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Photoperiod and vernalisation response of Mediterranean wheats, and implications for adaptation

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Summary

Hexaploid wheat has the largest cultivated area among crop plants due to its adaptability to different agroclimatic regions. A large part of this adaptability depends upon the variation in vernalisation and photoperiod requirements. A better understanding of the genetic control of flowering in wheat, as expressed by vernalisation requirements and photoperiod response, will guide breeders in targeting crosses of different types and will also improve our understanding of regional adaptation requirements. Characterisation of large numbers of breeding lines for photoperiod and vernalisation response in wheat is needed to assign the lines to geographic areas of most probable adaptation. Simple screening methods to quantify the effects of these two factors and their interaction are needed to assist breeding progress. Twenty wheat lines were evaluated for response to photoperiod and vernalisation under two controlled environments and under high ambient air temperatures in field conditions. Vernalised and non vernalised seedlings were transplanted into pots and placed in three photoperiod (8, 12 and 16 h light) cabinets, in the greenhouse or in growth chambers. Days to anthesis decreased with increasing length of photoperiod. Vernalised plants flowered earlier than non vernalised plants. There was a significant correlation between days to anthesis in the greenhouse and the growth chamber ($r = 0.88$, $P < 0.001$). Length of basal vegetative period, effects of vernalisation, and photoperiod from the two screening techniques were positively correlated with each other. Growth habit score, vernalisation requirement and heading date in the field were highly correlated with the main effect of vernalisation in the two controlled environments. The results indicated that selection for vernalisation response in a large number of genotypes can be achieved under high ambient air temperatures in the field. The selected material can subsequently be screened for photoperiod response under greenhouse conditions. Using these techniques, 49 local and improved cultivars from the Mediterranean region in west Asia and north Africa (WANA), showing differences in response to photoperiod, vernalisation, and earliness independent of vernalisation and photoperiod, affecting time to anthesis, were identified. Most old local cultivars were sensitive to both photoperiod and vernalisation. All the improved genotypes were insensitive to photoperiod. Responses to vernalisation were generally small under short photoperiods, but were more pronounced in long photoperiod, particularly in winter and facultative types from northern latitudes. These results should help to explain the adaptability of cultivars based on photoperiod and vernalisation requirements and their interaction.

Introduction

Wheat adaptation is the result of a complex interaction between the genetic background of varieties/populations and how these entities interact with environmental factors. The main objective of wheat breeders is to match genotypes to environments to reach the maximum yield stability across locations and years. This adaptation is achieved by complex combinations of morphophysiological traits. These traits, while quantitative in response to environment, are largely controlled by a few genes having large effects. These genetic characteristics of adaptation permit the manipulation of genes to meet specific environmental situations.

The *vrn* and *ppd* genes controlling flowering response provide an example of genes that can be manipulated to improve adaptation. Vernalisation requirement, photoperiod response, and temperature are the main determining factors in crop earliness. The processes determining the timing of flowering and development (i.e., vernalisation and photoperiod responses, and those influenced by growth temperature) can therefore be considered as highly significant to wheat's adaptation and hence, yield (Halloran, 1975; Pirasteh & Welsh, 1980).

An understanding of adaptation allows a better targeting of germplasm to specific environments, reduces the risk of crop failure, helps in the development of more realistic crop models, and allows better targeting of inputs to ensure maximum production (Appleton & Haggar, 1985). Characterisation of large numbers of breeding lines for vernalisation and photoperiod response in wheat is also needed to enhance adaptation. Off-season field plantings can be used to deduce genotype response to these two factors (Qualset & Puri, 1975). In this study we have examined a representative set of cultivars and breeding lines under controlled environments and compared the results with field responses. We show that with appropriate date of planting, genotypes can be efficiently classified simultaneously for vernalisation requirement and photoperiod response.

Materials and methods

Twenty wheat genotypes, divided into two groups based on their selection history under high ambient air temperatures, were studied. Three wheat cultivars were used as controls: Pitic 62, sensitive to vernalisation and insensitive to photoperiod; Stork, insensitive to both vernalisation and photoperiod; and Kabir 1, sensitive to both vernalisation and photoperiod.

The experiments were conducted during spring (February-June, 1992) at the International Centre for Agricultural Research in the Dry Areas (ICARDA), Tel Hadya, Syria, in a greenhouse maintained at $22/16 \pm 2$ °C day/night with a 12 h photoperiod. The experimental design was a modified split-plot design within each photoperiod. The main plots were the two vernalisation treatments and the subplots were the 23 genotypes. There were five replicates. Vernalised and non vernalised treatments of each genotype were placed in three separate growth cabinets inside a greenhouse with photoperiods of 8, 12, and 16 h. Each cabinet was covered by a thick, light-proof piece of cloth, with a thermo-hygrograph inside to monitor the temperature and relative humidity. An automatic ventilation fan was installed in a U-shaped tunnel in each cabinet to keep the inside temperature constant. Photoperiods were extended using fluorescent lamps with a light intensity of 400 μmole m^{-2} s^{-1} at the canopy level.

Vernalised seedlings were obtained by maintaining germinated seeds at 1-2 °C for 42 days. Non vernalised seeds were germinated at 20 °C, five days prior to transplanting. A total of 10 vernalised and non vernalised seedlings of each cultivar were transplanted into separate 2.5 L pots. Pots were moved at three day intervals within the photoperiod treatment to ensure a uniform environment. After two weeks, plants were thinned to five uniform plants per pot. The pots were irrigated regularly to field capacity, to maintain an adequate moisture supply. At weekly intervals, all tillers were removed, leaving only the main stem.

A similar experiment was conducted simultaneously using three separate growth chambers (Conviron Model E15, Manitoba, Canada), with a light intensity of 400 μmole m^{-2} s^{-1} at the canopy level

from a source of fluorescent and incandescent lamps. There were three replicates. Temperatures in the growth chamber were 20/14 °C day/night as described by Cao & Moss (1991).

Time to anthesis was recorded for the main stem in both experiments. The data were analysed by analyses of variance. Genotypes were characterised for their response to photoperiod and vernalisation according to Midmore (1980), and Midmore et al. (1982). The genotypes were characterised as sensitive to day length if anthesis was delayed in the vernalised short-day (12 h) plants (VS) by 16 or more days, compared to the vernalised long-day (16 h) plants (VL). Genotypes were characterised as sensitive to vernalisation if anthesis was delayed by seven or more days under long photoperiods (16 h) in non-vernalised plants (OL) compared to vernalised plants (VL). The following effects (days) were calculated: main effect of vernalisation (AV) = OL-VL; main effect of photoperiod (AP) = VS-VL; casal vegetative period (BVP) = days to anthesis in VL.

The 23 genotypes were evaluated under heat-stressed field conditions at Tel Hadya, Syria, (36°10′N, 36°56′E), during July-October, 1992. There was no rainfall during the crop season and the crop was irrigated weekly to field capacity by overhead sprinklers. Maximum and minimum air temperatures during the crop season are given in Figure 1. The experimental design was a randomised block design with three replicates. Each plot consisted of two rows, 2.5 m long and 20 cm apart.

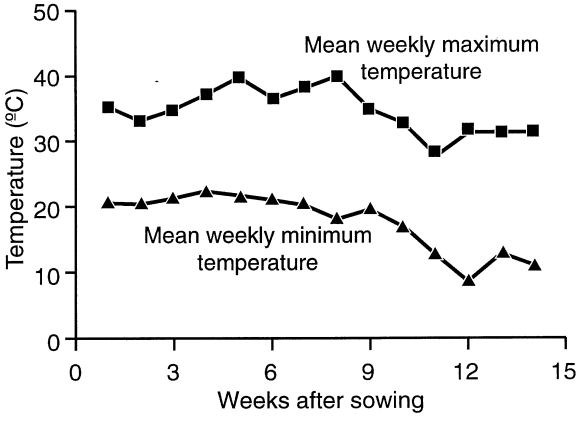

Figure 1. Mean weekly maximum and minimum air temperatures during the cropping season at Tel Hadya, Syria, 14 July, 1992.

Using a 1-9 scale, data were recorded for growth habit 20 days after seedling emergence (1 = erect, 9 = prostrate) and for vernalisation requirement (1 = low, all tillers headed; 9 = high, all plants remain vegetative and fail to reach the heading stage during the 90-day experimental period). Time to heading was recorded when 50% of plants in the plot reached ear emergence. Data were subjected to analyses of variance.

Using the above described techniques, 30 improved bread wheat cultivars (I), and 19 old cultivars (L) collected from the major wheat-growing areas of WANA (Figure 2), were characterised for their response to photoperiod and vernalisation. Five checks, characterised by Midmore et al. (1982) for their response to these two factors, were included in the 49 cultivars.

Results and discussion

In response to the various photoperiod and vernalisation treatments, there were large differences in days to anthesis (Table 1) in field, greenhouse, and growth chamber experiments. Days to anthesis decreased significantly ($P < 0.05$) with increasing light duration. Vernalised plants flowered earlier than non vernalised plants. Mean number of days to anthesis was lower in the greenhouse than in the growth chamber. The results from both controlled environments (greenhouse and growth chamber) confirmed the sensitivity of wheat development to photoperiod and vernalisation. Increasing duration of photoperiod or vernalisation resulted in earlier

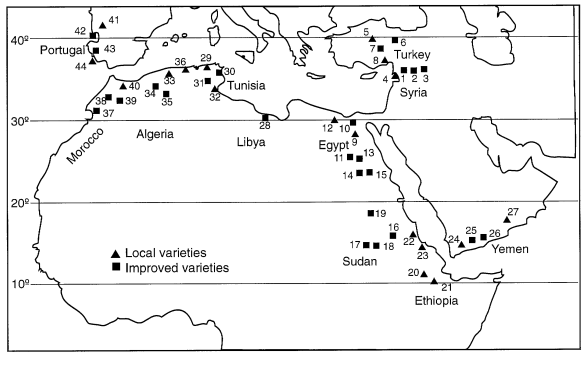

Figure 2. Source of local and improved wheat cultivars from the Mediterranean region.

Table 1. Main effect and interaction of photoperiod and vernalization for days to anthesis (mean of 23 genotypes), under green house and growth chamber conditions

Photoperiod	Days to anthesis from transplanting					
	Green house			Growth chamber		
	Vernalized	Non-vernalized	Mean	Vernalized	Non-vernalized	Mean
8	68.6	79.2	73.9	95.5	109.4	102.4
12	51.2	59.6	55.4	64.8	77.8	71.3
16	47.5	53.2	50.4	53.3	65.2	59.2
Mean	55.8	64.0	59.6	71.2	84.1	77.6
CV (%)			4.8			3.3
LSD (V)			0.5			0.3
LSD (P at same V)			0.8			0.7
LSD (V at same P)			0.9			0.5

flowering. Earlier flowering in the greenhouse could be due to the effect of light intensity and quality, higher temperatures, and lower competition among the plants. However, the responses of genotypes to photoperiod and vernalisation were similar in both experiments ($r = 0.88$, $P < 0.001$, data not presented).

Genetic differences in basal vegetative period (BVP), independent of sensitivity to photoperiod and vernalisation, have been suggested as a basis for developing varieties that are early or late irrespective of the prevailing day length and temperature conditions (Hunt, 1979; Ford et al., 1981; Masle et al., 1989; Penrose et al., 1991). Table 2 presents the means for basal BVP, the main effects of vernalisation, and the main effect of photoperiod for the 20 wheat genotypes and controls under the two controlled environments. The mean BVP of the selected group was earlier than that of the unselected group, suggesting that selection under high ambient temperatures in the field results in an advance in intrinsic earliness. Despite their responses to day length, the lines in both groups were classified as

Table 2. Mean days to anthesis in 16 h daylength with vernalization – basal vegetative period (BVP), 16 h daylength without vernalization (OL) and in 8 h daylength with vernalization (VS). Main effect of photoperiod (△P), and main effect of vernalization (△V) for the 20 wheat genotypes and checks (G) under green house and growth chamber

Genotype	Greenhouse					Growth chamber				
	BVP	OL	VS	△P	△V	BVP	OL	VS	△P	△V
Unselected (1–10)										
Mean	49.20	61.60	51.70	2.60	12.20	55.50	66.60	66.10	10.60	13.90
Selected (11–20)										
Mean	45.70	46.50	49.10	3.40	0.80	52.30	57.20	64.00	11.60	5.20
Checks										
Pitic 62	44.00	75.00	47.00	3.00 (–)	31.00 (+)	46.00	81.00	51.00	5.00 (–)	35.00 (+)
Kabir 1	52.40	85.60	77.20	24.80 (+)	33.20 (+)	52.40	93.80	81.80	29.40 (+)	41.40 (+)
Stork	46.00	47.60	43.70	–2.70 (–)	1.60 (–)	49.20	54.60	59.20	10.00 (–)	5.40 (–)
CV (%)	3.60	6.00	3.70	3.60	4.30	4.00				
LSD	2.17	4.05	2.35	2.43	3.45	3.28				

+ = senstive, – = insensitive.

Table 3. Correlation coefficents between basal vegetative period (BVP), main effects of vernalization (△V), and main effect of photoperiod (△P) in the green house and growth chamber with agronomic traits under heat-stressed field conditions (n=23)

	Green house			Growth chamber			Field		
	BVP	△V	△P	BVP	△V	△P	GH	VR	DHE
Green house									
BVP	–	0.15	–0.12	0.70***	0.13	0.16	0.19	0.33	0.40
△V			0.41*	–0.09	0.92***	0.28	0.75***	0.87***	0.91***
△P				0.00	0.43*	0.71***	0.16	0.17	–0.29
Growth chamber									
BVP					–0.27	0.06	0.00	0.07	0.26
△V						0.41*	0.65***	0.73***	0.74***
△P							0.08	0.17	–0.07
Field									
GH								0.87***	0.84***
VR									0.95***

GH = Growth habit; VR = Vernalization requirement; DHE = Days to heading.
*** $P < 0.001$.
** $P < 0.01$.
* $P < 0.05$.

insensitive to photoperiod, based on the classification system of Midmore et al. (1982). In contrast, there were clear differences between the lines in the unselected and selected groups in their response to vernalisation. These findings have implications for breeders interested in the targeting of germplasm to specific environments. Vernalisation sensitive genotypes, such as those in the unselected group, will show a marked delay in flowering in certain tropical or warm environments.

The results from the two controlled environments were compared with the results from the field (Table 3). The correlation coefficients between the main effect of vernalisation (0.92**), main effect of photoperiod (0.71**), and BVP (0.70**) in the two controlled environments were positive and significant. This suggests that the two controlled environments gave similar results when classifying genotype responses to photoperiod and vernalisation. Growth habit, vernalisation response, and days to heading in the field were positively correlated with each other and were also correlated with the main effect of vernalisation in the two controlled environments (Table 3). As the vernalisation requirements (<7 °C) were not met in the field experiment (Figure 1), the vernalisation-sensitive genotypes remained grassy and failed to reach heading. Prostrate growth when the vernalisation requirement is not met in the vernalisation-sensitive genotypes. Thus field evaluation under hot ambient air temperatures was effective in detecting the vernalisation sensitivity of the lines. These results are in agreement with the findings of Ortiz Ferrara et al. (1994) where the same parameters were used as selection criteria for heat-stressed environments.

Table 4. Long-term (1990-1995) mean maximum and minimum temperatures (°C), and day length in four different selection environments in Syria and Sudan

Environment	Planting date	Day length (h)	Temperature	
			Max.	Min.
TH-summer	15/06	15.5	33.9	17.1
TH-late	1/04	14.0	24.8	8.8
TH-normal	15/11	11.1	18.8	6.5
Wad Medani (Sudan)	25/10	12.2	37.3	19.7

TH = Tel Hadya, Syria.

Table 4 shows four selection environments used by the CIMMYT/ICARDA breeding program. These environments are very different and variable in terms of temperature and day length. By shifting segregating populations and selecting germplasm

Table 5. Days to anthesis of local and improved wheat varieties adapted in various countries of West Asia and North Africa under vernalized (V) and non-vernalized (O) treatment under long (L) photoperiod (16 h) and short (S) photoperiod (10 h), and the main effect of vernalization (△V), main effect of photoperiod (△P) and their interaction V × Æ

No. Cultivar	Type	Country grown	VL(BVP)	OL	VS	OS	△V	△P	V × P
Insensitive to V and P									
Anza	I	Check	50	49	63	67	–1(–)	13(–)	5
Jupateco 73	I	Check	55	61	64	77	6(–)	9(–)	7
Siete Cerros 66	I	Check	49	51	61	67	2(–	12(–)	4
Sonora 64	I	Check	55	52	63	62	–3	8(–)	2
Sakha 69	I	Egypt	48	46	60	66	–2(–)	12(–)	8
Sohag 2	I	Egypt	50	46	47	54	–4(–)	7(–)	1
Jouda	I	Morocco	46	50	57	66	4(–)	11(–)	5
Bohoth 111	I	Libya	45	49	55	57	4(–)	10(–)	–2
Merchouch	I	Morocco	47	49	59	59	2(–)	12(–)	–2
Saada	I	Morocco	50	46	56	57	–4(–)	6(–)	5
Cham 6	I	Syria	45	50	59	69	5(–)	14(–)	5
Mexipak 65	I	Syria	50	55	59	71	5(–)	9(–)	7
Tanit 80	I	Tunisia	51	54	58	64	3(–)	7(–)	3
Giza 160	I	Egypt	43	48	54	78	5(–)	11(–)	19
Sohag 3	I	Egypt	54	56	61	80	2(–)	7(–)	17
L-22	L	Morocco	49	52	58	71	3(–)	9(–)	10
Tejo	I	Portugal	54	53	64	78	–1(–)	10(–)	15
Condor	I	Sudan	46	50	57	71	4(–)	11(–)	10
Debeira	I	Sudan	55	50	67	80	–5–)	12(–)	18
El-Nilein	I	Sudan	47	50	57	77	3(–)	10(–)	17
Sonalika	I	Yemen	45	51	49	67	6(–)	4(–)	12
Sensitive to V and insensitive to P									
Zidane 89	I	Algeria	56	76	70	96	20(+)	6	
Zidi Okba	I	Algeria	47	58	59	71	11(+)	12(–)	1
Pitic 62	I	Check	52	73	62	89	21(+)	10(–)	6
Giza 164	I	Egypt	54	71	69	91	17(+)	15(–)	5
Centauro	I	Portugal	54	NF	62	NF	>50(+)	8(–)	–
Sasarieb	I	Sudan	53	74	64	86	21(+)	11(–)	1
Gomam	I	Syria	47	62	60	88	15(+)	13(–)	13
Florence Aurora	L	Tunisia	41	50	54	83	9(+)	13(–)	20
Byrsa	I	Tunisia	51	80	59	101	29(+)	8(–)	13
Bolal	I	Turkey	53	NF	60	NF	>50(+)	7(–)	–
Aziz	I	Yemen	50	66	54	91	16(+)	4(–)	21
Mokhtar	I	Yemen	52	71	65	81	19(+)	13(–)	–3
L-33	L	Yemen	51	74	63	97	23(+)	12(–)	11
Insensitive to V and sensitive to P									
Giza 155	L	Egypt	55	56	76	87	1(–)	21(+)	10
L-17	L	Ethiopia	50	53	68	66	3(–)	18(+)	–5
L-23	L	Ethiopia	46	49	64	70	3(–)	18(+)	3
L-66	L	Turkey	65	61	119	113	–4(–)	54(+)	–2
Sensitive to V and P									
L-1	L	Ethiopia	50	63	76	108	13(+)	26(+)	19
L-56	L	Tunisia	62	77	98	115	15(+)	36(+)	2
Gerek 79	L	Turkey	49	77	66	103	28(+)	17(+)	9
Mahon Demiaz	L	Algeria	61	102	98	NF	41(+)	37(+)	–
L-10	L	Algeria	63	102	106	NF	39(+)	43(+)	–
L-7	L	Ethiopia	50	78	96	NF	28(+)	46(+)	–
L-18	L	Egypt	72	83	NF	NF	11(+)	–	–
Almansor	L	Portugal	55	75	72	80	20(+)	17(+)	–12
Lodi	L	Portugal	51	NF	68	NF	>50(+)	17(+)	–
L-45	L	Syria	55	100	102	117	45(+)	47(+)	–30
Bezostaya 1	L	Turkey	56	NF	76	NF	>50(+)	20(+)	–

LSD for comparing genotypes within each photoperiod and vernalization= 2.40.

LSD for comparing a genotype across photoperiod and vernalization= 2.40.

I= improved cultivar, L= local cultivar.

+= sensitive, –= insensitive.

NF= did not flower.

under this range of environments, the breeding program has identified germplasm with low sensitivity to vernalisation and photoperiod.

Table 5 shows the 49 local and improved wheat cultivars that were evaluated for their response to photoperiod and vernalisation under controlled environment conditions. Based on the main effects of vernalisation and photoperiods, the varieties were grouped into four categories. Twenty one genotypes were classified as insensitive to both factors (Table 5). All except one (L-22) of the cultivars in this group were improved varieties, suggesting that most of the modern adapted wheats in low latitudes of WANA have been bred for insensitivity to both factors. This is not surprising considering that most of these cultivars are direct introductions from CIMMYT or CIMMYT/ICARDA germplasm and carry photoperiod insensitivity genes in their pedigree. Low sensitivity to photoperiod is a characteristic of new high-yielding wheat varieties targeted for the growing conditions of autumn and winter sowing in latitudes below 40° north and south, where often only the spring types are adapted. In the latitudes above 40°, where spring wheat grain yields are unstable often due to the lack of adequate winter hardiness, insensitivity to photoperiod has to be combined with vernalisation requirement and adequate winter hardiness.

Thirteen cultivars were sensitive to vernalisation and insensitive to photoperiod (Table 5). Eleven of these were modern improved cultivars. The reason for their vernalisation sensitivity can be traced back to the genetic background of these cultivars. Five, (Gomam, Giza 164, Sasarieb, Mokhtar, and Byrsa), were derived from winter x spring gene pool and have a common parent (Kavkaz) in their pedigrees. Zidane 89 is also a winter x spring derived variety having Weique Red Mace as one of its winter parents. The group contained two winter cultivars (Bolal and Centauro) adapted to higher latitudes, where vernalisation may have an adaptive role. In general, vernalisation requirement in spring wheats may serve little adaptive value in the rainfed areas of WANA. It is possible that the response observed here reflects genes for vernalisation carried from a winter parent.

The group characterised by insensitivity to vernalisation but high sensitivity to photoperiod is composed mostly of old cultivars and local spring wheat. Photoperiod sensitivity in these genotypes may be an adaptive mechanism to avoid early frost damage during heading in these regions.

Twelve old genotypes were sensitive to both photoperiod and vernalisation (Table 5). These were mostly winter types which failed to reach heading in the non vernalised treatment during the 125 days of the experiment.

Conclusions

The results presented in this paper suggest that fine tuning of the wheat crop can be achieved by modifying photoperiod and vernalisation sensitivity. Furthermore, selection for vernalisation response can be achieved under high ambient air temperatures in the field where a large number of lines can be screened. Subsequent screening for day length sensitivity and vernalisation requirements and their interaction can be carried out in the lines selected from the field, under greenhouse conditions using 12 and 16 h day lengths.

Time to flowering in spring wheat genotypes is controlled by basal vegetative period, photoperiod response and vernalisation requirement. In general, improved modern-day cultivars in the WANA region were insensitive to photoperiod and vernalisation. Photoperiod insensitivity would permit dissemination of improved cultivars to similar irrigated environments at lower latitudes. However, further increases in wheat production in rainfed regions are possible only where the maturity cycle of the improved cultivars is matched to take optimum advantage of favourable moisture and temperature. This can be achieved by utilising the intrinsic earliness, and combining it with a degree of photoperiod sensitivity for regional environments. Furthermore, the results should be of value in wheat breeding programs aiming to identify genotypes with a wide range of flowering behaviour in response to their photoperiod and vernalisation.

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