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COMBINING ABILITY OF COMMON WINTER WHEAT CULTIVARS (*TRITICUM AESTIVUM* L.) BY DATE TO HEADING AND DATE TO PHYSIOLOGICAL MATURITY

N. TSENOV * and E. TSENOVA
Dobrudzha Agricultural Institute, BG - 9520 General Toshevo, Bulgaria

Abstract

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This investigation was carried out with a view of evaluating the combining ability and the heritability regularities of a group of wheat cultivars which differed significantly by their date to heading (DH) and date to physiological maturity (DPM). Six common winter wheat cultivars were combined in a complete diallele crossing scheme. The two traits were represented as number of days from 1st January to the respective date for each of them. During three successive years, the early F_1 and F_2 hybrid generations were analyzed. They were grown in a randomized design, the distance between the rows being 20 cm and the distance between the plants in each row – 10 cm. Each cultivar was evaluated for combining ability and the breeding value of each combination was assessed for the above two traits.

The combining ability and the genetic parameters were calculated using the program Dial 98. Lack of reciprocal effect was established although the mother component strongly affected the phenotypic expression of the two traits. There were significant variations between the investigated cultivars in the expression of the two traits within 5-7 days. The values of GCA were predominant as a rule over the values of SCA in the variation analysis performed on the entire crossing scheme. This was evidence for some dominance of the genes with additive effect of the factors determining the two traits. GCA of each cultivar was directly related to the expression of the two traits, the correlation being as high as 0.95. The heritability of the two traits was analogous and resulted from complex combinations of genes with different effects (additive or dominant).

The higher the difference between the parental cultivars in a combination by the two traits, the higher the inherited DH and DPM values were. The regularities in the genetic control and the combining ability of the investigated cultivars by DH were completely analogous for the trait DPM, as well. This means that earliness could be easily evaluated by DH. Cultivars Pliska, Vratsa and Obriy had high combining ability towards earlier dates to heading and maturity. Cultivar Pryaspa had the latest dates in the diallele crossing scheme, but its breeding value implied successful breeding of earliness in combination with high productivity.

Key words: diallele analysis, winter wheat, date to heading, date to physiological maturity, combining ability

Abbreviations: DH – date to heading, DPM – date to physiological maturity, GCA – general combining ability, SCA – specific combining ability.

**E-mail: nick.tsenov@gmail.com*

Introduction

The results from the breeding for productivity are related to the combining ability of the cultivars used as components in hybridization with regard to the grain yield traits (Tsenov and Tsenova, 2004; Tsenov et al., 2005). The traits which ostensibly affect grain yield are the duration of the date to heading and to the date of maturity. Both are important for the adaptation of the wheat plant to the specific environment, especially under the annual seasonal variations in the climate of Bulgaria (Tsenov et al., 2009). According to Boyadjieva (2002); Foulkes et al. (2004), the two traits play a key role for obtaining high grain yields by adequate response to the environment, especially under stress. The term "duration of the vegetation period" is used in Bulgaria to define the time to heading (date to heading), and eventually to maturation (date to maturity). According to these traits, the cultivars can be divided into early, medium and late. The affiliation to any of these groups depends on the presence of various allelic combinations of the genes for vernalization and photoperiodism (Snape et al., 2001). The date to heading of winter wheat is affected significantly by genes for "intrinsic earliness", (*Eps*), which are genotype-specific (Stelmakh, 1998; Bullrich et al., 2002; Zhang et al., 2009).

These several different genetic systems related to the date to heading imply complex combinations difficult to study thoroughly. From the point of view of practical breeding, it is important to identify samples which can be used to develop early winter wheat forms (Tsenov et al., 2005) without even knowing in detail the specific genetic control of these systems. Furthermore, there are accessions with similar genetic control but with different dates to heading and maturity. Accessions with the same alleles in the major genes for vernalization and photoperiodism have demonstrated very different dates to heading (Tsenov, 2005; Zheleva et al., 2006). Therefore it is important to study the combining ability of each genotype for its efficient use in this direction. In this relation we performed diallele analysis on a group of cultivars, which were used for other purposes, to collect data on the heritability peculiarities of the dates to heading and maturity. There is few data on the heritability of the date to physiological maturity in literature. The duration of this period has been subjected to more investigations because it is related to the formation of grain and grain filling (Fayt and Fedorova, 2007; Herndl et al., 2008; Griffits et al., 2009). Furthermore, Tsenov (2009) found out that the cultivars differ considerably also by their date to physiological maturity, although date to heading was determining for the duration of the vegetation period on the whole.

The main aim of this investigation was to find out: 1) the combining ability of cultivars with different expression of the two traits; 2) the major regularities in the genetic control of the date to heading and the date to physiological maturity in combinations of cultivars contrasting by these two traits.

Material and Methods

Two hybrid generations were analyzed in a diallele crossing scheme which consisted of crosses between six common winter wheat cultivars: 1-Vratsa; 2-Kaloyan; 3-Pliska; 4-Obriy; 5-Slavyanka; 6-Pryaspa. The hybrid combinations were performed in a full diallele crossing scheme, method 1, model II of Griffing (1956), which involved the reciprocal crosses as well. Date to heading and date to physiological maturity were subjected to investigation. They were determined visually at stages 55 and 94, respectively, according to Zadoks et al. (1974) scale. They were considered traits, the values of which were represented as number of days from 1st January till the respective date for each of them. The means of the two traits were determined by marking single plants in the hybrid populations. The plants were selected from each of the respective hybrid progenies (F_1, F_2). The plants in the hybrid populations were grown during three successive years in three replications in a randomized block design with 20 cm distance between the rows and 10 cm distance between the plants in the row.

The combining ability effects of the cultivars in the scheme were calculated for each hybrid generation. The genetic parameters and the components of genetic variability of the trait according to Hayman (1956) and Jinks (1954) were also determined. The breeding value of each cross was calculated by the method described in Tsenov (1995). The combining ability of the parental cultivars, the broad-and-narrow sense heritability coefficients and the genetic parameters were calculated with the statistical program *Dial 98*.

Results

The variance analysis of the entire crossing scheme presented in Table 1 showed significant variations (a) between the values of the cultivars involved in the scheme for both investigated traits. The phenotypic expression of the traits was strongly affected by the dominant genes (b), the values being higher for DPM in general. The effect of the replications in the scheme was insignificant for both traits although the data were from several years, the environmental conditions being highly variable.

The female parent as a component in crossing had a strong effect (c) on the expression of the traits in the earliest hybrid generations without exception. It was highest for date to physiological maturity. Nevertheless, the effects of the reciprocal crosses (d) on the expression of the traits were insignificant. Therefore this investigation gives data only on the direct crosses. The high values of parameter (b1) were an indication that the parents with later date to heading possessed more dominant genes for this trait, and the parents with earlier date to heading carried recessive genes. Analogous was the situation with the other trait, which was even better, expressed.

The combining ability of the investigated cultivars was significant for both generations (Table 2). The absence of reciprocal effects is a prerequisite for objective analysis on the combining ability for both investigated traits.

The variation for DH was ostensible both for the cultivars included in the crossing scheme and for their combining ability. In both hybrid generations the GCA variances were 2.5 ÷ 3 times higher than the SCA variances (GCA / SCA = 3.01 – 2.26). This was an indication that in this crossing scheme the additive genes were predominant over the dominant ones.

For DPM, the combining ability of the cultivars was significant but the variances caused by the

Table 1

Variance analysis of the entire diallele crossing scheme according to Walters and Morton (1978)

Source	df	MS		F_1		F_2	
		DH	DPM	DH	DPM	DH	DPM
Replications	2	1.25	1.22	1.17 ns	1.22 ns	1.42 ns	1.55 ns
a	5	275.44	301.14	344.70 **	366.78 **	349.12 **	332.62 **
b	15	7.18	9.16	8.21 **	10.10 **	12.64 **	15.88 **
b1	1	33.22	35.55	42.53 **	49.73 **	45.31 **	51.51 **
b2	5	5.92	7.77	6.77 **	8.77 **	11.29 **	10.92 **
b3	9	6.11	7.88	7.55 **	9.47 **	8.58 **	9.11 **
c	5	54.71	65.26	55.6 **	68.88 **	60.21 **	66.61 **
d	10	5.52	6.31	2.67 ns	2.78 ns	1.97 ns	2.03 ns
error	70	0.83	1.16				

Table 2
Variance analysis for combining ability of the investigated traits

Source of variation	DF	F_1		F_2	
		MS	F	MS	F
Date to heading					
Genotypes		6.78	7.55 **	7.78	11.21 **
GCA	5	165.13	40.03***	144.09	37.72***
SCA	15	7.07	13.33***	8.05	16.75***
error	75	0.93		0.98	
GCA/SCA			3.01		2.26
Date to physiological maturity					
Genotypes		8.44	2.23 ns	9.18	2.42 ns
GCA	5	205.33	22.00***	214.11	25.22***
SCA	15	17.37	15.51***	18.25	16.92***
error	75	2.63		3.88	
GCA/SCA			1.42		1.49

different expression of the trait in the individual cultivars were low and insignificant (2.23, 2.42). The ratio GCA / SCA for DPM was considerably lower indicating balance in the expression of additive and dominant genes.

The GCA effects of the investigated cultivars differed considerably. Good combiners for efficient shortening of the date to heading are considered those parents which have negative values and vice versa. Cultivar Slavyanka had the lowest positive effect of GCA. The other cultivars were divided into two groups: with high positive effect – Kaloyan (3.33) and Pryaspa (2.27), and with negative values – Pliska (-2.44), Vratsa (-2.19) and Obriy (-2.17). The correlation between the DH level and its GCA was r = 0.95**. This indicated that the later the cultivar, the higher its GCA effects were. In this sense the best combiner towards shortening the date to heading was cultivar Pliska, and cultivars Vratsa and Obriy were equal. Work

Table 3
GCA effects of cultivars by date to heading

Generation		Vratsa	Kaloyan	Pliska	Obriy	Slavyanka	Pryaspa
F_1	Mean	126.6	133.7	122.6	124.8	129.3	130.6
	Effect	-2.19 *	3.33 **	-2.44 *	-2.17 *	1.20 ns	2.27 *
	Rank	2	6	1	3	4	5
	Error	P 0.05	2.16	P 0.01	3.22		
F_2	Mean	125.2	132.5	121.8	123.1	128.1	130.7
	Effect	-4.31**	4.24 **	-3.33 **	-3.79 **	3.14 *	4.05 **
	Rank	1	6	3	2	4	5
	Error	P 0.05	2.14	P 0.01	3.17		

Table 4

GCA effects for date to physiological maturity of the investigated cultivars

	Values	Vratsa	Kaloyan	Pliska	Obriy	Slavyanka	Pryaspa
F_1	Effect	-5.19 *	6.31 **	-5.68 *	-4.77 *	4.62 *	4.72 *
	Rank	1	5	2	3	4	6
	Mean	154	162.7	156.7	157.8	159.3	164.2
	Error	P 0.05=3.66		P 0.01=5.82			
F_2	Effect	-5.31 **	6.92 **	-5.75 **	-4.94 **	4.94 *	5.15 **
	Rank	1	6	2	3	4	5
	Mean	155.7	162.3	155.8	158.1	160.1	164.9
	Error	P 0.05=4.44		P 0.01=6.17			

on shortening of the date to heading of cultivar Kaloyan would be most difficult.

Similar is the situation with the trait DPM. Most suitable for shortening of the time to maturity were cultivars Pliska (-5.68), Vratsa and Obriy (-5.19 and -4.77, respectively).The ranking of the other cultivars was analogous to the ranking by DH. Here the effects of cultivar Slavyanka were significant in both generations. It is interesting to point out that the highest GCA was demonstrated by cultivar Kaloyan, which, however, was not the latest in this crossing scheme in the two hybrid generations. The latest cultivar Pryaspa had almost the same GCA effects as cultivar Slavyanka, which was with about 4 days earlier. This is an indication that it can be compromisingly used in breeding

Table 5

SCA effects for date to heading of the investigated hybrid generations

Generation	Parents	SCA effects					
		2	3	4	5	6	mean
F_1	1. Vratsa	0.30 **	-0.36**	-0.31*	-0.13	0.38 **	-0.3
F_2		0.11	-0.30**	-0.27 **	0.22 *	0.35 **	-0.33
F_1	2. Kaloyan		0.21*	0.11*	0.35*	0.55 **	1.22
F_2			0.12	0.19*	0.37	0.43 **	1.11
F_1	3. Pliska			-0.43 **	-0.18 *	-0.17 *	-0.78
F_2				-0.47 **	-0.16 *	-0.21 *	-0.84
F_1	4. Obriy				-0.05	-0.13**	-0.28
F_2					-0.1	-0.19*	-0.29
F_1	5. Slavyanka					0.54 **	0.54
F_2						0.51 **	0.51
F_1	6. Pryaspa						0.42
F_2							0.39
F_1	LSD	0.05	0.07	0.09			
F_2		0.01	0.09	0.12			

Table 6
SCA effects for date to physiological maturity of the investigated hybrid generations

Generation	Parents	SCA effects					
		2	3	4	5	6	mean
F_1	1. Vratsa	0.38 *	-0.42 *	-0.41 *	-0.18	0.31 *	-0.32
F_2		0.19	-0.28 *	-0.32	-0.38 *	0.41 *	-0.38
F_1	2. Kaloyan		0.18	0.18	0.44 *	0.59 *	1.39
F_2			0.11	0.22 *	0.52 *	0.53 *	1.38
F_1	3. Pliska			-0.38 *	-0.27 *	-0.27 *	-0.92
F_2				-0.41 *	-0.21 *	-0.27 *	-0.89
F_1	4. Obriy				-0.15	-0.21 *	-0.36
F_2					-0.21 *	-0.28 *	-0.49
F_1	5. Slavyanka					0.57 *	0.57
F_2						0.49 *	0.49
F_1	6. Pryaspa						0.92
F_2							0.89
F_1	LSD	0.05	0.12	0.14			
F_2		0.01	0.19	0.21			

for earliness although it reaches physiological maturity latest. The probable reason for this is the presence of an early spring cultivar (Era) in its pedigree (Panayotov, 1988).

The data on SCA effects for DH in the respective crossing combinations are given in Table 5. Although the two hybrid generations were grown in different years, their values for each cross were similar. However, these values were radically different in Vratsa/Kaloyan (0.30** ÷ 0.11) and Vratsa/Slavyanka (-0.13 ÷ -0.22). In the other crosses the values were unidirectional and similar; therefore the crossing combinations with cultivar Vratsa given above should be considered exceptions.

In this case, too, the early cultivars had significant and negative values. The calculation of the mean values by the female parent revealed the strong effect of cultivars Kaloyan, Slavyanka and Pryaspa towards later date to heading. From this point of view the data on SCA demonstrated the same tendency as GCA for each variety. The behavior of cultivar Pryaspa is again interesting to note. Its SCA values were comparatively low (0.42 – 0.39) in comparison to the earlier cultivars Kaloyan and Slavyanka. Highest SCA effects towards shortening of the date to heading were found in the crossing combinations with cultivar Pliska. In cultivars Vratsa and Obriy the values were very close: about 0.30. The crossing combination Pliska / Obriy was much more promising in breeding for earliness (-0.43 ÷ -0.47) than the combination Vratsa/ Pliska (-0.30 ÷ -0.36). The effect of the early cultivars Pliska and Obriy was very strong in the crosses with the later parents expressed through the negative levels of their values.

Discussions

Since it becomes clear that the same cultivars have both high specific and general combining ability, the question remains unclear which of the parents will be efficient in breeding, the ones with high GCA or the ones with high SCA. To throw more light on the problem which parent possessed good combining ability, the breeding values of

Table 7
Breeding value of the parents for the two investigated traits

Cross		DH	DPM
1 Vratsa	Kaloyan	0.75	1.65
	Pliska	-6.38	-11.32
	Obriy	-6.52	-10.46
	Slavyanka	-1.04	-0.75
	Pryaspa	0.28	0.05
2. Kaloyan	Pliska	1.07	1.05
	Obriy	0.96	1.97
	Slavyanka	6.32	11.88
	Pryaspa	7.44	12.11
3. Pliska	Obriy	-6.32	-10.96
	Slavyanka	-0.89	-1.18
	Pryaspa	-0.11	-1.05
4. Obriy	Slavyanka	-0.89	-0.25
	Pryaspa	0.02	-0.15
5. Slavyanka	Pryaspa	5.74	10.25

each crossing combination was calculated. For maximum clarity the mean value of each trait obtained from the two hybrid generations is given in Table 7.

It is evident from the data that, on the whole, breeding for early forms is more probable in the

Table 8
Components and parameters of genetic variability for date to heading

Components and parameters	F_1		F_2	
	DH	DPM	DH	DPM
D	27.9**	58.1 **	26.8**	56.6 **
H1	4.31 ns	4.17 ns	3.27 ns	3.47 ns
H2	6.88 *	6.44 *	5.99 *	5.02 *
F	7.74 *	6.67 *	5.76 *	5.13 *
hh	10.22 **	9.88 *	10.11 *	8.55 *
E	0.51	0.52	0.48	0.54
$\sqrt{H1/D}$	0.43	0.38	0.42	0.35
kd	0.49	0.5	0.52	0.5
h	2.82 *	2.97 *	2.77 *	2.37 *
D+E	0.79 *	0.81	0.82	0.75
H^2	0.63	0.58	0.65	0.56
h^2	0.75	0.7	0.72	0.69

crosses between the early cultivars. The later one of the components is (by both traits), the more the breeding value of the cross tends towards later dates to heading and maturity. This was very clear in the crossing combinations of cultivars Kaloyan and Slavyanka. In these combinations the tendency was most evident. In the crossing combinations of cultivar Pryaspa there were some deviations from this regularity, provided that this was the latest cultivar in the crossing scheme. Almost all its combinations had breeding values more favorable than the values of cultivar Kaloyan. There was highest probability of obtaining early forms in the crosses of cultivar Pliska regardless of the level of the traits of the other component. These data confirm to a large extent the results from the use of this cultivar (Tsenov, 2000). This is the first cultivar from the breeding of DAI which combines high productivity with earliness to a highest degree (Petrov et al., 1982). The early dates to heading and maturity had been achieved 10 years earlier by Rachinski (Rachinski, 1977), who developed cultivar Roussalka, a parent of Pliska (Panayotov et al., 1993). This cultivar has been justifiably used in mass breeding and there already are several released varieties which involve it in their pedigrees (Kostov et al., 1998; Tsenov et al., 1998; 1999; Tsenov et al., 2009) and are now distributed in mass production.

The combining ability clarifies to some extent the problem of which of the involved genotypes can be used as a donor (Tsenov, 1995) to transfer a trait in new lines. In this case the heritability regularities and the effect of the environment on the traits are important.

The data on the genetic parameters (Table 8) show that in both generations there is an additive – dominant system of heritability of the two traits. Although parameter D (additive genes) had significant and very high values, the level of the traits in the crossing scheme was strongly affected by dominant genes (H2). Such effect implies presence of recessive genes as well. This presence was confirmed by the values of parameter (kd) which indicated some predominance of the recessive genes by number. The variations of the two parents by each investigated trait were significant because the values of parameter (hh) were very high. The heritability of this trait was partially dominant towards the later date to heading ($\sqrt{(H1/D)}$=0.41).

The trait earlier date is due to the action mainly of additive genes (Shoran et al., 2003) present in both parent. When combining two early cultivars, the heritability mode is intermediary. The higher the difference between the values of the two traits, the mode of inheritance tends towards dominance of the later parent. Such regularities have been reported by other authors as well (Shoran et al., 2003; Haq and Tanach, 1991; Tsenov et al., 2005).

The heritability of (H^2) was stable by generations and traits and completely confirmed the low and insignificant values of parameter (E). However, about 20 % of the phenotypic expression of the traits was due to the genotype x environment interaction (D+E). The share of the additive gene effects was considerable and varied from 2/3 to 3/4 from the entire genetic control of the trait (h^2=0.69 ÷ 0.75). This was a sound evidence for the presence of complex interaction between individual genetic systems resulting in plants differing by DH and DPM. The knowledge available on the different alleles of genes for vernalization (*Vrn*), photoperiodism (*Ppd*) and intrinsic earliness (*Eps*) implies that the variations in the earliness of each cultivar are the result from the unique combinations between them. The researches carried out up to now (Zheleva et al., 2006; Todorovska et al., 2009; Kolev et al., 2010) on Bulgarian wheat cultivars reveal similar genetic control of vernilization requirements and photoperiod sensitivity. However, the values of DH and DPM of the Bulgarian cultivars varied rather significantly (Tsenov, 2009).

A self-evident conclusion is that the expression of the trait in each cultivar is the result from the unique combination of genes which exist in almost all chromosomes of wheat (Worland and Snape, 2001; Shindo et al., 2003). Probably these are the *Eps* genes; according to many authors their effect is determining under field conditions and is very strongly related to their phenotypic expression: 0.79 ** and 0.68** (Borner, 2002; Hanocq et al., 2005).

It can be concluded that the efficiency of breeding for early forms is related to the systematic study on the suitability (combining ability) of each cultivar. This is because breeding is simultaneously and obligatorily performed for all elements of productivity (Tsenov and Tsenova, 2004). To achieve practical results in this respect, it is necessary to identify accessions with good combining ability by a complex of traits (Tsenov, 1995; Tsenov et al., 2005). This is the only way to compensate for the avoidance of late cultivars which however posses a number of traits and properties valuable for breeding. It also provides a favorable prerequisite for their adequate and large-scale use in breeding work. In our case Pryaspa is such a cultivar: it is a carrier of high productivity and excellent resistance to leaf diseases. Furthermore, there is data that cultivar Yantar (from which Pryaspa was derived) has high combining ability for number of kernels per spike and number of productive tillers (Tsenov and Tsenova, 2004), which is, on the whole, highly favorable for breeding.

Conclusions

- The heritability of the two investigated traits was analogous and resulted from complex combinations of genes with different action (additive or dominant).
- The higher the difference between the parental cultivars in a combination by the traits, the mode of inheritance tends towards dominance of later DH and DPM.
- The regularities in the genetic control and the combining ability of the investigated cultivars were completely analogous for DH and DPM. This means that earliness can be reliably evaluated by DH.
- Cultivars Pliska, Vratsa and Obry possess high combining ability towards shorter time to heading and maturity.
- Cultivar Pryaspa was the latest variety in the crossing scheme but its breeding value implied successful breeding for earliness combined with high productivity.

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