Theor Appl Genet (2003) 107:768–772
DOI 10.1007/s00122-003-1317-x

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Genetics of growth habit (spring vs winter) in common wheat: confirmation of the existence of dominant gene *Vrn4*

Received: 11 April 2002 / Accepted: 31 March 2003 / Published online: 1 July 2003

Abstract The number of dominant *Vrn* genes in common wheat, *Triticum aestivum* L., is estimated. Data were obtained supporting Pugsley's and Gotoh's data on the presence of a dominant gene *Vrn4* in near-isogenic line 'Triple Dirk F'. The presence of a dominant gene *Vrn4* in line 'Gabo-2' of cultivar 'Gabo', which was used by Pugsley as a donor of the gene *Vrn4* for the near-isogenic line 'Triple Dirk F', was also confirmed. The *Vrn2* and *Vrn4* relationship and their chromosomal location are discussed. It was demonstrated that the dominant *Vrn8* gene which was introgressed from *Triticum sphaerococcum* to common wheat by Stelmakh and Avsenin is allelic to *Vrn4*. While genes *Vrn6*^{sc} and *Vrn7*^{sc} which were introgressed from rye, *Secale cereale* L., by the above-mentioned authors are not allelic to the genes *Vrn1, Vrn2, Vrn3* and *Vrn4*.

Keywords *Triticum aestivum* · Growth habit (spring vs winter) · Introgressive lines · Dominant gene *Vrn4*

Introduction

Increasing knowledge about the genetics of growth habit (spring vs winter) will contribute to a better understanding of the evaluation of adaptation in wheats and promote their breeding for specific environments. Studies on growth-habit genetics in common wheat, *Triticum aestvum* L., were started at the beginning of the last century [for reviews see Gotoh (1979) and Flood and Halloran (1986) among others]. Åkerman and MacKey (1949) reported that the spring growth habit in common wheat is controlled by one, two, or occasionally, three dominant genes *S* (*S* is the abbreviation for the German word 'Sommer') and that the winter growth habit is controlled by recessive alleles at these loci. The presence of even one dominant allele leads to the spring growth habit. Tsunewaki and Jenkins (1961) also suggested the existence of three loci determining growth habit – *Sg1, Sg2*, and *Sg3* (*Sg* is the abbreviation for the English word 'spring growth'). Sears (1944) revealed that nullisomic 5D 'Chinese Spring' plants were the latest to mature among all the aneuploids that he produced in this cultivar, and suggested that the gene for early maturity resides on chromosome 5D. Tsunewaki and Jenkins (1961) designated this gene as *Sg1* and located another dominant gene for the spring growth habit, *Sg2*, in chromosome 5A. The third dominant gene, *Sg5*, was located in chromosome 5B by Singh (1967). Thus, the three homoeologous group-5 chromosomes possessed dominant genes for the growth habit. At present, *Vrn1, Vrn2* and *Vrn3* have been mapped using DNA markers (Galiba et al. 1995; Snape et al. 1998; Barrett et al. 2002; Iwaki et al. 2002).

Pugsley (1971), in agreement with the above-mentioned investigators, concluded that the spring growth habit was controlled by any of three dominant genes or their combinations. He re-designated these genes as *Vrn1, Vrn2* and *Vrn3*. *Vrn1* was equated with S_k, *Vrn2* with S_s, and *Vrn3* with the 'Chinese Spring' gene *Sg1* (Pugsley 1972). He found a further dominant gene in cultivar 'Gabo' (Pugsley 1972), which was earlier described by Knott (1959). This gene was listed as *Vrn4* by McIntosh (1973). Maystrenko (1974) equated *Vrn1* and *Vrn3* with *Sg2* and *Sg1*, earlier located in chromosomes 5A and 5D, respectively (Tsunewaki and Jenkins 1961). However, the erroneous equating of *Vrn2* and *Vrn4* and their chromosome location by Maystrenko (1980) was accepted by McIntosh et al. (1998) in the "Catalogue of gene symbols for wheat". The *Vrn1* gene is now designated *Vrn-A1, Vrn2* (or *Vrn4*) is designated *Vrn-B1*, and *Vrn3* is designated *Vrn-D1* (McIntosh et al. 1998). One more common wheat dominant gene *Vrn-B4* (*Vrn 5*) was located in 7BS (Law and Wolfe 1966).

Communicated by J.W. Snape

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The aim of this study is to demonstrate the separate existence of the dominant gene *Vrn4* and to discuss the possible number of dominant *Vrn* genes in common wheat.

Materials and methods

Pugsley's near-isogenic line (NIL) 'Triple Dirk F', which Dr. T. Gotoh has provided me, was used in the investigation. Prof. D. Knott supplied seed of the original line of cultivar 'Gabo', 'Gabo-2' (K4417F98), which had a gene nonallelic to *Vrn1* and *Vrn2* according to his investigation (Knott 1959) and which was used by Pugsley (1972) as donor of the dominant gene *Vrn4* for NIL 'Triple Dirk F'. The genetic control of growth habit in NIL 'Triple Dirk F' and line 'Gabo-2' was determined by hybridisation with tester NIls 'Triple Dirk D', 'Triple Dirk B', 'Triple Dirk E' with the dominant genes *Vrn1, Vrn2* and *Vrn3*, respectively, and winter cultivars 'Bersée', 'Uliyanovka' and 'Skorospelka 35'. To identify the *Vrn* genotype, segregation in the F_2 was scored according to the scheme of Dzhalpakova et al. (1996), i.e. 3 months after sowing, when all the standard spring cultivars had already headed, and when it was possible to classify the hybrid plants as spring (ear emerged) or as winter (no visible ear formation). The segregation ratio for each cross was determined and compared with the expected segregation ratio using the chi-square test.

'Bersée' mono5D was produced by Worland (1988).

The genes $Vrn6^{sc}$ and $Vrn7^{sc}$ were introgressed from rye, *Secale cereale* L., to common wheat by Stelmakh and Avsenin (1996). The *Vrn8* was introgressed from *Triticum sphaerococcum* Perciv. (Stelmakh and Avsenin 1996).

Hybrid dwarfness was estimated as described by Hermsen (1962). The experiments were conducted under field conditions in Novosibirsk.

Results

The data obtained for checking the NIL 'Triple Dirk F' are presented in Table 1. It was established that the spring growth habit of 'Triple Dirk F' was controlled by a single dominant gene which was not allelic to the dominant genes *Vrn1, Vrn2, Vrn3* or *Vrn5* (Table 1).

The result of the attempt to locate the gene *Vrn4* on chromosome 5D is presented in Table 2. It is obvious that, according to the data obtained, chromosome 5D is not the critical chromosome for the gene. F_2 segregation in the cross of the winter wheat cultivar 'Bersée' with 'Triple Dirk' was performed with that expected for a single gene. The F_2 from the selected monosomic plant of 'Berseé' mono5D with 'Triple Dirk' also segregated monofactorily. If *Vrn4* were located in 5D, this cross should have segregation with an increase of the spring habit offspring relative to the winter habit types; therefore, *Vrn4* is not located on chromosome 5D. The result of checking line 'Gabo-2' is also presented in Table 2. The cross 'Skorospelka 35' × 'Gabo-2' segregated for two genes. Both crosses of 'Triple Dirk D' (*Vrn1*) and 'Triple Dirk F' (*Vrn4*) with 'Gabo-2' failed, and segregation indicated that 'Gabo-2' possessed *Vrn1* and *Vrn4*.

The assays for determining the hybrid dwarf genotypes of the 'Triple Dirk' NILs are presented in Table 3. The only 'Triple Dirk' NIL that segregated for hybrid dwarfness in crosses with 'Saratovskaya 29' and K-43376 (both genotypes D_1D_1 d_2d_2 d_3d_3 d_4d_4) was in 'Triple Dirk B'. The ratio of normal:dwarf plants was not expected 13:3 (χ^2 = 17.85, $P < 0.05$) at the end of vegetation in the field conditions of Novosibirsk. It is connected with something that is very difficult to identify

Table 1 F_2 segregation for growth habit and tests of conformity to one, two and three gene ratios in various crosses of Triple Dirk F possessing *Vrn4*

Tester lines	Segregation into winter vs spring forms in the F_2 generation		χ^2 Value for ratio*		
	Spring	Winter	3:1	15:1	63:1
'Uliyanovka'	114	44	0.68	125.79	709.76
'Triple Dirk D' (*Vrn1*)	146	11	27.11	0.15	30.25
'Triple Dirk B' (*Vrn2*)	154	9	32.98	0.15	16.61
'Triple Dirk E' (*Vrn3*)	140	9	28.57	0.01	19.42
'Chinese/Hope 7B' '(*Vrn3 Vrn5*)'	155	3	44.97	5.11	0.12

* Values for significance of P = 0.05 is 3.84

Table 2 Results of checking hypotheses of dominant gene *Vrn4*-location on chromosome 5D and identification of the *Vrn* genotype of cultivar 'Gabo-2'

Cross combination	Segregation into spring vs winter in the F_2 generation		χ^2 Value for ratio*	
	Spring	Winter	3:1	15:1
'Bersée' × 'Triple Dirk F'	15	4	0.16	7.11
mono5D Bersée × 'Triple Dirk F' (selected monosomic F_1 plants)	44	12	0.38	22.02
'Skorospelka 35' × 'Gabo-2'	46	3	9.31	0.00
'Triple Dirk D' × 'Gabo-2'	171	0	–	–
'Triple Dirk F' × 'Gabo-2'	256	0	–	–

* Values for significance of P = 0.05 is 3.84

Table 3 Identification of the hybrid dwarfness gene *D2* in Pugsley's near-isogenic lines

Near-isogenic lines (with dominant gene)	Segregation into normal vs dwarf forms in the F_2 generation	
	Normal plants	Dwarf type-I plants
'Triple Dirk D' (*Vrn1*)	$190^a/98^b$	$0^a/0^b$
'Triple Dirk B' (*Vrn2*)	$118^a/39^b$	$8^a/2^b$
'Triple Dirk E' (*Vrn3*)	$187^a/273^b$	$0^a/0^b$
'Triple Dirk F' (*Vrn4*)	$165^a/94^b$	$0^a/0^b$

[a] Cross combination with cultivar 'Saratovskaya 29'
[b] Cross combination with K-43376

Table 4 Tests for allelism between introgressed genes $Vrn6^{sc}$, $Vrn7^{sc}$ and *Vrn8*, and common wheat genes *Vrn1, Vrn2, Vrn3* and *Vrn4*. TDD – 'Triple Dirk D'; TDB – 'Triple Dirk B'; TDE – 'Triple Dirk E'; TDF – 'Triple Dirk F'

Lines with *Vrn* genes	Segregation into winter vs spring plants in the F_2 generation[a]				
	Winter cultivar	TDD (*Vrn1*)	TDB (*Vrn2*)	TDE (*Vrn3*)	TDF (*Vrn4*)
$Vrn6^{sc}$	59:10*	123:14	128:12	120:6	49:6
$Vrn7^{sc}$	43:61**	53:3	100:7	191:16	56:11***
Vrn8	93:32	202:15	298:24	75:5	253:0

[a] * The spring/winter ratio; ** and *** not significant for 3:1 and 15:1 ratios at $P_{0.05} = 3.84$, respectively

the dwarf type II phenotype during, and even more difficult, at the end of vegetation simultaneously with spring:winter segregation. The calculation is complicated with the uncertainty of plant classification into late spring or the dwarf II type. The expected segregation ratio 13:3, when using 'Saratovskaya 29', was easily observed only under short-day conditions (Maystrenko and Troshina 1975). In this case the phenotype of plant type dwarf II is not considerably different from the plant phenotype of the dwarf I type. According to this reason the dwarf allele of cultivar 'Saratovskaya 29' was designated as D_1^{ppd} (Maystrenko and Troshina 1975). In our experiments only heterozygotes *D1- D2d2* and *D1d1 D2-* are not definitely identified at the end of vegetation under the Novosibirsk environment in hybrids with this cultivar and, due for this reason, the expected segregation ratio shifts to 15:1. At present, having the information at our disposal, it is possible to identify the plant phenotype of the dwarf II type. The ratio in hybrids with Saratovskaya 29 here is 111:15 ($\chi^2 = 0.35$, $P > 0.05$) and in hybrids with K-43376 is 36:5 ($\chi^2 = 1.03$, $P > 0.05$).

Stelmakh and Avsenin (1996) reported on the introgression of the dominant genes $Vrn6^{sc}$ and $Vrn7^{sc}$ from rye *S. cereale*, and *Vrn8* from *T. sphaerococcum* to common wheat. The segregation data for these lines with Pugsley's NILs are presented in Table 4. The first two genes were not allelic to *Vrn1, Vrn2, Vrn3, Vrn4* or the spring habit gene in *T. sphaerococcum*. It is worth noticing that complicated conjugation was often observed in F_1 hybrid-meiosis of lines $Vrn6^{sc}$ and $Vrn7^{sc}$ with tester lines. Sometimes there were 3–5 polyvalents formed per cell. The chromosome with the line gene $Vrn7^{sc}$ has sites homoeologous to chromosome 5A in the long arm. It is large and has unequal arms (arm ratio 1:3). Micronuclei with a high frequency were observed in tetrads. Sometimes delays and bridges were observed in AI and AII. All these allow me to conclude that the chromosome has 5R chromatin by which, probably, the deviation from theoretically expected segregation ratios was with the winter cultivar (see Table 4). Line $Vrn6^{sc}$ has the rye chromosome unlike 5R.

Discussion

The number of dominant *Vrn* genes in common wheat is important since it modifies growth habit (spring vs winter), and allows the development of varieties with different vegetative periods.

The dominant gene *Vrn4*

Lakerbai and Rigin (1982) and Stelmakh (1987) could not identify the dominant gene *Vrn4* in Pugsley's NILs based on the cultivar 'Triple Dirk' supplied by the former USSR. Based on the results of analysis of these lines, and also on checking the genotypes of a number of cultivars possessing *Vrn4* according to Maystrenko's suggestion, Stelmakh (1987) rejected the likely existence of *Vrn4* in common wheat. In contrast Gotoh (1979) also using Pugsley's NILs identified four dominant *Vrn* genes, one in each of the four lines. The present work also confirmed the presence of *Vrn4* in 'Triple Dirk F'.

The dominant gene *Vrn4* probably occurs at a low frequency in the gene pool of hexaploid wheat (Goncharov 1998; Goncharov and Shitova 1999). Its distribution is confirmed for certain regions of China and India (Iwaki and Kato 1998; Goncharov and Shitova 1999). Under the Novosibirsk environment, the near-isogenic lines 'Triple Dirk B' and 'Triple Dirk F' with the dominant genes *Vrn2* and *Vrn4*, respectively, do not differ significantly in ear emergence times (Goncharov and Rigin 1989). The cultivars possessing *Vrn2* or *Vrn4* could not be distinguished by phenotype in the middle latitudes, and this might have been a reason why the dominant gene

Vrn4 was not included in European breeding programs (Goncharov 1998). Gotoh (1979) noted that *Vrn4* is not responsive to vernalization treatment, but is sensitive to low temperature. It would be of interest to examine its phenotypic expression on a wider range of geographic areas to evaluate its adaptation to certain environments.

The line 'Gabo-2', a selection from 'Gabo', has the dominant gene *Vrn4* as well as *Vrn1* (Table 3).

Chromosomal localisation of the *Vrn4* and *Vrn2* genes and their allelism

As the data in Table 1 show, the *Vrn4* and *Vrn2* genes are not allelic. It appears that Maystrenko (1980) erroneously located *Vrn2* in chromosome 2B, and *Vrn4* in chromosome 5B. Consideration of her error is beyond the scope of this paper. To locate the gene for spring growth habit, Maystrenko (1980) used monosomic lines of cultivar 'Saratovskaya 29' which, according to Tsilke (1973), has the dominant complimentary gene *D1*. It appears possible that Maystrenko confirmed hybrid dwarf and winter phenotypes in her field experiments, leading to the erroneous chromosome location. At the time when Maystrenko was identifying the genes *Vrn*, the line 'Triple Dirk F' carrying the gene *Vrn4* was not available in the former USSR, hence, precluding an appropriate tool of allelism with *Vrn2*. Regretfully, the chromosome location of *Vrn4* must be considered unknown. While there are suggestions of its location in chromosome 7A (Law and Scarth 1984) or chromosome 5D (Kato et al. 1993), Goncharov and Gaidalenok (1994) concluded that chromosome 7A does not carry a dominant *Vrn* gene, and, in the current work, *Vrn4* was shown not to be located on chromosome 5D (Table 3). It is possible that the *Vrn4* is not homoeologous to other discovered common wheat *Vrn* genes. For the same reason gene *Vrn4* has not been mapped using DNA markers.

The dominant gene *Vrn5*

Law and Wolfe (1966) identified the gene *Vrn5* in the substitution line 'Chinese Spring (Hope 7B)', and they localised it on chromosome 7B.

The dominant genes $Vrn6^{Sc}$, $Vrn7^{sc}$ and *Vrn8*

It is clear that genes $Vrn6^{sc}$ and $Vrn7^{sc}$ are also non-allelic to the four dominant genes (*Vrn1* to *Vrn4*) described earlier for common wheat. The experiments carried out do not allow me to identify the introgression type. It is only possible to note that not point-like build-in of the rye genes to the wheat genome occurred. Probably, translocation including a considerable segment of rye chromosome 5R took place in the line $Vrn7^{sc}$; inclusion of the whole rye chromosome is possible in line $Vrn6^{sc}$. However, the presence of segregation with tester lines carrying common wheat dominant genes *Vrn* allows one to conclude that lines with dominant genes $Vrn6^{sc}$ and $Vrn7^{sc}$ have no dominant *Vrn* genes of common wheat.

It seems that the putative gene *Vrn8* is *Vrn4*. *Vrn8* was introgressed by Stelmakh and Avsenin (1996) from *T. sphaerococcum* and was designated as *Vrn8* due to its non-allelism with genes *Vrn1, Vrn2* and *Vrn3*, because of Stelmakh's (1987) earlier evidence for the non-existence of gene *Vrn4*. *Vrn4* was detected in a number of other accessions of *T. sphaerococcum* (Goncharov and Shitova 1999).

The conclusion from the results here is the presence of five non-allelic dominant *Vrn* genes in hexaploid wheat, which, alongside with genes for earliness *per se* and photoperiodic response (*Ppd*), determine a wide range of variation for the duration of the vegetative period. Variation can be increased by means of two other non-allelic genes $Vrn6^{sc}$ and $Vrn7^{sc}$ introgressed from rye (Stelmakh and Avsenin 1996), and probably with new *Vrn* genes described in the diploid species *Aegilops squarrosa* L. (Goncharov and Chikida 1995) and *Aegilops speltoides* Tausch (Goncharov and Konovalov 1996), donors of the basic D and B(G) genomes of polyploid wheats.

Acknowledgements The author is grateful to Dr. T. Gotoh (AFFTIS, Tokyo, Japan) who kindly provided the near-isogenic line 'Triple Dirk F', and Drs. T. Gotoh and A.J. Worland (JIC, Norwich, GB) for critical reading of the manuscript. Special thanks to Prof. D. Knott (Saskatchewan University, Canada) for supplying line 'Gabo-2', Dr. A.J. Worland for mono5D Bersée and Dr. V.I. Avsenin (BGI, Odessa, Ukraine) for lines with the dominant $Vrn6^{Sc}$, $Vrn7^{sc}$ and *Vrn8* genes. The author is also grateful to the anonymous Referees for their remarks and valuable advice that contributed to the improvement of this paper. All experiments were carried out according to the current Russian legislation.

References

Åkerman Å, MacKey J (1949) Försök till stegrande av vårvetets avkastning. II. Korsningar mellan vår-och höstvete: Beskrivning av Svalöfs Ellavårvete (in Swedish). Sveriges Utsadesforenings Tidskrift 59:105–117

Barrett B, Bayram M, Kidwell K (2002) Identification of AFLP and microsatellite markers for vernalization response gene *Vrn-B1* in hexaploid wheat using reciprocal mapping populations. Plant Breed 121:400–406

Dzhalpakova KD, Goncharov NP, Bersimbaev RI (1996) Genetic control of growth habit in common wheat cultivars from Kazakhstan. Russian J Genet 32:62–66

Flood RG, Halloran GM (1986) Genetics and physiology of vernalization response in wheat. Adv Agron 39:87–125

Galiba G, Quarrie SA, Sutka J, Morgounov A, Snape JW (1995) RFLP mapping of the vernalization (*Vrn1*) and frost resistance (*Fr1*) genes on chromosome 5A of wheat. Theor Appl Genet 90:1174–1179

Goncharov NP (1998) Genetic resources of wheat related species: the *Vrn* genes controlling growth habit (spring vs winter). Euphytica 100:371–376

Goncharov NP, Chikida NN (1995) Genetics of growth habit in *Aegilops squarrosa*. Russian J Genet 31:343–346

Goncharov NP, Gaidalenok RF (1994) Role of chromosomes of wheat homoeological group 7 in growth habit control. Russian J Genet 30:1071–1074

Goncharov NP, Konovalov AA (1996) Inheritance of glucose phosphate isomerase, awnedness, hairy glume and growth habit in *Aegilops speltoides* and *Aegilops aucheri*. Russian J Genet 32:571–576

Goncharov NP, Rigin BV (1989) The number of genes *Vrn* controlling spring growth habit in common wheat (in Russian). Bull Appl Bot, Genet Breed 128:71–74

Goncharov NP, Shitova IP (1999) Genetics of growth habit in old-local and local cultivars of hexaploid wheats. Russian J Genet 35:386–392

Gotoh T (1979) Genetic studies on growth habit of some important spring wheat cultivars in Japan, with special reference to the identification of the spring genes involved. Japan J Breed 29:133–145

Hermsen JGTh (1962) Hybrid necrosis as a problem for the wheat breeder. Euphytica 12:1–6

Iwaki K, Kato K (1998) Geographical variation of the *Vrn* genotype in wheat caused by the selection for adaptability to winter coldness. In: Slinkard A (ed) Proc 9th Int Wheat Genet Symp, vol. 4. Saskatoon, Canada, pp 39–41

Iwaki K, Nishida J, Yanagisawa T, Yoshida H, Kato K (2002) Genetic analysis of *Vrn-B1* for vernalization requirement by using linked dCAPS markers in bread wheat (*Triticum aestivum* l.). Theor Appl Genet 104:571–576

Kato K, Nakagawa K, Kuno H (1993) Chromosomal location of the genes for vernalization response, *Vrn2* and *Vrn4*, in common wheat, *Triticum aestivum* L. Wheat Inf Service 76:53

Knott DR (1959) The inheritance of rust resistance. IV. Monosomic analysis of rust resistance and some other characters in six varieties of wheat including Gabo and Kenya Farmer. Can J Plant Sci 39:215–228

Lakerbai AO, Rigin BV (1982) Genetics and phenotype of near-isogenic lines of cultivar Triple Dirk (in Russian). Bull Vavilov All-Union Institute of Plant Industry 122:55–58

Law CN, Scarth R (1984) Genetics and as potential for understanding the action of light and the flowering process. In: Vince-Prue D (ed) Light and flowering process. Academic Press, London, pp 193–209

Law CN, Wolfe MS (1966) Location of genetic factors for mildew resistance and ear emergence time on chromosome 7B of wheat. Can J Genet Cytol 8:462–470

Maystrenko OI (1974) Identification of chromosomes caring genes *Vrn1* and *Vrn3* inhibiting winter habit in wheat. EWAC Newslett 4:49–52

Maystrenko OI (1980) Cytogenetic study of the growth habit and ear-emergence time in wheat (*Triticum aestivum* L.). In: Well-Being of mankind and genetics, vol. 1, book 2. Proc 14th Int Congress of Genetics. MIR, Moscow, Russia, pp 267–282

Maystrenko OI, Troshina AV (1975) Discovering new alleles controlling hybrid dwarfness under short day in wheat. In: The problem of theoretical and applied genetics: information materials for 1974 (In Russian). ICG, Novosibirsk, pp 52–53

McIntosh RA (1973) A catalogue of gene symbols for wheat. In: Sears ER, Sears LMS (eds) Proc 4th Int Wheat Genet Symp. University of Missouri, Columbia, USA, pp 893–937

McIntosh RA, Hart GE, Devos KM, Gale MD, Rogers WJ (1998) Catalogue of gene symbols for wheat. In: Proc 9th Int Wheat Genet Symp, vol. 5. Saskatoon, Canada, pp 1–235

Pugsley AT (1971) A genetic analysis of the spring-winter habit of growth in wheat. Aust J Agric Res 22:21–31

Pugsley AT (1972) Additional genes inhibiting winter habit in wheat. Euphytica 21:547–552

Sears ER (1944) Cytogenetic studies with polyploid species of wheat II. Additional chromosomal aberrations in *Triticum vulgare*. Genetics 29:232–246

Singh MP (1967) Monosomic analysis in wheat. Heredity 22:591–596

Snape JW, Semikhodskii A, Sarma R, Korsun V, Fish L, Quarrie SA, Gill BS, Sasaki T, Galiba G, Sutka J (1998) Mapping vernalization loci in wheat and comparative mapping with other cereals. In: Sinkard AE (ed) Proc 9th Int Wheat Genet Symp, vol. 3. University Extension Press, University of Saskatchewan, Saskatoon, pp 156–158

Stelmakh AF (1987) Growth habit in common wheat (*Triticum aestivum* L. em Thell.). Euphytica 36:513–519

Stelmakh AF, Avsenin VI (1996) Alien introgression of spring habit dominant genes into bread wheat genomes. Euphytica 89:65–68

Tsilke RA (1973) Finding of genes of hybrid dwarfness in two strains of spring wheats (in Russian). Genetika (Moscow) 9:13–17

Tsunewaki K, Jenkins BC (1961) Monosomic and conventional gene analysis in common wheat. II. Growth habit and awnedness. Jpn J Genet 46:428–443

Worland AJ (1988) Catalogue of monosomic series. In: Miller TE, Koebner RMD (eds) Proc 7th Int Wheat Genet Symp, vol. 2. Cambridge, pp 1399–1403