended on the specificity of involved genes, rye genome, as well as on the genetic background of the initial wheat lines according to the *Ppd* system. The expression of the *Vrn* genes was noted to be inhibited by the genetic background of *Triticale* (Table 1). All *Triticale* lines headed later than the initial wheat lines. The lines where winter rye was used as a parental component of crossing headed much later.

The *Triticale* lines developed on the basis of TD wheat lines were shown to head earlier than *Tritica-*

Table 1. **Number of days before heading under spring growing of common wheat lines (nearly isogenic in the *Vrn* gene system) of cvs. 'Triple Dirk', 'Mironovskaya 808' and *Triticale* developed on their basis**

Wheat and *Triticale* lines	Mean over 6 years	1995	1996	1997	1998	1999	2000
Wheat lines				**Number of days before heading**			
TD D (*Vrn 1*)	**49.0**	47	51	53	45	45	53
TD B (*Vrn 2*)	**55.7**	55	60	58	53	52	56
TD F (*Vrn 1 Vrn 2*)	**47.8**	44	50	52	44	45	52
TD E (*Vrn 3*)	**50.5**	47	55	54	48	46	53
Mean of line set of wheat TD	**50.8**	**48.3**	**54.0**	**54.3**	**47.5**	**47.0**	**53.5**
M 808-1 (*Vrn 1*)	**51.3**	50	56	54	47	45	56
M 808-2 (*Vrn 2*)	**64.2**	63	68	64	65	59	66
M 808-3 (*Vrn 3*)	**52.7**	51	58	56	53	45	53
M 808-12 (*Vrn 1 Vrn 2*)	**49.2**	49	52	52	44	45	53
M 808-13 (*Vrn 1 Vrn 3*)	**49.3**	49	52	53	44	45	53
M 808-23 (*Vrn 2 Vrn 3*)	**52.5**	53	56	55	50	46	55
Mean of line set of wheat M 808	**53.2**	**52.5**	**57.0**	**55.7**	**50.5**	**47.5**	**56.0**
***Triticale* lines**							
TD D × AR (*Vrn 1*)	**54.2**	54	55	54	51	52	59
TD B × Voskhod (*Vrn 2*)	**62.2**	63	73	58	58	58	63
Mean of *Triticale* lines developed on the basis of TD	**58.2**	**58.5**	**64.0**	**56.0**	**54.5**	**55.0**	**61.0**
M 808-1x AR (*Vrn 1*)	**67.5**	64	67	65	65	66	78
M 808-3 × Voskhod (*Vrn 3*)	**59.3**	56	69	61	57	56	57
M 808-3 × AR (*Vrn 3*)	**61.5**	56	73	62	60	55	63
M 808-12 × Voskhod (*Vrn 1Vrn 2*)	**63.3**	57	68	63	64	59	69
M 808-13 × Voskhod (*Vrn 1Vrn 3*)	**65.3**	63	74	66	64	62	63
M 808-13 × Voskhod (*Vrn 1Vrn 3*)	**59.0**	55	61	59	59	59	61
Mean of *Triticale* lines developed on the basis of M 808	**62.7**	**58.5**	**68.7**	**62.7**	**61.5**	**59.5**	**65.2**

le developed on the basis of spring analogs of cv. M808. Molecular-genetic investigations showed that this phenomenon was not associated with translocations or mutations in the location region of vernalization genes of wheat and resulted from the influence of genetic materials of rye on the expression of the *Vrn* genes [6].

The analysis of the overwintering level of the wheat lines of cvs. TD and M808, differing in reaction to photoperiod has shown that both gene systems play an important role in their adaptation to conditions of winter growing (Table 2). Wheat lines of cv. TD with the genes *Vrn 1* or *Vrn 1 Vrn 2* (the ripest) practically did not overwinter (0–5%) over the experimental years, while in later lines of the same cultivars with *Vrn 2* or *Vrn 3* survived 20–25% of plants. At the same time plants of spring analogs of M 808 survived up to 100% in some years. It should be noted that winter lines of TD C and M808 have overwintered 80–90% and 95–100%, respectively. The difference in their overwintering level is accounted for by the influence of the *Ppd* gene system. Recessive *ppd* genes of cv. M 808 determine a rather high winter resistance of its spring analogs with dominant *Vrn* genes. At the same time the presence of dominant *Ppd* genes in the genotype of TD lines decreases winter hardiness. Dominant alleles of the *Vrn* and *Ppd* genes exert an effect on the winter hardiness level of wheat plants by suppressing their requirements to vernalization and photoperiodic sensitivity.

The overwintering degree of the developed *Triticale* lines proved significantly higher than that of parental wheat lines, which is accounted for by the influence of rye chromosomes (Table 2). *Triticale* differed in the overwintering degree depending on both the systems of *Ppd* and *Vrn* genes of wheat and rye genomes. *Triticale* developed on the basis of spring analogs of cv. M808 overwintered better than the forms produced on the basis of TD lines (on the average over the past 5 years of testing: 74.6; 49.5% respectively). The *Triticale* lines where winter rye was used as a paternal component of crossing overwintering better (up to 100%). The phenotypic correlations between the NDH of wheat and *Triticale* plants under spring growing and the percentage of their

Table 2. **Overwintering of common wheat lines (nearly isogenic in the *Vrn* gene system) of cvc. 'Triple Dirk', 'Mironovskaya 808' and *Triticale* lines synthesized on their basis**

Wheat and *Triticale* lines	Mean over 5 years	1996	1997	1998	1999	2000
Wheat lines	% of plants that remained after overwintering					
TD D (*Vrn 1*)	**1.8**	5	0	–	0	2
TD B (*Vrn 2*)	**11.3**	20	0	–	0	25
TD F (*Vrn 1 Vrn 2*)	**1.7**	0	0	–	–	5
TD E (*Vrn 3*)	**8.3**	0	0	–	–	25
Mean of line set of wheat TD	**7.6**	**6,3**	**0**	**–**	**0**	**24.3**
TD C (*vrn1 vrn2 vrn3*)	**87.0**	**80**	**90**	**90**	**85**	**90**
M 808-1 (*Vrn 1*)	**86.0**	85	70	90	85	100
M 808-2 (*Vrn 2*)	**94.0**	90	85	100	95	100
M 808-3 (*Vrn 3*)	**85.0**	90	80	80	85	90
M 808-12 (*Vrn 1 Vrn 2*)	**61.0**	60	20	70	75	80
M 808-13 (*Vrn 1 Vrn 3*)	**57.0**	60	20	60	65	80
M 808-23 (*Vrn 2 Vrn 3*)	**60.0**	85	55	30	40	90
Mean of line set of wheat M 808	**73.8**	**78.3**	**55.0**	**71.7**	**74.2**	**90.0**
M 808 (*vrn1 vrn2 vrn3*)	**97.0**	**100**	**95**	**95**	**100**	**95**
***Triticale* lines**						
TD D × AR (*Vrn 1*)	**28.0**	0	15	20	25	80
TD B × Voskhod (*Vrn 2*)	**71.0**	75	41	58	95	86
Mean of *Triticale* lines developed on the basis of TD	**49.5**	**37.5**	**28.0**	**39.0**	**60.0**	**83.0**
M 808-1 × AR (*Vrn 1*)	**58.6**	55	18	39	97	84
M 808-3 × Voskhod (*Vrn 3*)	**90.8**	100	79	89	91	95
M 808-3 × AR (*Vrn 3*)	**71.8**	100	32	59	89	79
M 808-12 × Voskhod (*Vrn 1 Vrn 2*)	**71.2**	83	26	69	92	86
M 808-13 × Voskhod (*Vrn 1 Vrn 3*)	**85.6**	99	52	89	96	92
M 808-13 × Voskhod (*Vrn 1 Vrn 3*)	**70.0**	88	23	59	89	91
Mean of *Triticale* lines developed on the basis of M 808	**74.6**	**87.5**	**38.3**	**67.3**	**92.3**	**87.8**

overwintering were strongly positive. Thus, late forms and lines of *Triticale* may be grown quite successfully under Belarussian conditions at underwinter sowings, with an essential gain in the productivity of plants being achieved and ripening being promoted [7].

Thus, a comparative study on the phenotypic expression of dominant *Vrn* genes in common wheat and *Triticale* on two genetic backgrounds with *Ppd* genes ('Triple Dirk' and 'Mironovskaya 808') showed their role in the manifestation and variability of the heading rate (NDH) and revealed the influence of the *Vrn* and *Ppd* genes on winter hardiness in the plant samples studied.

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