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Allelic diversity of the *Vrn* genes and the control of growth habit and earliness in wheat

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Abstract. Wheat is one of three main food crops around the world, which has the largest distribution area due to its adaptation to the different environments. This review considers polymorphisms and allelic variation of the vernalization response genes *Vrn* controlling the major adaptation traits in wheats (the genus *Triticum* L.): growth habit (spring *vs.* winter) and length of vegetative period (earliness). The review summarizes available information on the allelic diversity of the *Vrn* genes and discusses molecular-level relationships between *Vrn* polymorphisms and their effect on growth habit (spring *vs.* winter) and earliness (length vegetative period in spring plants) in di-, tetra- and hexaploid wheat species. A unique attempt has been made to relate information on mutations (polymorphisms) in dominant *Vrn* alleles to the values of the commercially most important trait "length of plant vegetative period (earliness)". The effects of mutations (polymorphisms) in the recessive *vrn* genes on vernalization requirement in winter wheats are considered, and this trait was formalized. The evolution of the winter/spring growth habit in the genus *Triticum* species is discussed. A scheme of phylogenetic interactions between *Vrn* alleles was constructed on the basis of these polymorphisms; the paper considers the possibilities to enhance the diversity of polymorphisms for the dominant *Vrn* genes and their alleles using wheat related species and rarely used alleles and discusses the prospects of breeding for improved earliness for concrete agroecological zones.

Key words: wheat; *Vrn* genes; winter/spring growth habit; length of plant vegetative period; earliness.

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Аллельное разнообразие генов *Vrn* и контроль типа и скорости развития у пшениц

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Аннотация. Пшеница, являясь одной из трех основных продовольственных культур мира, занимает самый широкий ареал за счет адаптивности к разнообразным условиям возделывания. В обзоре рассматриваются полиморфизм и аллельная изменчивость генов *Vrn* (от англ. *response to vernalization*), контролирующих важнейшие адаптационные признаки пшениц – тип (яровость *vs.* озимость) и скорость развития у диких и возделываемых видов пшениц (род *Triticum* L.). Суммируется информация об аллельном разнообразии генов *Vrn* и обсуждается связь полиморфизмов этих генов на молекулярном уровне с их влиянием не только на признак «тип развития (яровость *vs.* озимость)», но и на признак «скороспелость (длина вегетационного периода яровых растений, ДВП)» у ди-, тетра- и гексаплоидных видов. Предпринята попытка связать полученную информацию о мутациях (полиморфизмах) доминантных аллелей генов *Vrn* с выраженностью наиболее важного с хозяйственной точки зрения признака «продолжительность ДВП (скороспелость)», которая ранее в обзорах не предпринималась. Рассматривается влияние мутаций (полиморфизмов) в последовательностях рецессивных генов *vrn* на признак «потребность в яровизации» у озимых форм растений пшениц и выполнена его формализация. Обсуждается эволюция озимости/яровости в роде *Triticum*. На основе выявленных полиморфизмов построена схема филогенетических взаимодействий аллелей генов *Vrn* и рассматриваются возможности расширения полиморфизма по доминантным генам *Vrn* и их аллелям за счет видов-сородичей и редко используемых алелей и перспективы селекции на изменение ДВП (скороспелости) для конкретных зон возделывания.

Ключевые слова: пшеница; гены *Vrn*; яровость; озимость; длина вегетационного периода; скороспелость.

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Introduction

Many of the cultivated and wild herbaceous plant species growing in temperate climates have developed the spring growth habit (cryophobic plants) or the winter growth habit (cryophilic plants) as adaptations to natural environments (Gupalo, Skripchinsky, 1971). The spring plants complete their entire development cycle during a single vegetation season, while the winter ones do not proceed to reproduction unless they have been exposed to low temperatures.

In wild and cultivated wheat species, delays in transition from vegetative to reproductive development are controlled by the vernalization response genes *Vrn* regulating growth habit (spring *vs*. winter) and earliness, the vernalization requirement duration genes *Vrd* controlling duration of vernalization treatment in winter wheats, and the photoperiod sensitivity/insensitivity gene *Ppd* for response to photoperiod. Any of the dominant genes *Vrn*: *Vrn-1* (Yan et al., 2003), *Vrn-3* (Yan et al., 2006) and *Vrn-D4* (Kippes et al., 2016), controls spring growth habit and is epistatic over the recessive alleles of these genes. An exception is the dominant gene *Vrn2* described in *Triticum monococcum* L. (Yan et al., 2004a) and controlling winter growth habit: this gene expression are destroyed in polyploid wheat species.

An any dominant allele of the gene *Vrn*, except *Vrn2*, is enough for a plant to become a spring (Pugsley, 1971; Yan et al., 2004b; Fu et al., 2005; Knippes et al., 2018). Winter hexaploid wheat varieties are homozygous for the recessive alleles of all the three *Vrn-1* genes at once (Stelmakh, 1987); while winter tetraploids, for two genes, *Vrn-A1* and *Vrn-B1*, because the dominant genes *Vrn-3* and *Vrn-D4* have no recessive alleles, and so all winter varieties carry their null-alleles. No interaction between *Vrd* and *Vrn* has been described. A number of investigations have proposed schemes for the interaction between the *Vrn* with *Ppd* (Chen A. et al., 2014). However, the mechanisms underlying the interactions between these genes are not yet fully understood (Goncharov, 2012; Kiseleva, Salina, 2018). The *Vrn* genes are estimated to account for about 75 % of the control of variability of the trait duration of the vegetative period (DVP), and the *Ppd* genes, for about 20 % (Stelmakh, 1981). The third group of loci, EPS (earliness *per se*), controlling earliness *per se*, is under polygenic control (van Beem et al., 2005; Royo et al., 2020) and explains only about 5 % of DVP variation (Stelmakh, 1981).

The *Vrn-1* controlling the adaptability of wheat to environments (the traits spring/winter growth habit and earliness) are transcription factor genes (Trevaskis et al., 2003; Yan et al., 2003) that determine the expression of many genes involved in response to environmental stresses. Mutations in such genes not only disrupt their function, but also cause remarkable phenotypic changes. In wheat, DVP (earliness) is one of the important traits allowing the wild and cultivated species to take full advantage of the spring-summer season. At the same time, the *Vrn* genes have direct effects on plant productivity, yield and resistance to stresses, such as drought, low temperatures, pests and diseases, to mention a few (Zotova et al., 2019).

This paper considers the results of the modern molecular and genetic studies concerning spring/winter growth habit control and the effect of the allelic diversity of the *Vrn* genes on DVP in spring plants.

How many VRN loci does wheat have?

To date, six dominant *Vrn* genes (three *Vrn-1*: *Vrn-A1*, *Vrn-B1*, and *Vrn-D1*) (Yan et al., 2003), two *Vrn-3* (*Vrn-A3*, and *Vrn-B3*) (Nishimura et al., 2018), one *Vrn-D4* (Kippes et al., 2016)) and one recessive gene, *vrn-2* (Yan et al., 2004a) have been described as the ones controlling spring growth habit. Let us consider their main features.

VRN-1 locus. In di-, tetra- and hexaploid wheats, the spring growth habit is most commonly controlled by the *Vrn-1* genes (Genotypes…, 1985; Catalogue…, 1987; Goncharov, 1998; Lysenko et al., 2014; among others). These genes are located in distal part of long arms of the homeologous group 5 chromosomes: *Vrn-A1* on 5AL (Law et al., 1976; Galiba et al., 1995; Dubcovsky et al., 1998), *Vrn-B1* on 5BL (Barrett et al., 2002; Iwaki et al., 2002) and *Vrn-D1* on 5DL (Law et al., 1976). It has been shown that the *Vrn-1* genes are orthologous to the *Arabidopsis thaliana* (L.) Heynh. closely related *CAULIFLOWER* (*CAL*), *APETALA1* (*AP1*) and *FURITFULL* (*FUL*) meristem identity genes controlling the reproductive/flowering meristem transition (Ferrándiz et al., 2000; Yan et al., 2003; Preston, Kellogg, 2006; Dhillon et al., 2010). As was found, in *Arabidopsis*, *FUL* controls not only the development of carpels and fruits, but also flowering time (Ferrándiz et al., 2000). Later, another gene, *WAP1* (*Wheat APETALA1*) were characterized as AP1-like MADS-box gene in common wheat), was found and characterized as an activator of the transition from vegetative to reproductive development (Yan et al., 2003). It was shown that *WAP1* in wheat corresponds to *Vrn-1* (Trevaskis et al., 2003). *WAP1* expression begins before the transition to reproductive phases and continues until maturity (Murai et al., 2003).

The dominant *Vrn-A1* alleles have insertions and/or deletions in the promoter regions as well insertions and/or deletions and single nucleotide polymorphisms (SNPs) in the first intron, which the native recessive gene *vrn-A1* does not (Supplementary Material)[1]. Deletions in the first intron is what differentiates most of the dominant *Vrn-B1* alleles differ from the recessive *vrn-B1* allele. Additionally, deletions or insertions within the first intron are features of the dominant *Vrn-D1* alleles.

Although molecular biological methods allowed a large number of alleles of the dominant *Vrn* genes to be described (Yan et al., 2004a, b; Fu et al., 2005; Liu et al., 2012; Milec et al., 2023), the effects of these alleles on the duration of

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[1] Supplementary Material is available
https://vavilov.elpub.ru/jour/manager/files/Suppl_Smolen_Engl_27_8.pdf

vernalization treatment and flowering time were not always identified (see Supplementary Material).

VRN-2 locus. The *Vrn2* gene (*Vrn-A^{m}2*) has been revealed only in the diploidic wheat *T. monococcum* (Dubcovsky et al., 1998). This gene was mapped to the distal part of the long arm of chromosome 5A^m within the segment translocated from 4A^{m}S (Dubcovsky et al., 2006). The VRN-2 locus includes two completely linked zinc finger-CCT domain genes *ZCCT1* and *ZCCT2* that act as flowering repressors down-regulated by vernalization (Yan et al., 2004a). However, it was established that the main determinant for *Vrn-2* expression in diploid wheat *T. monococcum* and *T. boeoticum* Boiss. and barley *Hordeum vulgare* L is day length (Dubcovsky et al., 2006; Trevaskis et al., 2006).

The sequence of the *Vrn-2* genes was revealed in the winter common wheat Jagger and 2174. No allelic variants of *Vrn-A2* in the A genome or *Vrn-D2* in the D genome were found (Chen Y. et al., 2009). Two duplicated copies of *Vrn-B2* were found in 2174. The *Vrn-B2* allele was not found in Jagger, suggesting this variety carries a null allele of this gene. The null-allele had no effect on flowering time in a segregated population. Mapping of *Vrn-B2* showed that both of its copies in 2174 were closely associated with a SNP on chromosome 4BL, suggesting that the *Vrn-B2* duplicates were located in a tandem-like manner at the same locus. Identical *Vrn-B2* sequences have been found in contig sequences of chromosomes 4BS, 2BS and 5DL in Chinese Spring (CS) (International Wheat Genome Sequencing Consortium..., 2018). In *Aegilops squarrosa* L. (=syn. *Ae. tauschii* Coss.), the sequence of the gene *Vrn-D2* was not found (Chepurnov et al., 2023). Thus, the gene *Vrn-2* in tetra- and hexaploid wheats is inactivated (Tan, Yan, 2016).

VRN-3 locus. The dominant gene *Vrn-B3* (formerly *Vrn 5* or *Vrn-B4*) was mapped to the short arm of chromosome 7B using 82 recombinants obtained from crosses between CS and the substitution line CS/Hope 7B (Yan et al., 2006). The gene is activated by vernalization and long day; it has been identified as an orthologue of the gene *FLOWERING LOCUS T* (*FT*) in *Arabidopsis* (Yan et al., 2006; Cockram et al., 2007). It is not easy to understand the role of *TaFT* in flowering regulation, because both common wheat and barley each possesses a 78 % identical paralogous copy of *FT2* (*TaFT2* and *HvFT2*, respectively) (Yan et al., 2006; Faure et al., 2007). As the *TaFT*/*TaFT2* duplication event took place after these cereals and *Arabidopsis* split off, this event is unrelated to the duplication of *FT*/*TSF*, the twin sister of *FT* found in *Arabidopsis* (Li, Dubcovsky, 2008).

The dominant gene *Vrn-A3* (homologous to *Vrn-B3*) has only been revealed in tetraploid wheats and mapped on the short arm of chromosome 7A (Nishimura et al., 2018). It is unlikely that it has homologs in common wheat, and it must be inactive as is *vrn-2* in *T. monococcum*.

VRN-4 locus. The dominant gene *Vrn-D4* was discovered in the line Gabo-2 (Knott, 1959; Pugsley, 1972; Goncharov, 2003) selected from the Australian commercial common wheat cv. Gabo. This gene was localized on chromosome 5D (Kato, 1993) and mapped to the centromeric region of the same chromosome (Kippes et al., 2015). The most current hypothesis is that the dominant gene *Vrn-D4* can have emerged in polyploid wheats due to a translocation of a ~290 kb-fragment of the long arm of chromosomes 5A to the proximal part of the short arm of chromosome 5D (Kippes et al., 2015). The translocated segment includes a *Vrn-A1* copy that carries mutations in the coding and regulatory regions (Kippes et al., 2015).

The gene is expressed at earlier stages of spring plants[2], and its sequence does not contain any of mutations that were previously described for the dominant gene *Vrn-A1* and that endow common wheat with spring growth habit (Yan et al., 2003, 2004b). The dominant gene *Vrn-D4* has instead three SNPs in the first intron, where the binding site for the TaGRP2 protein described as a negative regulator for *Vrn-A1* is located (Fu et al., 2005).

At present, no B-genome genes homologous to *Vrn-4* are known. As the dominant gene *Vrn-D4* has not been found in *Ae. tauschii*, the D-genome donor to hexaploid wheat (Chepurnov et al., 2023), it can be concluded that this mutation occurred in polyploids.

Thus, spring wheat carry mutations in the promoter or the first intron of the *Vrn* genes (Yan et al., 2004b; Fu et al., 2005). At the same time, most of the dominant alleles of the *Vrn-1* genes described to date (*Vrn-A1a*, *Vrn-A^{m}1a*, *Vrn-A1b*, *Vrn-A1d*, *Vrn-A1e*, *Vrn-A^{m}1g*, *Vrn-A1h* and *Vrn-A1i*) carry mutations in the promoter regions, within the VRN box, including SNPs, indels or its full elimination (Shcherban, Salina, 2017). The mutations found in the *Vrn* genes are presented in Supplementary Material. Chromosomal locations of the *Vrn* genes are detailed in Table 1. They were confirmed by molecular biological studies (Kiseleva, Salina, 2018).

The fact that the dominant alleles of the *Vrn-1* genes carry insertions and deletions that the recessive (intact) alleles do not may be an indication that they are evolutionarily younger (Milec et al., 2023). This allows their phylogenetic relationships to be inferred (see the Figure).

Vernalization of winter and spring wheats and its molecular and genetic network

Vernalization is the need of winter plants adapted to temperate climates for exposure to low temperatures, ensuring the transition of them from vegetative to reproductive development. A requirement for vernalization is an adaptive trait that helps prevent flowering before winter and permits flowering in the favorable conditions of spring. Winter plants are assumed to carry recessive (native) alleles of the

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[2] See scales for growth and development in cereals (Efremova, Chumanova, 2023).

Table 1. Designation and localization in chromosomes of genes for growth habit in spring and winter wheat (after Goncharov (2012) with addition)

Phenotype	Haploid genotype	Allelism and chromosomal localization	Reference
Tetra- and hexaploid wheats according to hypothesis and data of K. Tsunewaki, B.S. Jenkins (1961) and K. Tsunewaki (1962)			
Spring	*Sg1Sg2Sg3** *sg1sg2sg3* *Sg1sg2Sg3**	*Sg1*–$Sg1^{c}$–*sg1* (5D)	Tsunewaki, Jenkins, 1961; Tsunewaki, 1962
	$Sg1^{c}Sg2^{c}Sg3$*	*Sg2*–$Sg2^{c}$–*sg2* (5A)	
	$Sg1^{c}Sg2Sg3$* $Sg1^{c}Sg2Sg3$*	*Sg3*–*sg3* (2B)	
	*sg1sg2sg3Sg5**	*Sg5*–*sg5* (5B)	Singh, 1967
Winter	*sg1sg2Sg3*		Tsunewaki, 1962
According to A.T. Pugsley (1972) hypothesis and to a number of author data			
Spring	*Vrn-A1vrn-B12vrn-D1*	*Vrn-A1*–*vrn-A1* (5AL)	Law et al., 1976
	vrn-A1Vrn-B12vrn-D1	*Vrn-B1*–*vrn-B1* (5BL)	Barrett et al., 2002
	vrn-A1vrn-B12Vrn-D1	*Vrn-D1*–*vrn-D1* (5DL)	Law et al., 1976
	vrn-A1vrn-B12vrn-D1Vrn-B3	*Vrn-B3* (7BS)**	Yan et al., 2006
	vrn-A1vrn-B12vrn-D1Vrn-A3	*Vrn-A3* (7AS)**	Nishimura et al., 2018
	vrn-A1vrn-B12vrn-D1Vrn-D4	*Vrn-D4* (5DS)**	Kippes et al., 2014
	and an any combination of dominant genes		
Winter	*vrn-A1vrn-B1vrn-D1*		Pugsley, 1972
Diploid *T. boeoticum* and *T. monococcum* according to J. Dubcovsky et al. (1998) hypothesis and to a number of author data			
Spring	*Vrn-A1vrn-A2*	*Vrn-A1-vrn-A1* (5AL)	Dubcovsky et al., 1998
	vrn-A1vrn-A2	*Vrn-A2*–*vrn-A2* (4AL)	Yan et al., 2004b
Winter	*vrn-A1Vrn-A2*		Dubcovsky et al., 1998

* Spring growth habit is observed for any allelic state of the gene *Sg3*.
** The gene does not have recessive alleles.

vrn genes, with mutations in any of them leading to partial or complete inhibition of response to vernalization (Fu et al., 2005; Milec et al., 2023) and to a conversion of winter growth habit to spring ones. Spring plants form ears without vernalization, even though late-ripening spring forms, including the facultative growth ones[3], may respond to vernalization by promoting earliness and a reducing DVP. Vernalization in the late-ripening spring plants is poorly studied. In southern latitudes, vernalization is believed to provide autumn-sown late-ripening spring plants protection against damage from early-autumn light frosts.

A major obstacle to the study of the transition from vegetative to reproductive development is misidentification of the functions performed by the alleles of the *Vrn* genes. The misidentification arose from a terminological confusion started by Australian scientists A.T. Pugsley (1968) and R.A. McIntosh (1973), who were unfortunate to replace "spring growth" (Tsunewaki, 1962) with "response to vernalization" (Pugsley, 1971) (see Table 1). This term replacement were certain reasons (Pugsley, 1968); however, they were rather speculative. Years went by, but even so J. Dubcovsky, a molecular biologist, overlooked the issue and allowed this terminological mess to become part of the subsequent editions of "Catalogue of Gene Symbols for Wheat" (McIntosh et al., 2013). Note that the gene symbol *Sg* (spring growth) has immediate relevance to the

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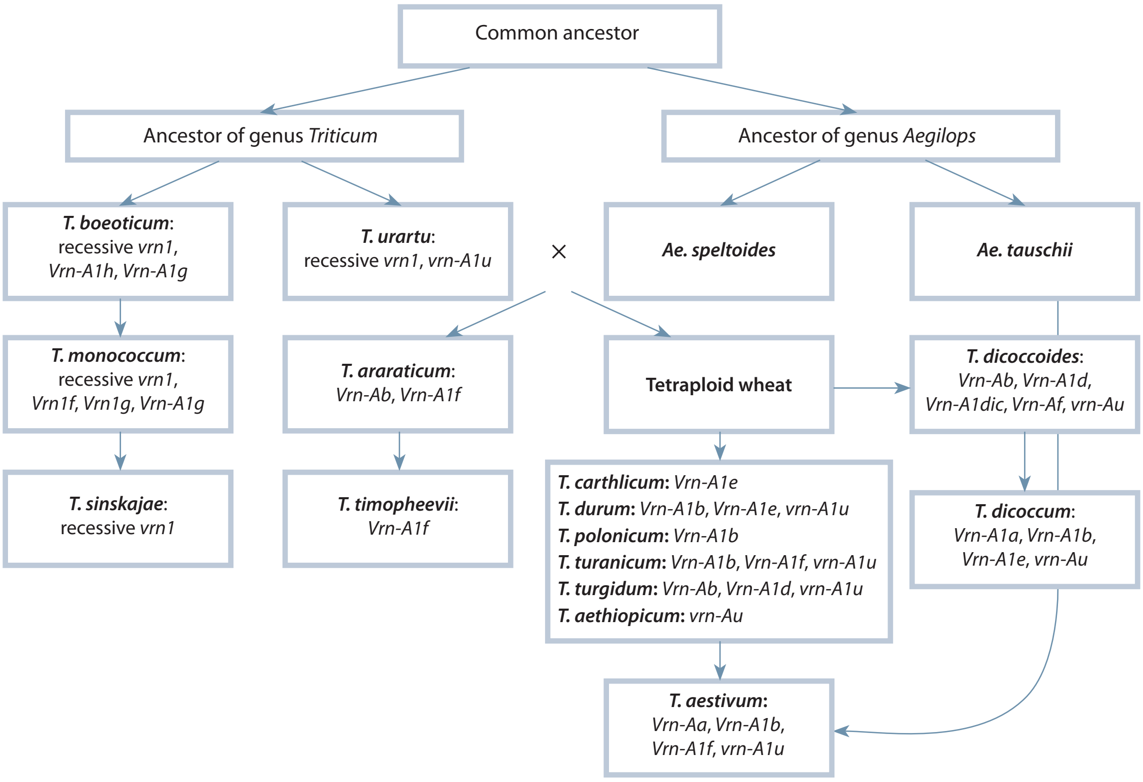
[3] Facultative growth habit is an agrotechnological characteristic. Facultative growth habit plants can be both autumn-sowing and spring-sowing as reserve crops. At present, the State Register of RF includes three facultative growth habit cultivars produced in the Lukyanenko National Grain Center (Krasnodar, Russia) (State Register…, 2023).



Scheme of *Triticum* and *Aegilops* genera evolution (according to Goncharov, 2011, with additions).

Different alleles of *Vrn-A1* gene among wheat species are presented in appropriate boxes next to the species names. Section *Timopheeevii* is presented in grey boxes, while section *Monococcon*, *Dicoccoides* and *Triticum* are in white ones (after Konopatskaia et al., 2016, with additions).

trait spring growth habit *vs.* winter growth habit and allows this trait to be explicitly formalized (Goncharov, 2004). In this case, the classification of the trait is genotype-based, not phenotype-based (Steinfort et al., 2017).

Need to pay attention that genotyping and phenotyping data may be inconsistent (see Table 2 in M. Makhoul (2022)). This relates to autumn-sown spring cultivars in the southern regions of the Eastern Hemisphere (Makhoul et al., 2022). Unfortunately, it is becoming more and more popular to state (postulated) the phenotypes depending on the sowing season (Steinfort et al., 2017). While, the phenotyping has to base solely on growth habit of plant (spring *vs*. winter). A.T. Pugsley (1983) begins his terminology-related considerations with "winter growth habit", that is, the physiological condition of a wheat plant requiring treatment to low temperatures (vernalization) and, consequently, having "response to vernalization" before it can come to reproductive phase.

And only the next step (question) is about phenotyping based on growth habit (spring *vs*. winter). The trait has to phenotyped as a qualitative morphological one (Goncharov, 2004). Plant phenotypes differ in that some plants switch to reproductive growth within a single spring-summer season and some do not. Wheat varieties are phenotyped with respect to this trait in the summer, at high positive temperatures, during ontogenesis after planting in the field or a greenhouse.

Response to vernalization is a quantitative trait, and so the accessions should be phenotyped using low temperatures (vernalization). In this case, the ultimate question is one about the duration of vernalization treatment (Dolgushin, 1935). Spring plants, even late-ripening ones, do not require vernalization to proceed to reproductive growth. Producing a unified approach for phenotyping spring/winter will make it possible to correctly compare all available research results.

In the database Wheat Trait Ontology, the traits plant growth habit (vernalization) and earliness are in the same subclass Development of class Trai and are associated with plant phenotype (Nédellec et al., 2020). The trait response to vernalization is not there, it is in the subclass Response to environmental conditions, meaning are the response of plants to the influence of the external environment (to a stress factor).

An important part of a unified approach to defining and phenotyping a trait is not only the terminology, but also the symbols of wheat genes. After the power to decide was shifted from one group of researchers (Ausemus et al., 1946) to another (McIntosh et al., 1973), the misleading terms "response to vernalization" became "legalized".

Table 2. Polymorphism of recessive alleles of the *Vrn* genes in winter wheat

Gene/locus	Allele	Mutation	Accession	Reference
Diploid wheat ($2n = 2x = 14$)				
Vrn-A1	*vrn-A1u*	Identical to sequences of polyploid wheats	*T. urartu* Thum. ex Gandil. IG 44829	Golovnina et al., 2010
VRN-2 (*ZCCT1*)	*vrn2*	Point mutation at position 35 in the coding region of the CCT domain	*T. monococcum* DV92	Yan et al., 2004a
	vrn2	Complete deletion of *ZCCT1*	*T. monococcum*	
	vrn2	Data not present	*T. monococcum* TRI 17025	Shcherban et al., 2015b
Tetraploid wheat ($2n = 4x = 28$)				
Vrn-A1	*vrn-A1b.3*	Deletion of the "T" upstream and the 20 bp deletion downstream of the VRN-box	*T. turgidum* PI 223173, *T. durum* PI 655432	Muterko et al., 2016
	vrn-A1b.4	»	*T. dicoccoides* PI 466941	
Hexaploid wheat ($2n = 6x = 42$)				
Vrn-A1	*vrn-1a/vrn-A1b*	SNP in exon 4	Jagger (PI 593688)/2174 (PI 602595)	Chen Y. et al., 2009
	vrn-A1b.3	Deletion of the "T" upstream and the 20 bp deletion downstream of the VRN-box	*T. spelta* L. PI 168680 *T. vavilovii* Jakubz. PI 428342	Muterko et al., 2016
Vrn-B1	*vrn-B1*	5′ UTR 1-bp deletion + 8 bp start of a 2nd deletion	i: Triple Dirk C	Yan et al., 2004b
Vrn-D1	*vrn-D1*	5′ UTR 1-bp deletion + 15 bp start of a 2nd deletion	i: Triple Dirk C	
Vrn-D1	*vrn-D1r*	SNP polymorphism CArG-boxes of the *vrn-A1* promoter		Strejčková et al., 2021; Makhoul et al., 2022
Vrn-B3		Null-allele	cv. Yanzhan 4110	Chen F. et al., 2013

Note. Mutations in the recessive alleles of the gene *vrn-A1* in hexaploid wheat (Chen Y. et al., 2009) and the gene *Vrn-2* in diploidic wheat (Yan et al., 2004b) are in the coding regions.

That is why, although *Vrn* is a legal abbreviation and late-ripening spring and facultative (intermediate) growth habit varieties have response to vernalization, we will be using a more relevant term "growth habit (spring *vs*. winter)" throughout. We suggest the term "vernalization response" be left only for winter wheat (Fayt et al., 2018). Whether or not the recessive genes *vrn* really control vernalization response in winter varieties is still a question. Let us have a closer look at the matter.

Polymorphism of the recessive alleles of *Vrn* genes in winter wheat

All dominant *Vrn* genes known to date that control the qualitative difference between spring and winter wheats have been cloned. Two mutually exclusive hypotheses have been proposed: one stating that the duration of vernalization treatment in winter plants depends on the variability of the recessive alleles *vrn-A1* for winter growth habit (Pugsley, 1971; Chen Y. et al., 2009, 2010) and the other stating that it depends on a system of genes independent of them (Gotoh, 1979; Bulavka, 1984; Fayt, 2003, 2006a, b; Stelmakh et al., 2005) and unrelated to the expression of the recessive *vrn* genes.

This process has been poorly studied genetically and not studied at all at the molecular and biological level. Now it is obvious that the polymorphisms for the recessive genes *vrn* in winter wheat varieties do not explain differences in the duration of vernalization treatment between these varieties (Table 2). Not a single exception invalidating this genetic model has been reported in the studies, in which a large number of cultivars/germplasms from wheat species with different ploidy levels were screened using molecular markers for the recessive alleles of the each of *Vrn-1* genes (Yan et al., 2003, 2004a, b; Fu et al., 2005; Bonnin et al., 2008; Zhang X.K. et al., 2008; Santra et al., 2009; Chen Y. et al., 2010). The polymorphism for the *Vrn-3B* and *Vrn-4D* genes, in which the recessive allele is represented only by only as a null allele, makes an exception.

The alleles that have SNPs in exon 4 of the recessive gene *vrn-A1* are associated with the regulation of the development of winter plants and are designated *vrn-A1a* in Jagger (PI 593688) and *vrn-A1b* in 2174 (PI 602595). In a field assessment of a population of 96 recombinant inbred lines from crosses between Jagger and 2174, Y. Chen et al. (2009) showed that the *vrn-A1a* plants had an earlier onset of shooting. At the same time, the effects of the alleles on the duration of vernalization treatment have not been checked experimentally.

Plants with the 3_SNPs haplotype showed higher transcription levels of the gene *Vrn-A1* than 1_SNP plants (Kippes et al., 2018). An assumption was made that the single nucleotide polymorphism in the regulatory region of the first intron should probably be associated with differences in the duration of vernalization treatment in the winter wheat. However, the attempt made by N. Kippes et al. (2018) to associate the SNPs in the recessive gene *vrn-A1* with the duration of vernalization treatment cannot be recognized successful: the authors used the winter near-isogenic line Triple Dirk C, a derivative of the spring cv. Triple Dirk, and in our experiments, Triple Dirk C plants, in the field, progressed into shooting (and some came to ear) within four months without vernalization (Goncharov, 2012).

It can be concluded that none of the known changes (point mutations) in the sequences of the recessive genes *vrn* has any effect on the duration of vernalization treatment in the winter wheat accessions (see Table 2).

Note that isogenic lines for the *Vrd* genes controlling variation in the duration of vernalization treatment in winter common wheat have long since been created (Fayt, 2006b) and can now be used in molecular and biological experiments. These genes reside on the winter common wheat's chromosomes: *Vrd1* on 4A and *Vrd2* on 5D (Fayt et al., 2007).

Allelic variability at the VRN locus and winter growth habit. Mutations in the regulatory regions of the *Vrn-1* gene are associated with prevalent spring growth habit, while the point mutations of a gene (or genes) at the VRN-2 locus (the *vrn-2a* allele) or the deletion of an entire gene (the *vrn-2b* allele) are also associated with spring growth as a recessive trait in diploid wheat *T. monococcum* and barley *H. vulgare* (Yan et al., 2004b; Dubcovsky et al., 2005). No multiple allelism of the dominant gene *Vrn-2* controlling winter growth habit has been revealed. This offers indirect evidence that this gene is not associated with the duration of vernalization treatment in the diploid *T. monococcum* or *T. boeoticum*. What genes control it at barley is not known either.

Variability of dominant alleles of the *Vrn* genes in spring accessions of di-, tetra- and hexaploid wheats and their effect on duration of the vegetative period

The number of works analyzing the distribution of the dominant genes *Vrn* and their alleles in the main wheat cultivation areas is impressive (Catalogue…, 1987; Goncharov, 1998; Fu et al., 2005; Zhang X.K. et al., 2008; Lysenko et al., 2014; Smolenskaya et al., 2022; and others). Differences of the regions by alleles is shown (Genotypes…, 1987; Stelmakh, 1990; Goncharov, 1998). As far as modern spring common wheat are concerned, *Vrn-A1a* is prevalent in cold-winter areas where spring wheat are sown only in the spring. By contrast, the dominant alleles of the homologous genes *Vrn-B1a* and *Vrn-D1a* are highly frequent in the varieties cultivated in the Mediterranean climate, where spring wheats are sown in the autumn (Stelmakh, 1990; Zhang X.K. et al., 2008; Shcherban, et al., 2015a). Noteworthy, *Vrn-D1a* emerged in Southern Europe in the 1930s together with photoperiod-insensitivity and reduced height genes coming from Japanese common wheat (Goncharov, 2012). The question as to whether the dominant gene *Vrn-B3* can be widely used outside China (Bonnin et al., 2008) requires special close consideration. This gene has not been found in Russia's cultivars (Lysenko et al., 2014), nor has it been found in the progeny of the variety Hope (Goncharov, Gaidalenok, 2005), the gene *Vrn-B3* donor for the isogenic line CS/Hope 7B.

Facultative growth habit plants. In English-language literature, facultative growth plants are known as "intermediate" (Flood, Halloran, 1986). According to B.V. Rigin and the colleagues, the spring growth habit in them should be determined by the dominant *Vrn-A1* gene (Genotypes…, 1985), while in A.F. Stelmakh' opinion, exclusively by the dominant gene *Vrn-B1* (Stelmakh, 1981). In Chinese wheat, the facultative growth habit plants possess the dominant allele *Vrn-D1b* (Zhang X.K. et al., 2008).

Because facultative growth habit plants (sometimes called semi-spring) play an important role in wheat production in some areas (Fayt et al., 2018), 689 Chinese varieties were studied for the frequency and distribution of the allele *Vrn-D1b* in them. The results showed that allele *Vrn-D1a*, *Vrn-D1b* and *vrn-D1* were present in 27.3, 20.6 and 52.1 % of the specimens, respectively. Pedigree analysis indicates that *Vrn-D1b* originated from Chinese landraces (Guo et al., 2015).

A study of F_2 hybrid segregating for *Vrn-D1b* and *Vrn-D1a* in greenhouse long-day conditions without vernalization showed that the *Vrn-D1b* homozygote plants would heading 32 days later than *Vrn-D1a* homozygotes. Because *Vrn-D1b* has the same deletion in the first intron as does *Vrn-D1a* and a single nucleotide mutation in the promoter region and is associated with facultative growth habit, the authors proposed that the mutation in the promoter can change the basal activity level of gene *Vrn-D1*, which is already active due to the deletion in the first intron (Zhang J. et al., 2012).

Copy number of the *Vrn* genes. Change in the copy number (CNV) of the *Vrn-1* genes is one of the sources of genetic variability in hexaploid wheat (Díaz et al., 2012; Würschum et al., 2015). In most cases, CNV is associated with changes in gene *Vrn* expression (Muterko, 2023); however, data on their effect on the DVP are inconsistent.

Hexaploid wheat species (2*n* = 6*x* = 42)

The most economically important point in the study of allelism of the dominant genes *Vrn* is the search for their functional association with the DVP. Data on DVP (earliness) in spring wheat are quite inconsistent. According to K.A. Flaksberger (1938), it is in a range between 76 and 140 or more days. Other authors report variations from 70–80 to 120–130 days (Kumakov, 1980). Opinions differ as to how to classify commercial common wheat varieties by maturity (Goncharov N.P., Goncharov P.L., 2018), as this classification has a clear-cut region-specific flavor. At the same time, earliness can be associated with different combinations of the dominant alleles of the *Vrn* genes (see Supplementary Material).

VRN-A1 allele. The distribution of spring common wheat into ripeness groups revealed that this trait is influenced by a combinations of certain dominant genes *Vrn* and their alleles (Stelmakh, 1993; Likhenko et al., 2014; Smolenskaya et al., 2022). Spring varieties with the dominant gene *Vrn-A1* are usually more early-ripening than the varieties with dominant genes *Vrn-B1* and *Vrn-D1* (Stelmakh, 1993). It has been demonstrated the main contributor to the reduction in duration between emergence of plant seedlings and heading is the dominant allele *Vrn-A1a*, while *Vrn-A1b*, in contrast, accounts for later heading (Efremova et al., 2016). Additionally, the varieties with the dominant allele *Vrn-A1b* is rare in Siberia, 8 % (Smolenskaya et al., 2022). The *Vrn-A1a* has an insertion in promoter region and *Vrn-A1b*, in contrast, a deletion (Yan et al., 2004b).

B.V. Rigin and the colleagues (2021) stated that the ultra-ripening lines Rico (K-65588) and Rimax (K-67257) had the shortest time from emergence plant shootings to heading among all spring common wheat accessions in the VIR collection. Their genotypes revealed dominant alleles for three *Vrn* genes at once, *Vrn-A1*, *Vrn-B1* (respectively *Vrn-B1a* or *Vrn-B1c*), and *Vrn-D1*.

Any of the dominant alleles, *Vrn-A1a* or *Vrn-A1b*, disables response to vernalization, while any of the dominant alleles of the *Vrn-B1* or *Vrn-D1* genes induces a residual response and leads to later flowering (Stelmakh, 1993). These data were confirmed by studies showing that the dominant alleles *Vrn-A1a* and *Vrn-A1b* in combination with the dominant gene *Vrn-B1* can provide optimum flowering time and potentially high yield in the Pacific Northwest region of the USA, while spring wheat varieties with the dominant gene *Vrn-D1* may have advantage in Idaho and Oregon, where the vegetation periods are longer (Santra et al., 2009).

VRN-B1 allele. A novel allele, *Vrn-B1c*, probably associated with earlier ripening in late-ripening spring varieties was revealed using near-isogenic lines with different alleles of the *Vrn-B1* gene (Shcherban et al., 2012a). Its prevalence among common wheat varieties in Western Siberia and the North Kazakhstan, when spring growth habit being under monogenic control, was demonstrated (Shcherban et al., 2012b). In the absence of epistatic effects of the dominant *Vrn-A1* gene, this allele causes earlier heading than does *Vrn-B1a* (Shcherban et al., 2013). The effect of *Vrn-B1f* on heading time is similar to that of *Vrn-B1c*, but the mechanism of its regulation most likely appears to be different (Strejčková et al., 2021).

VRN-D1 allele. The dominant gene *Vrn-D1* occurs only in hexaploid wheat cultivars in the Asian region and some Italian varieties (Stelmakh, 1993; Goncharov, 1998). K. Iwaki and the colleagues (2000, 2001) found the dominant allele *Vrn-D4* in a large number of common wheat cultivars from different regions worldwide (55 cultivars out of 272 studied). The highest frequency of occurrence was observed in accessions from India and the bordering countries (Iwaki et al., 2000, 2001). This dominant gene had previously been found in most accessions of the Indian hexaploid endemic species *T. sphaerococcum* Perciv. (Goncharov, Shitova, 1999).

The dominant allele *Vrn-D^{t}1* with a 5.4-kb deletion in the first intron was found in spring plants of *Ae. tauschii* from the Middle East (Takumi et al., 2011). One more dominant allele was described later (Chepurnov et al., 2023). This allele has effect on heading time.

All the variants identified in three *Vrn-1* homeologs in wheat were designated as separate alleles, but not all of them were experimentally confirmed to have any effect on DVP (earliness) (see Supplementary Material).

VRN-B3 allele. The nucleotide substitutions or insertions/deletions in the copies of the *FT* gene (*Vrn-B3*) in the A and D genomes in 239 local, old local and modern commercial cultivars from different regions cause DVP polymorphisms (Bonnin et al., 2008). In contrast to *Vrn-1*, the homeologous copies of the *FT* gene showed no evidence of epistatic interactions (Bonnin et al., 2008). *TaFT* overexpression in transgenic *T. aestivum* plants considerably accelerated flowering compared to the non-transgenic control (Yan et al., 2006).

The absence of isogenic lines does not allow its different alleles to be compared for the strength of their phenotypic manifestation. Note that, line 620 with *Vrn-B3* had much later heading (Goncharov, 2012). Later heading was also observed in cultivars carrying various *Vrn-B3* alleles, *Vrn-B3a* and *Vrn-B3b* (Chen F. et al., 2013), and *Vrn-B3d* and *Vrn-B3e* (Berezhnaya et al., 2021).

Two hundred and seventy eight Chinese spring common wheat cultivars were characterized using molecular markers of the *Vrn-A1*, *Vrn-B1*, *Vrn-D1* and *Vrn-B3* genes. The varieties possessing from three to four dominant *Vrn* genes, including the rare dominant gene *Vrn-B3*, were the earliest (30–31 days to heading on average), and one-, two-, or three-gene combinations, including the dominant gene *Vrn-A1*, but not *Vrn-B3*, followed (38 days to heading on average). On the basis of these data, the dominant *Vrn-1* genes were ranked according to the amount of their influence on DVP reduction in the Chinese cultivars: *Vrn-A1* > *Vrn-B1* > *Vrn-D1* (Zhang X.K. et al., 2008). This ranking is not the same as those reported elsewhere (Gotoh, 1979; Goncharov, 2003).

VRN-D4 allele. The dominant gene *Vrn-D4* has a weaker effect on DVP than have the *Vrn-A1*, *Vrn-D1* or *Vrn-B3* genes (Kippes et al., 2014), but stronger than *Vrn-B1* (Gotoh, 1979; Goncharov, 1998).

Tetraploid wheat species (2*n* = 4*x* = 28)

Based on the analysis of *Vrn-A3* expression using sister lines, earlier flowering in accession TN26 of *T. dicoccum* Schrank ex Schuebl. than in accession TN28 of *T. pyramidale* Perciv. is due to a 7-bp insert in the promoter region of the gene which, this insert including a *cis*-element of the GATA box (Nishimura et al., 2018). The analysis revealed the presence of the early-flowering alleles of *Vrn-A3* in spelt wheat from Ethiopia and India and their absence in the accessions of *T. durum* Desf. and common wheats. These results led the authors to the conclusion that the *Vrn-A3a-h1* and *Vrn-A3a-h2* alleles should be useful in breeding for earliness in durum and common wheat (Nishimura et al., 2021).

T. carthlicum Nevski and *T. dicoccum* accessions possessing the *Vrn-B1c* allele with a retrotransposon insertion passed to flower without vernalization. Transcripts in the winter DH-lines possessing the recessive *vrn-B1* allele were observed no sooner than after vernalization (Chu et al., 2011).

Two spring accessions, PI 208912 (Iraq) of *T. turgidum* and PI 74830 (China) of *T. durum* and one winter accession PI 221422 (Serbia) of *T. turgidum* started to flower without vernalization. However, they did so substantially later than plants with the dominant *Vrn-A1* or *Vrn-B1* genes. Interestingly, winter accession PI 221422 started to flower 25 days later than did spring accessions PI 208912 and PI 74830. All of them have recessive *vrn-B1* alleles and null alleles *vrn-B3*. It is proposed that their late flowering is due to the *Vrn-A1i* allele (Muterko et al., 2016).

The combination of the dominant *Vrn-A1* and *Vrn-B1s* alleles was associated with early flowering the tetraploid species *T. dicoccum* and *T. dicoccoides* (Körn. ex Asch. et Graebn.) Schweinf. (Muterko et al., 2016). *Vrn-A1* allelism is a possibility in *T. dicoccum* (Rigin et al., 1994).

The gene's allelic variant coming from *T. militinae* Zhir. et Migusch. was designated *Vrn-A1f*-like. QTL analysis showed that it caused a 1.9–18.6-day delay in the flowering time of Tähti and Mooni, depending on cultivation conditions (Ivaničová et al., 2016).

In all *T. timopheevii* (Zhuk.) Zhuk. accessions studied, the spring growth habit was associated with the dominant *Vrn-A1f-ins* and *Vrn-A1f-del/ins* alleles (Golovnina et al., 2010; Shcherban et al., 2016). The same allele was found in wild *T. araraticum* Jakubz. (Golovnina et al., 2010). Noteworthy, this species has an extremely limited number of spring forms (Goncharov, 1998).

Diploid wheat species (2*n* = 2*x* = 14)

It is possible that the pattern of inheritance in diploid wheats is more sophisticated than it used to be thought before, as spring growth habit in the wild *T. boeoticum* has recently been shown to be under digenic control (Fu Hao, Boguslavskyi, 2023). Similar results obtained for the *T. monococcum* by L. Smith (1939) have remained unnoticed. Spring accessions of *T. urartu*, the A^u-genome donor for polyploid wheat species, were found to have a *Vrn-A1* mutation typical for the section *Triticum* species (Golovnina et al., 2009). However, as few as four *T. urartu* accessions from among 400 studied were spring (Goncharov, 1998), of which two were "odd" in that they were *T. urartu* phenotypically (with velvety pubescence of leaves), but *T. boeoticum* karyotypically (Adonina et al., 2015) and, therefore, *Vrn-A1* polymorphism is most likely to have emerged no sooner than in polyploid wheats.

In field conditions, *T. monococcum* with various deletions in the promoter region of the *Vrn-A1f* and *Vrn-A1g* alleles showed 59–60 days to heading on average and did not differ significantly from each other in terms of this measure ($p = 0.842$) (Chepurnov, Blinov, 2022).

Enhancing the diversity of polymorphisms in the *Vrn* genes and prospects in breeding for reduced duration of the vegetative period

The polymorphism in dominant *Vrn* genes controlling spring growth habit in varieties of Siberia and the European part of Russian Federation is extremely low (Lysenko et al., 2014; Smolenskaya et al., 2022). In 75 % of the cultivars in Siberia, this trait is under digenic control exerted by the dominant *Vrn-A1* and *Vrn-B1* genes; in 25 %, under monogenic control exerted by dominant genes (among 24 cultivars, 19 are controlled by a single dominant gene *Vrn-A1* and 5, by a single dominant gene *Vrn-B1*). Trigenic control was discovered for one cultivar, Tulun 15, (Likhenko et al., 2014). The conclusion made by E.A. Moiseeva and N.P. Goncharov (2007) that spring growth habit in the of Western and Eastern Siberian wheat cultivars is controlled by two dominant *Vrn* genes has been confirmed. An increased prevalence of the allele *Vrn-B1c* in West Siberian cultivars and of the allele *Vrn-B1a* in East Siberian cultivars has been observed, suggesting their selectivity to environments of these regions (Smolenskaya et al., 2022). Other regions of the Russian Federation have not yet been considered with this amount of scrutiny (Lysenko et al., 2014).

Our assumption is that, the level of DVP-related polymorphism in spring wheat cultivars in Siberia in particular and Russia in general can be enhanced by introgression of the dominant alleles of the *Vrn* genes from their wild ancestor (Goncharov, Chikida, 1995; Goncharov, 1998) or by using rare alleles that are present in their gene pool (Stelmakh, Avsenin, 1996; Koval, Goncharov, 1998) but have not been studied by a molecular genetic methods and are rarely used in the breeding. Note that *T. urartu* Thum. ex Gandil. – the donor of the A^u genome of polyploid wheats does not carry any mutation that could be new to spring common wheat (Golovnina et al., 2010). The use of the diploid species *T. monococcum* carrying the A^b genome (Goncharov et al., 2007; Nishiura et al., 2018) appears to be impracticable either, due to its evolutionary unrelatedness to cultivated wheat. Consequently, the model based on *T. monococcum* is not successful, as it leads modern plant cultivation nowhere.

The aim of the future efforts is to develop a simple model predicting wheat phenology, with effects of vernalization and photoperiods taken into account. New facts about the expression of the *Vrn* genes, their allelic composition, and interaction with other genes will allow us to learn more about the associations known to date (Distelfeld et al., 2009; Jin, Wei, 2016; Krasileva et al., 2017; Kiseleva, Salina, 2018; Milec et al., 2023). This knowledge will undoubtedly contribute to increasing the efficiency of next generation breeding.

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