Breeding for earliness and thermo-tolerance in wheat suited to early, late and very late sowing in northwestern India

Vinod, J. B. Sharma, R. S. Tomar, Bhanwar Singh and S. M. S. Tomar*

Division of Genetics, Indian Agricultural Research Institute, New Delhi 110012

(Received: April 2011; Revised: December 2011; Accepted: January 2012)

Abstract

Wheat varieties WR 544, HD2285, Sonalika, Halna, Raj3765 and PBW373 recommended for late sown conditions in India (i.e., on or after 25th December) along with contrasting check HD2687 released for timely sown conditions (i.e., 1 to 15th November) and C306, a rainfed cultivar (last week of October and first week of November) were studied to know the genetic basis of flowering time. The date of flowering and maturity were comparatively evaluated by planting them on 20th September, 15th November, 25th December and 15th of January over a period of more than four years. The photoperiod insensitivity in these genotypes was determined by a Ppd-D1 allele. Gene expression in response to vernalization was examined based on pedigree analysis. It was found that each of these genotypes carries Vrn-A1, Ppd-D1 genes except late flowering genotypes, HD2687 and C306, which carried vrn-A1 and Ppd-D1 alleles. The days to flowering of 20th September sown crop ranged from 44 to 56 (photo insensitive), except the cultivars HD2687 and C306 which flowered in 83 and 93 days and expressing their response to vernalization. WR544 demonstrated tremendous resilience with respect to flowering and other agronomical traits under 20th September and 25th December sown crop since it flowered in 44 days and thus characterized as an ultra early flowering genotype. It involves spring wheat Sonora 64 in its pedigree originating from Mexico. Sharbati Sonora, a mutant of Sonora 64 has been identified to carry Vrn-A1 and Ppd-D1 alleles. Similarly Raj3765 and Halna involved Ciano and Sonora 64 in their parentage both carrying Vrn-A1 and Ppd-D1 alleles making these cultivars as photo insensitive. It can therefore, be conclusively said that both the alleles Vrn-A1 and Ppd-D1 have been introduced in Indian genotypes from Mexican germplasm. The combined average yield of WR544 and Raj 3765 sown on 20th September (early sown, autumn) and 25th December (late sown, winter) over two seasons was 70.2 and 62.8 q/ ha respectively. This indicated that the crop sown in September can be harvested in the month of December leaving enough time for preparation and raising subsequent wheat crop on the same piece of land. Since WR544 out yielded all the varieties tested, it can therefore be popularized for early autumn and late sowings.

Key words: Spring wheat, winter wheat, photosensitive, photoinsensitive, Ppd and Vrn genes

Introduction

Wheat is widely grown crop in both higher and lower latitude areas (from zero masl to higher altitude of Tibet) at optimum temperature of about 25°C with minimum and maximum growing temperatures of 3 to 4°C and 30 to 32°C, respectively [1]. With the advent of early maturing genotypes, cultivation of wheat is technically feasible even in much warmer areas with adequate source of moisture available during the growing season.

Prior to the introduction of dwarf wheats, India was cultivating tall, photosensitive and late maturing genotypes. Wheat production in India increased dramatically after the introduction of dwarf wheats, Lerma Rojo (Rht1) and Sonora 64 (Rht2) in 1965. The dwarfing genes (Rht1, Rht2) provided lodging resistance by reducing the plant height genetically and perhaps by pleiotropic effect on yield through increased tiller number and the biomass. Incidentally, photoperiod insensitive genes (Ppd1, Ppd2) were also introgressed into CIMMYT breeding programme at the same time as the two dwarfing genes [2]. Photoperiod insensitivity is determined by genes Ppd-D1 (Ppd1), Ppd-B1 (Ppd2) and Ppd-A1 (Ppd3) located on group 2 chromosomes 2D, 2B and 2A, respectively, having major influence on the trait [3-4]. Genes determining photoperiod response have also been found on 3D [5], 4B [6] and 6B [7] and on all chromosomes of group 1 [8]. Both photoperiod-

^{*}Corresponding author's e-mail: smstomar@yahoo.co.in; smstisgpb@gmail.com
Published by Indian Society of Genetics & Plant Breeding, F2, First Floor, NASC Complex, PB#11312, IARI, New Delhi 110 012
Online management by indianjournals.com

insensitive (*Ppd-D1*) and height reducing(*Rht1* and *Rht2*) genes got introduced into Indian cultivars from Mexico and are now widely distributed in indigenously developed cultivars. *Ppd* genes make cultivars differently sensitive to day length [9] and therefore, wheat is characterized by a large capacity for adaptation to diverse environmental conditions [10]. Photoperiod sensitivity does affect primordial initiation of double ridge and terminal spikelet. Therefore, flowering time is a key adaptive trait ensuring that plant sets its flowers at an optimum time for pollination and seed development [11]. The *Ppd1* gene maintains the required balance between vegetative and reproductive phases including the grain growth period to optimize the source-sink relationship for promoting yield.

Generally, based on the growth habit, wheat cultivars are classified into two ecotypes, winter and spring types, depending on cold temperature requirement to initiate flowering. The vegetative growth and heading time in wheat are determined by three major factors i.e., vernalization requirement, photoperiod sensitivity and narrow sense earliness [12]. Narrow sense earliness is an environment-independent trait [13]. However, some genotypes fall in between with respect to days to flowering and are called facultative. These wheats are photosensitive and partially sensitive to vernalization. The difference between winter and spring growth habit is mainly controlled by the major loci Vrn-A1, Vrn-B1and Vrn-D1 (located in group 5 chromosomes) for vernalization [14]. The winter habit trait is generally recessive (vrn) to spring habit (Vrn). The variation noticed in flowering time is mainly due to multiple alleles at Vrn-A1 and Vrn-D1 [15]. Among all these genes Vrn-A1 is most potent in reducing the vernalization requirement. For instance, Vrn-A1 does not require vernalization treatment at all, whereas, Vrn-B1 and Vrn-D1 require vernalization for 15-30 days [16].

The winter wheats grown in temperate climate during autumn experience snow fall and chilling for vernalization, where the day length in winter season is insufficient, hence they mature in more than 10 months. Whereas in countries of South Asia, North Africa and Middle East and the lower latitudes, spring wheats are usually planted in late autumn and early winter and mature in summer. Indian sub-continent falls under later category. The potential yield of winter wheat can be enhanced by extending the growing season by delaying flowering with photoperiod sensitive genes. Production in wheat (winter or spring) is strongly influenced by flowering date [17], which is controlled by both *Vrn* and *Ppd* loci. The conditions prevailing in Indian sub-

continent, southern Europe and Australia are entirely different, where wheat crop suffers from hot summer conditions towards ripening phase causing desiccation, resulting into yield losses. Therefore late flowering wheats are not suitable but the genotypes carrying photo-insensitive genes are better adapted under these conditions.

Normally wheat in India, is sown in the month of November; if sown early in the month of September and October, it experiences relatively high temperature which may affect germination. When the crop is sown in mid December to mid January, it faces high temperature at the time of maturity. Thus, the time of flowering is crucial which is a complex biological process regulated by environmental and developmental factors, representing the phenomenon of interaction between numerous genes [18]. India being a subtropical country, the day length is one of the most important factors affecting the rate of wheat development. Plant breeders and agronomists are engaged in developing improved cultivars and the cultural techniques to allow wheat to grow under adverse conditions. The progress made towards these improvements has been encouraging [19] but further research is necessary to achieve stable production from optimum as well as harsh environments. A study comprising several experiments was conducted during the last decade to explore the possibilities, if the sowing of wheat could be preponed to early autumn season in September to accommodate two crops in succession on the same piece of land within the same time frame. The results obtained are presented here.

Material and methods

Different centers in the country engaged in wheat breeding have released short duration cultivars to suit the early and late planting of wheat so that they can fit well in the crop rotations in order to harvest maximum yield from same piece of land. The material comprised early maturing genotypes, WR544, HD2285, Halna, Raj3765, Sonalika, PBW373 and late maturing genotypes, HD2687 and C306. The parentage of all the cultivars is given in Table 1. Wheat is generally planted in the first week to 15th of November and matures in second week of April, while rainfed varieties are sown in the last week of October and matures in the last week of March. The early genotypes as mentioned above are suitable for late and very late sowing in winter season commencing on 15th December and ending the 15th January in north western and north eastern plains zones of the country. Some of the early maturing genotypes

Table1. Pedigree of the cultivars used in the study

1	WR544	Kalyansona/HD1999//HD2204/DW38
2	HD2285	HD1912/HD1952/3/HD1962/E4870/K65/6/HD2160/HD2189 Expanded form= 36896//CJ54/P4160E/3/HUAR/4/KAL Sib/5/SLsib/NP852/4/PJ Sib/P14//KT54B/3/K65/6/HD2160/7/SL Sib/NP852/4/Pjsib/P14//KT54B/3/K65/5*SKA
3	Halna	HD1982(YT54/N10B//HD845)/K816 (CNO Sib//SON64/KLRE/3/8156
4	Raj3765	HD2402/VL639 (VL421/CPAN1535) [VL421= N64/Y50E//Gaboto(Bage2018//H44/Sinvalocho/3/Bage1971.37)] [HD2402 = HD2177//CNO67/BB/HD2160/4/HD2236] [HD2177= SL SIB/NP852/4/PJ SIB/P14//KT54B/3/K65/5/KAL] [HD2236=CNO SIB/NO/3/C273/NP875/PI SIB/4/HD1981] [HD1981=YT54/N10B//HD845]
5	Sonalika	MIDA-U/K117A//2*TH/3/FN/4*TH/4/AN/5/YT54/N10B//LR/6/B4946-A4-18-1/Y53/3*Y50
6	PBW373	ND/VG/1944//KAL/BB/3/YACO 'S'/4/Vee# 5 'S'
7	HD2687	CPAN2009/HD2329 (SL SIB/NP8522/4/PJ SIB/P14//KT54B/3/K65/5/SKA/6/HD2160) [HD2160=MZ*3//YT54/N10B/3/CAL/4/TOB/CTFN/5/HD1949 (Moti)] [HD1949= YT54/N10B//NP852]
8	C306	Regent1974/CHZ//2*C591/3/P19/C281 [C591= Type9/8B; C281= C591/NP4]

CNO = Ciano; CAL = Calida; CTFN = Centrifen; BB = Blue Bird; FR = Frocor; KF = Kenya Farmer; KAL = Kalyansona; M = Mazoe; NAD = Nadadores; P = Platina; SL = Safed Lerma; SN = Sonora; TOB = Tobari66; TZPP = TezanosPintos Precoz; Y = Yaqui; YT = Yektana; 8156 = Penjamo "S"/Gabo 55

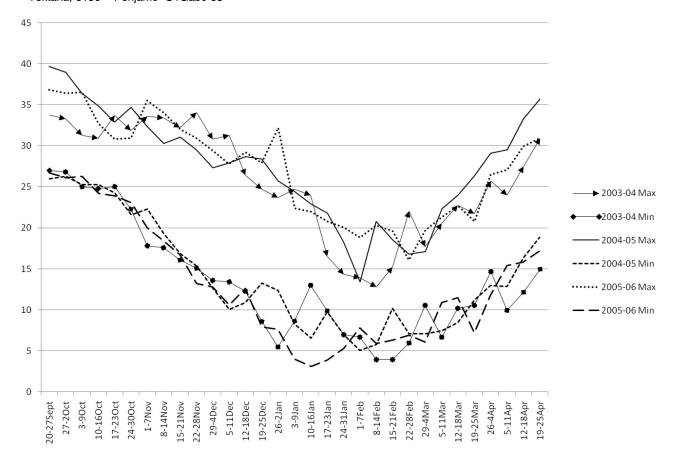


Fig. 1. Weekly average of minimum and maximum temperature during September to April in the year 2003 to 2006

were tested under Short Duration and Heat Tolerance Nursery by Directorate of Wheat Research, Karnal over the years and across the locations from 1995-96. WR544, a genotype developed at IARI, New Delhi was selected from this nursery and tested in all India Wheat Coordinated Trials under late and very late sown conditions across the locations in all wheat zones during 1998-2002. To test the relative earliness and yield, cultivars WR 544, HD2285, Halna, Raj3765, Sonalika, PBW373 and HD2687 were sown on 20th September, 15th November, 25th December and 15th of January over a period of two years (2003-04 and 2004-05). September sowing was done to know the effect of sowing date on flowering. The material was planted in RBD in four rows of 3 meters in three replications. The data were recorded on days to flowering, days to maturity, number of spikes m⁻², number of grains/spike, 1000 grain weight and yield per square meter. WR 544, HD2285, Halna, Raj3765, Sonalika, PBW373, HD2687 and C306 were also planted in two rows of two meter each on 20th September from 2005-06 to 2007-08 to know the influence of date of flowering on maturity and thousand grain weight. The early harvested crops sown in September were kept in shed till they were dried and threshed to record various characters. The minimum and maximum temperatures recorded during the crop season are shown in Fig. 1. The results of multi-location trials conducted under late sown and very late sown conditions on early maturing varieties WR544, Sonalika, HD2285, K8962, Raj3765, Halna, HD2643, HD2402, HP1744, NW1014, PBW373 by the All India Coordinated Wheat Improvement Project during 2000-2001 were also taken as reference (Table 5) for comparing the results of present study.

Results and discussion

The mean of grain yield and its attributing traits recorded in the experiment conducted during 2003-04 to 2004-05 is given in Tables 2-3 and the mean and range on three agronomical traits recorded in the experiment conducted during 2005-06 to 2007-08 is given in Table 4. All the varieties sown during 2003-04 and 2005-06 on 20th September flowered earlier compared to 15th November sowing but the flowering time was almost similar when sown on 15th of January indicating that all the cultivars are photoinsensitive. The days to flowering of all the early genotypes ranged from 44 to 56. However, the cultivar HD2687 flowered in >80 days displaying its photosensitivity (Table 3). The days to flowering in September sown crop during 2005-06 to 2007-08 ranged from 43 to 61 except in case of C306 and HD2687, which flowered in 83 and 93 days respectively (Table 4). Out of 8 genotypes studied,

WR544 demonstrated tremendous resilience with respect to adaptability under very early and very late sowing conditions. The September sown crop of WR544 and Halna matured in 87 and 89 days respectively, (Table 3) while remaining genotypes took =90 days to reach physiological maturity (earhead turning to pale yellow but the foliage of the plant remained green). WR544 recorded the highest yield (326 g m⁻²) in September sown crop, which was higher in comparison to all other genotypes followed by HD2285 and Raj3765, both giving 313 g m⁻². The higher yield of WR544 is ascribed to the production of more number of spikes m⁻² (352.5), more number of grains/spike (33.7) and comparatively higher thousand grain weight (40.5) (Table 2). The mean yield of WR544 in 25th December sown crop was 376 g m⁻², followed by PBW373 (364 g m⁻²) which was also higher than other varieties. The yield of WR544 is comparable to the results reported by the All India Wheat Improvement Project from 2000 to 2001 under late sown (364 g m⁻²) and under very late (318 g m⁻²) sown conditions (Table 5) [20]. WR544 has also shown its superiority in yield under very late sown (15th January sown crop) conditions giving 32.8 g/ha yield, which was higher than all other varieties. The cultivars C306 and HD2687 matured in 143 and 153 days during 2005-06 to 2007-08 making them unsuitable under September sowings. However, HD2687 gave significantly higher yield (517 g m⁻²) ascribed to more number of spikes m⁻² (466.2) in comparison to all the cultivars tested under 15th November sown crop. The crop of WR544 sown in September matured early than the crop sown on 15th November (normal sowing time) and on 15th January. Also the yield of normal sown crop was 27% higher than the early and very late sown crop (Table 2). This indicated that the crop sown in September can be harvested in the month of December leaving enough time for preparation and raising subsequent wheat crop on the same piece of land. It is therefore possible to cultivate autumn crop and winter crop in continuation with considerable advantage in total production per unit area. If wheat crop is sown before 20th September, it likely to suffer from late rains and thus under high temperature of >30°C the seeds may get decayed, thus affecting germination and leading to poor crop stand. By the last week of September the temperatures are more or less 30°C.

Resilience of WR544

The warmer environment of September under which wheat crop is grown hastens the flowering time and hence WR544 flowered in 44 days which was 37-39

Table 2. Yield (q/ha) and its attributing traits (mean) in cultivars planted at Delhi in four dates of sowing during 2003-04 to 2004-05

Trait	Date of sowing	Conditions	WR 544	HD 2285	Halna	Raj 3765	Sonalika	PBW 373	HD 2687	CD at 5%
Height	20 Sept.	Early	85	91	75	90	90	84	81	4.58
	15 Nov.	Normal	93	100	90	94	101	93	101	6.31
	25 Dec.	Late	91	91	85	87	97	89	89	2.49
	15 Jan.	Very Late	90	84	77	84	90	84	81	6.38
No. of spikes m ⁻²	20 Sept.	Early	352.5	347.4	339.2	350.6	321.1	351.0	309.5	13.83
	15 Nov.	Normal	395.4	379.5	361.5	380.6	352.5	375.8	466.2	6.23
	25 Dec.	Late	367.5	386.0	328.2	356.1	305.9	398.2	407.7	9.09
	15 Jan.	Very Late	341.5	344.5	321.6	341.9	321.7	34.2	<200*	12.89
No. of grains/spike	20 Sept.	Early	33.7	32.2	32.5	32.6	28.4	32.6	47.1	3.30
	15 Nov.	Normal	43.4	40.2	37.6	35.7	34.2	47.4	50.4	5.02
	25 Dec.	Late	39.7	33.1	33.2	31.3	33.9	28.4	44.7	3.41
	15 Jan.	Very Late	29.8	28.9	27.1	27.0	28.8	27.6	28.2*	3.53
TGW(g)	20 Sept.	Early	40.5	39.1	34.3	38.7	40.1	36.8	3.46	2.6
	15 Nov.	Normal	37.8	36.7	35.2	39.3	39.4	35.8	34.0	2.78
	25 Dec.	Late	37.8	35.7	32.8	36.7	33.6	33.6	31.5	2.96
	15 Jan.	Very Late	37.5	35.4	28.0	34.0	33.5	32.3	20.0*	3.4
Yield q/ha	20 Sept.	Early	32.6	31.3	29.7	31.3	27.8	28.9	29.0	1.34
	15 Nov.	Normal	44.5	43.7	41.4	41.0	38.7	43.4	51.7	2.78
	25 Dec.	Late	37.6	31.5	29.5	34.4	31.0	36.4	28.2	0.68
	15 Jan.	Very Late	32.8	30.5	27.7	30.6	26.2	31.3	#	1.70

^{* =} Insufficient population due to very poor germination and growth, TGW = Thousand grain weight; # = Crop affected by high temperature, data not considered

Table 3. Days to flowering and maturity of genotypes carrying different vernalization and photo-insensitive genes in cultivars sown at four sowing dates during 2003-04 to 2004-05

Varieties		Days to		Days to	maturit	Ту	Proposed gene(s)		
	20 Sept.	15 Nov.	25 Dec.	15 Jan. 2	20 Sept	.15 Nov.:	25 Dec	. 15 Jan.	
	Early	Normal	Late	Very late	Early	Normal	Late	Very late	
WR544	44	75	67	62	87	134	103	94	Vrn-A1, Vrn-B1, vrn-D1, Ppd-D1
HD2285	52	82	74	65	90	137	105	94	Vrn-A1, Ppd-D1
Halna	51	79	65	62	90	138	107	93	Vrn-A1, Vrn-B1, Vrn-D1, Ppd-D1
Raj3765	49	83	74	66	104	139	119	93	Vrn-A1, Vrn-B1, Vrn-D1, Ppd-D1
Sonalika	51	81	73	63	91	137	109	93	Vrn-A1, vrn-B1, Vrn-D1, Ppd-D1
PBW373	56	87	81	73	105	136	111	101	Vrn-A1, vrn-B1, Vrn-D1, Ppd-D1
HD2687	81	104	94	>75	123	146	139	>105	vrn-A1, Vrn-B1, Vrn-D1, Ppd-D1
C306*	-	-	-	-	-	-	-	-	vrn-A1, Vrn-B1, Vrn-D1, Ppd-D1

^{*}Tested during 2005-06 to 2007-08

days and 49 days earlier than HD2687 and C306 (Table 3 and 4) respectively, as both showing partial photo sensitivity. Thus WR544 can be characterized as an ultra-early flowering genotype. This cultivar does not require any vernalization treatment but flowers very early, it can therefore be concluded that it carries *Vrn-A1* gene (Table 3). Among all the VRN genes *Vrn-A1*

is most potent in reducing the vernalization requirement. For instance, *Vrn-A1* does not require vernalization treatment at all, whereas, *Vrn-B1* and *Vrn-D1* require vernalization for 15-30 days [16]. The findings are in accordance with earlier reports that *Vrn-A1* promotes early flowering. Iqbal [21] studied Pakistani spring wheat cultivars and concluded that 39 percent carry *Vrn-A1*

either alone or in combination of Vrn-B1 and Vrn-D1. Wheat cultivars with Vrn-A1 flower the earliest where as those with dominant Vrn-D1 and/or Vrn-B1 flower later under non vernalization conditions [22]. Conversely, C306 responds partially to vernalization and may carry either Vrn-B1 or Vrn-D1 or both these genes along with vrn-A1. The cultivar C306 involves Regent, a winter wheat in its pedigree presumably deriving vrn-A1 gene from it. The other varieties although flowered early (49 to 56 days) but were late than WR544. The WR544 also matured in 87 days, which is early in comparison to other late sown and early flowering varieties, HD2285, Halna, Raj3765, Sonalika and PBW373 released for late sown conditions for north western plains zone. These varieties may carry similar or a different allele for photoperiod insensitivity.

The combined average yield of WR544 sown on 20th September (early sown, autumn) and 25th December (late sown, winter) over two seasons was 70.2 q/ha where as that of Raj 3765 was 62.8 q/ha. However, under normal conditions (15th November) WR544 gave 44.5 g/ha as compared to HD2687 (51.7 q/ha), a timely sown variety. HD2687 takes an average of more than 145 days to maturity, when sown on 15th November and more than 140 days (range 141-146 days) when planted on 20th September, whereas the total number of days (mean) taken to maturity by WR544 under early and late sown conditions are only 190 days fitting well in the season for two crops (Tables 3 and 4). It is characterized with the unique photo period response providing adaptation to a broad range of environments. Kato and Yokoyama [23] concluded that early flowering conferred by an alteration of photoperiod response was important for regional adaptation by avoiding stresses associated with high temperature. The wheat crop in Indian subcontinent suffers from early as well as terminal heat stress considerably. WR544 has shown a greater plasticity under early and late heat stress as compared to other early flowering genotypes, indicating that it possesses genes for thermo-tolerance. Heat stress is

experienced at both ends of cropping season. At high temperature plant undergoes excessive respiration over photosynthesis and cause injury [24-25]. High temperature during early growth stages in a photo sensitive genotype HD2687 adversely affects the appearance of first node and reduction in tillers/plant, lower biomass thereby resulting in reduced sink capacity as the number of grains/spike are reduced. Ruwali and Bhawsar, [26] had also reported reduction in number of tillers/plant, grain number/plant and 1000 grain weight in their studies.

It is suggested, therefore, that two crops of WR544 can easily be taken and the production can substantially be increased, if the sowing of some of the early flowering genotypes like WR544 is advanced to mid or last week of September. Such a practice can be followed only when the preceding crop is of early maturing types viz., maize (baby corn and fodder), jowar (fodder) pearlmillet (fodder), vegetable cowpea, groundnut, upland paddy and summer mungbean. The selection of such genotypes is based on early flowering with shorter vegetative phase and proportionately larger grain growth period producing larger sink size with high adaptability to adverse temperatures, initial longer photoperiod and moderate to high humidity. Among all the varieties tested, WR544 gave higher yield (Table 2) indicating its suitability for very early, early (timely sown) and late sown conditions. The vegetative growth of September sown crop of HD2687 (vrn-A1, Vrn1-B1 and Vrn-D1) prolonged and it flowered in 104 days making it unsuitable for early sowing. The delayed flowering may be due to its longer vegetative growth period ascribed to Vrn genes. C306 carry vrn-A1, Vrn-B1 and Vrn-D1 genes making it partially photosensitive and vernalization responsive, affecting the time of flowering and maturity (Dr. Neelu Jain, Personal communication). Therefore, both these cultivars are totally unsuitable for very early and very late sown conditions. Shinoda and Sasakuma [13] reported that two near isogenic lines carrying Vrn-A1 for the spring type and vrn-A1 for the

Table 4. Mean and range (in parenthesis) for different agronomical traits in 20th September sown crop over three years (2005-06 to 2007-08)

Traits	WR544	HD2285	Halna	Raj3765	Sonalika	PBW373	HD2687	C306
Days to heading	43	56	48	53	46	61	83	93
	(39-45)*	(51-67)	(45-55)	50-60)	(45-49)	(58-70)	(79-91)	(89-101)
Days to maturity	86	92	90	89	91	105	143	153
	(83 - 88)	(87 - 95)	(86-92)	(87 - 93)	(89-93)	(101 - 120)	(141-146)	(151-163)
1000 grain weight (g)	42	40	39	38	44	42	34	39
	(38-46)	(38-46)	(37 - 42)	(36-44)	(41-47)	(38-44)	(33-36)	(37-43)

Table 5. Adaptability to changes under irrigated, very late sown agronomic conditions during 2000-2001 (Dates of sowing x variety)

Trait	Conditions	WR544	HD2643	HD2285	Raj3765	HP1744	NW1014	PBW373
Yield q/ha	Normal	43.9	40.7	43.2	40.0	40.9	38.7	47.4
	Late	36.4	37.2	37.5	35.4	35.5	36.0	32.4
	Very late	31.8	30.9	31.4	30.0	25.2	26.2	33.3
	Mean	37.4	36.3	37.4	35.1	33.9	33.4	37.7
Ear heads/sq.m	Normal	385.3	366.2	369.5	390.6	370.3	352.5	375.8
	Late	360.5	407.7	436.0	406.1	372.0	405.9	418.2
	Very late	361.5	357.7	354.5	361.9	293.7	341.7	388.2
	Mean	369.1	376.6	393.1	388.2	358.8	373.4	391.1
No. of grains/earhead	Normal	35.4	28.4	38.2	32.7	35.4	34.2	37.4
	Late	36.7	24.7	31.1	30.3	29.3	33.9	27.4
	Very late	29.8	26.9	28.7	26.0	29.2	28.8	27.1
	Mean	31.5	26.4	32.8	29.7	32.6	32.6	30.6
1000 grain weight (g)	Normal	36.8	44.0	36.7	39.3	36.7	39.4	36.8
	Late	37.8	39.5	35.7	36.7	34.6	33.6	32.6
	Very late	37.5	37.2	35.4	34.0	33.2	33.5	31.9
	Mean	37.0	42.8	35.9	36.7	35.3	33.9	34.0

Source: Progress Report-Crop Improvement, AICWBIP, Directorate of Wheat Research, Karnal

winter type critically differed in their heading time. Worland and Law [27] studied the effect of *Ppd1* in comparison to *ppd1* and found that the presence of this gene accelerated flowering by more than 7 days in a substitution line in the background of Cappelle-Desprez. They also observed pleiotropic effect of *Ppd1* on reduction in plant height, spikelet number, grain size and growing period leading to reduction in overall yield. High temperature effects on grain development in the cultivars carrying *ppd1* were noticed by Worland et al. [28-29], but the cultivars having *Ppd1*, which is photoinsensitive allele, showed advantage in yield under similar conditions. They also suggested that the two photoperiod insensitive varieties Ciano67 and Mara might carry different alleles at the *Ppd1* locus.

Varieties involved in the present study are semidwarf carrying either *Rht1* or *Rht2* derived from CIMMYT (Mexico) germplasm in their pedigree (Table 1). WR544 is an ultra-early flowering genotype involving Mexican genotype Sonora64 in its pedigree (Fig. 2). Maystrenko [30] identified *Vrn-A1* and *Ppd-D1* alleles in Sharbati Sonora, a mutant of Sonora 64 (photo-insensitive). Based on pedigree, it can be conclusively said that both the alleles *Vrn-A1* and *Ppd-D1* have been introduced in Indian genotype WR544 from Mexican germplasm. The genes *Ppd1* and *Ppd2* [26] promoting insensitivity to photoperiod are present in spring cultivars, however *Ppd2* is weaker gene for photoperiod insensitivity. Arbuzova *et al.* [31] reported that non-sensitivity to daylength and ultra ripening in Sharbati Sonora is determined by three dominant genes Ppd1, Ppd2 and Ppd3 and typical for samples from south latitude of the earth with short day light. In the conditions of temperate climate the cultivars usually carry 1-2 Ppd genes which make them differently sensitive to day-length [9]. The days to heading of the varieties under study, except C306 and HD2687 ranged from 44 to 56 and 62 to 73 days in September sown and January sown crops, respectively. A perusal of Table 1 and 3 reveals that the early flowering genotypes viz., Raj3765, Halna, Sonalika, HD2285 and PBW373 involve in their parentage the Mexican germplasm and therefore, may carry different alleles of Ppd and Vrn genes. Halna and Raj3765 involve Ciano and Sonora 64, both carrying Ppd-D1 gene. Kowalczyk et al. [32] found that lines carrying Ppd-D1 flowered earlier (3-5 days) than the lines with ppd-D1 and the substitution line of Mara 2D flowered earlier than the line with Ciano 2D. However, these results were in contrast with the findings of Worland et al [28] who established that Ppd-D1 originating from Ciano acceletrated heading date to a greater extent than the allele from Mara. It was also proposed that the Ciano67 allele might have advantageous pleiotropic effect; however, these differences may also be due to linked genes associated with complete chromosome substitution. In the present study WR544 flowered earlier than Halna and Raj3765, which are likely to carry Ppd-D1 from Ciano. Another early flowering cultivar, Sonalika carries Thatcher (VrnA1a) in its parentage; the allele controlling heading time is presumably inherited from Thatcher. The presence of Ppd-D1 allele in Sonalika can be traced to Lerma Rojo (Table 1). The Ppd-D1a allele is generally considered the most potent for photoinsensitivity [33]. The WR544 sown on 25th December produced a higher yield of 37.6 g/ha compared to all the late sown varieties, and the control HD2687 which produced only 28.2q/ ha. Under very late sown conditions, only PBW373 gave higher yield of 33.8 g/ha. WR544 produced a combined yield of 70.2q/ha, followed by Raj3765 (65.7 q/ha) in September and December sown crops. Other varieties comparatively gave lesser combined grain yield. Table 2 indicate that in early sowing, PBW373 produced an average 34.6 grains/spike, which is higher than WR544 (33.7), but the 1000 grain weight of WR544 was much higher (40.5) than PBW373 (36.8). The genotypes carrying Ppd-D1 gene were characterized by higher kernel weight/spike compared to the genotype carrying ppd-D1 allele [29] .Utilization of genes controlling time of flowering may help the breeders to be able to select genotypes which can adjust the life cycle to suit differing

environmental conditions. The recombinant genotypes derived from the crosses between photoperiod sensitive spring and photoperiod insensitive winter type wheat behaved differently under autumn and spring sowing. Advantage in both heading dates and yield per m⁻² were observed in genotypes with *Ppd-D1a/Vrn-A*, *vrn-D1* and *Ppd-D1b/Vrn-A1*, *vrn-D1* allele combination [34].

The number of spikelets/spike in WR544 was also higher. Since all the tested varieties flowered early and carry *Ppd-D1* allele, but the WR544 carry additional factors enhancing the number of spikelets/spike, number of grains/spike and 1000 grain weight leading to higher yield under very early (20th September) and late (25th December) sowings. The variety WR544 suitably released in 2003 [35] for very late sown conditions fits well in crop rotations such as, Potato-Wheat, Sugarcane- wheat, *Brassica* (early Toria)-wheat.

Yield gains in wheat are most likely to be achieved by simultaneously increasing both source as well as sink strength [36]. The reproductive stages of development from initiation of floral primordia to anthesis

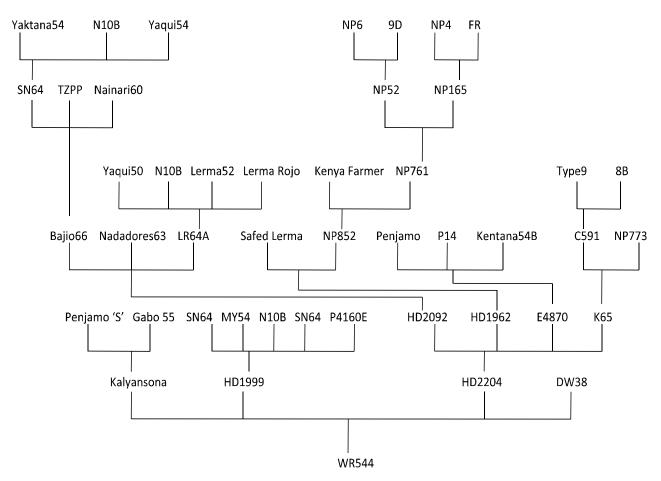


Fig. 2. Pedigree of WR544

are pivotal in determining yield. During this period, grain number per spike is determined. The duration of spike growth relative to other phenological stages is variable and the genetic basis for this variation is associated with sensitivities to photoperiod and vernalization. The capacity of WR544 being single gene dwarf genotype with high tillering facilitate competition for physical space as well as increasing the potential for uptake of nutrients and water. It showed tolerance to heat stress at sowing in September as well as at the time of maturity in April. Efficient and cost effective evaluation is necessary to identify such genotypes. There were significant differences in the number of days to heading in September and January sowings. The lines with Ppd-D1 gave significantly less spikelets/spike than the ppd-D1 but characterized with higher kernel weight/spike [32]. The reduced grain size in the genotypes having ppd-D1 allele is presumably a consequence [28-29] of the effect of high temperature on the grain development, which results in yield advantage for plants with the photoperiod insensitive alleles of *Ppd-D1*. Foulkas et al. [37] concluded that the effect of Ppd-D1 on yield potential and late season drought resistance may offer scope for breeding winter wheat cultivars with more efficient production of grain dry matter per unit area with improved harvest index. Most of the varieties recommended for late sown conditions, including the varieties considered for the present study, have better grain filling and are likely to possess late heat tolerance and carry Ppd-D1 alleles. The technology developed could be extended to non-traditional areas of wheat cultivation, where short winter conditions prevail.

Acknowledgement

The authors are grateful to Dr. (Ms.) Neelu Jain, Division of Genetics, IARI, New Delhi for confirming the genotype with respect to vernalization and photoperiod insensitive genes in varieties studied.

References

- Briggle L. W. 1980. Origin and botany of wheat. *In*: Wheat *documenta ciba-geigy* E. Hafliger (ed.), p. 6-13. Vasle, Switzerland.
- Curtis B. C. 2002. Wheat in the world. *In*: Bread Wheat-Improvement and Production, B. C. Curtis, S. Rajaram and H. Gomez Macpherson (eds.), FAO of the United Nations, Rome Pp. 103-116.
- 3. **Law C. N., Sutka J. and Worland A. J.** 1978. A genetic study of day length response in wheat. Heredity, **41**: 185-191.

- Snape J. W., Butterworth K., Whitechurch E. and Worland A. J. 2001. Waiting for fine times: genetics of flowering time in wheat. Euphytica, 119: 185-190.
- Miura H. and Worland A. J. 1994. Genetic control of vernalization and day length responses and earliness per se by the homoeologous group 3 chromosomes in wheat. Plant Breed., 113: 160-169.
- Halloran G. M. and Boydell C. W. 1967. Wheat chromosomes with genes for photoperiodic response. Canad. J. Genet. Cytol., 9: 394-398.
- 7. **Faridi N. I.** 1988. Genetical studies of grain protein and developmental characters in wheat. PhD. thesis, University of Cambridge.
- Law C. N., Suarez E. J., Miller T. E. and Worland A. J. 1998. The influence of the group 1 chromosomes of wheat on ear-emergence times and their involvement with vernalisation and day length. Heredity, 80: 83-91.
- 9. **Aliev A. B. and Maystrenko O. I.** 1986. A precise determination of number of genes involved in photoperiodic response in spring wheats with different sensitivity to neutral short daylight. Cereal Res. Commun., **14**: 129-132.
- Worland A. J., Appendino M. L. and Sayers E. J. 1994. The distribution of genes influencing ecoclimatic adaptability in European winter wheat varieties. Euphytica, 80: 219-228.
- Cockeram J., Jones H. Leigh F. J., Sullivan D. O., Powell W., Lauri D. A. and Greenland A. J. 2007. Control of flowering time in temperate cereals: genes, domestication and sustainable productivity. J. Exp. Bot., 58: 1234-1244.
- 12. Law C. N. and Worland A. J. 1997. Genetic Analysis of Some Flowering Time and Adaptive Traits in Wheat. New Phytologist, 137: pp. 19-28.
- Shinoda C. and Sasakuma T. 2002. Genes responding to vernalization in hexaploid wheat. Theor. Appl. Genet., 104: 1003-1010.
- McIntosh R. A., Yamazaki Y., Dubcovskyi J., Rogers J., Morris C., Somers D. J., Appels R. and Devos K. M. 2008. Catalogue of gene symbols for wheat. Proc. 11th Int. Wheat Genet. Symp. R. Appels, R. Eastwood, E. Lagudah, P. Langridge, M. Mackey, L. McIntyre and P. Sharp (eds.). Sydney University Press, Sydney, 143-150.
- 15. **Pugsley A.T.** 1972. Additional genes inhibiting winter habit in wheat. Euphytica, **21**: 547-552.
- Kato K. 1988. Method of evaluation of chilling requirement and narrow sense earliness of wheat cultivars. Japan. J. Breed., 38: 172-186.
- White J. W., Herndl M., Hunt L. A., Payne T. S. and Hoogenboom G. 2008 Simulation -based analysis of effects of *Vrn* and *Ppd* loci on flowering in wheat. Crop Sci., 48: 678-687.

- Dubcovsky J., Loukoianov A. and Bonafide M. 2007. Regulation of flowering time in wheat. *In*: Wheat production in stress environments. pp. 659-665.
- Tomar S. M. S. 2005. A century of wheat research in India - The way ahead. Paper presented at celebrations and scientific centenary convention, March 16-19, 2005. IARI, New Delhi.
- 20. **Anonymous.** 2002. Annual progress Report- Crop Improvement. All India Coordinated Wheat and barley Improvement project. Directorate of Wheat Research, Karnal.
- 21. **Iqbal M., Shahzad A. and Ahmed I.** 2011. Allelic variation at the *Vrn-A1,Vrn-B1,Vrn-D1, Vrn-B3* and *Ppd-D1a* loci of Pakistani wheat cultivars. Electonic J. Biotech., D.O.I:10.2225/vol14-issue1-fulltext-6.
- Goncharov N. P. 2004. Response to vernalization in wheat: its quantitative and qualitative nature. Cereal Res. Commun., 32: 323-330.
- Kato K. and Yokoyama H. 1992. Geographical variation in heading characters among wheat landraces, Triticum aestivum L, and its implication for their adaptability. Theor. Appl. Genet., 84: 259-265.
- Reynolds M. P., Trethowan R. M., Ginkel Mv. and Rajaram S. 2001. *In*: M.P Reynolds, J. I. Qrtiz-Monasterio and A. MacNab (eds.), Application of physiology in wheat breeding. CIMMYT, 2-10.
- 25. **Nagarajan S. and Rane J.** 2002. Physiological traits associated with yield performance of spring wheat (*Triticum aestivum* L.) under late sown conditions. Indian J. agric. Sci., **72**: 135-40.
- Ruwali K. N. and Bhawsar R. C. 1998. Effect of high temperature on grain development of wheat under late sown irrigated conditions. *In:* Wheat Research Needs Beyond 2000 AD. Proc Int. Conf., pp. 68-69. Karnal, India.
- Worland A. J. and Law C. N. 1986. Genetic analysis of chromosome 2D of wheat. Z. Pflanzenzuchtg, 96: 331-345.
- 28. **Worland A. J.** 1996. The influence of flowering time genes on environmental adaptability in Europeon wheats. Euphytica, **89**: 49-57.
- Worland A. J., Borner A., Korzun V., Li W. M., Petrovíc S. and Sayers E. J. 1998. The influence of photoperiod genes on the adaptability of European winter Wheats. Euphytica, 100: 385-394.

- Maistrenko O. I. and Aliev E. B. 1985. Chromosomal location of genes responsible for photoperiodic reactiuon in a non-sensitive spring variety of common wheat Sharbati Sonora. Cereal Res. Commun., 13: 363-369.
- 31. Arbuzova V. S., Efremova T. T., Laikova O. I., Maystrenko O. I. and Pshenichnikova T. A. 2003. The development, maintenance and use of cytogenetic collection of wheat and its derivative forms as a part of biological diversity of cereals. Proc. 12th, EWAC Conference, 1-6 July, 2002, Johnn Innes Centre, Norwich, U.K. EWAC Newsletter, 1-6.
- Kowalczyk K., Worland A. J. and Miazga D. 2003. Pleiotropic effect of Ppd-D1 on yield and its components in recombimnant lines of common wheat. Proc. 12th, EWAC Conference, 1-6 July, 2002, Johnn Innes Centre, Norwich, U.K. EWAC Newsletter, 1-6.
- Blake N. K., Lanning S. P., Martin J. M., Doyle M., Sherman J. D., Naruoka Y. and Talbert L. E. 2009. Effect of vernalization for major growth habit genes on maturity and yield in five spring wheat populations. Crop Sci., 49: 1211-1220.
- 34. Kolev S., Ganeva G., Christov N., Belchev I., Kostov K., Tsenov N., Rachovska G., Landgeva S., Ivanov I., Abu-Mhadi N. and Todorovska E. 2010. Allele variation in loci for adaptive response and plant height and its effect on grain yield in wheat. Biotechnol & Biotechnol Eq., 24: 1807-1813.
- 35. **Tomar S. M. S., Singh B. and Vinod.** 2004. Pusa Gold (WR544) a new variety for very late sown condition. Intensive Agriculture, **42**: 18-19.
- 36. Slafer G. A., Calderini D. F. and Miralles D. J. 1996. Yield components and compensation in wheat: Opportunities for further increasing yield potential. *In*: Increasing yield potential in wheat - Breaking the barriers. M. P. Raynolds, S. Rajaram and McNab (eds.), Workshop Proceedings. Cd. Obregon, Mexico, 28-30 March 1996. Mexico DF CIMMYT.
- Foulkes M. J., Sylvester-Bradley R., Worland A. J. and Snape J. W. 2004. Effects of a photoperiod response gene Ppd-D1 on yield potential and drought resistance in UK winter wheat. Euphytica, 135: 63-73.