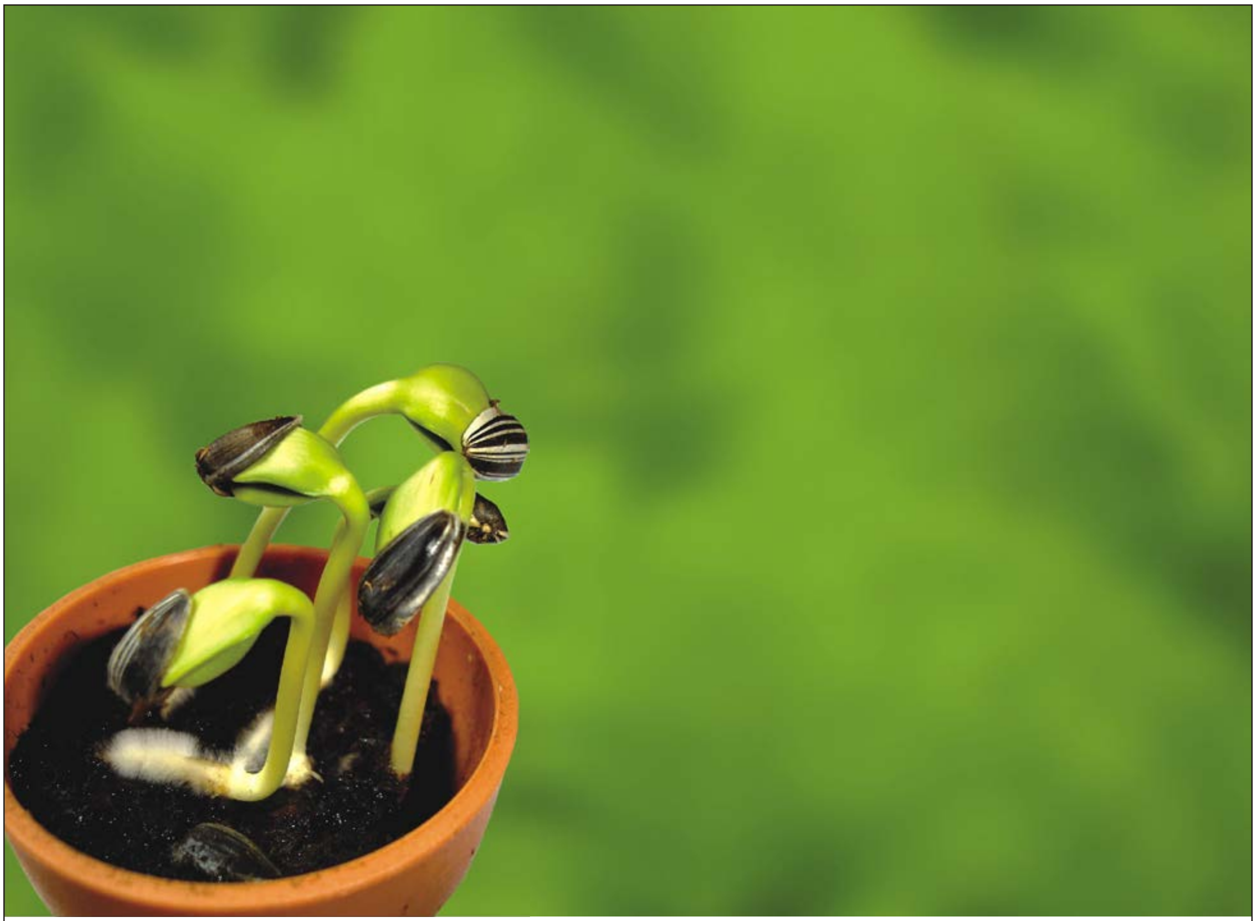

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Phenotyping and Genotyping through F_1 and F_2 Generation the Promising Crosses

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ABSTRACT

In the attempt of understanding the importance of the first generations in wheat breeding, a controversial experimentation procedure was used with F_2 generation preceding F_1. Ten bread wheat F_2's and their parents were evaluated in dense stand followed by the evaluation of the ten F_1's and their parents in isolation environment for two successive years. Three criteria groups were used; a) the heterosis of F_1 and F_2 according to their parents, b) the productivity and stability *per se* of F_1 and F_2 and c) the general/specific combining ability of parents. Heterosis alone proved of little significance in connecting the performance of both generations compared to standard check heterosis. The highest yielding F_2 was the only cross exhibiting negative heterosis and heterobeltiosis in F_1 while it was significantly higher in F_2 and equal in F_1 for standard check heterosis constituting it a safe criterion. The second criteria group indicated significant correlation between the stability of F_1 and F_2 with the productivity of the crosses in total being equal to each other giving another linkage factor between the two generations. The diallel analysis of both experiments pinpointed the importance of the information provided by the F_2 generation thus constituting it far more valuable than the information of F_1. The data indicated that non heterotic F_1's should not be discarded as a combined use of all the criteria can evaluate and discriminate more accurately the promising materials.

Key words: Bread wheat, general combining ability, heterosis, yield potential

INTRODUCTION

In a breeding program hybridization is the principal procedure in order to develop genetic variance (Poehlman and Sleper, 1995). In wheat, the breeding schemes involve pure line hybridization with their main expression being applied in CIMMYT's wheat breeding programs. A quick reviewing glance on wheat breeding techniques shows that hybridization followed by pedigree selection, was applied from 1944-1985 while, from 1985 until the second half of the 1990's, the modified pedigree/bulk method (Van Ginkel *et al.*, 2002), was preferred. Under this modification many wheat varieties that are cultivated throughout the world were developed. In the late 1990's the selected bulk method (Singh *et al.*, 1998; Van Ginkel *et al.*, 2002) replaced the modified pedigree/bulk method by improving resource use efficiency.

The identification of promising segregating material and the selection of genotypes with high yielding potential is a classical practice that takes place during the first generations. According to many researchers (Valentine, 1979; Bernardo, 2002), if maximizing yield is the main target the opportunity for selection in early generations should not be lost. Furthermore, Hallauer and Miranda (1988) referred that, in self pollinated species in F_2 populations, the phenotypic variance is distributed among and within the populations. Considering the fact that with self-fertilization the loss of heterozygosity and an increase of homozygosity occurs at a rate of 50% for each generation, the F_2 generation will be 50% homozygous and the percentage of homozygosity will increase with every generation of self fertilization (Stoskopf, 1999). Thus, the F_2 generation is the crucial generation for the selection procedure to set off.

Various criteria have been suggested for identifying promising crosses. Many breeders (Nass, 1979; Fasoulas, 1988; Roupakias *et al.*, 1997; Singh *et al.*, 2004; Kotzamanidis *et al.*, 2008) point out the importance of heterosis in F_1 generation, as a criterion for the promising crosses to be evaluated in F_2. The use of heterosis along with combining ability proposed for the discrimination of high yielding hybrids (Ali Avci, 2005) while heterosis and low inbreeding depression indicates promising material (Chowdhry *et al.*, 2001). Furthermore, exploitation of heterosis in the attempt of increasing yield has been reported in many crops (Khan *et al.*, 2004; Sofi *et al.*, 2007; Alghamdi, 2009; Selvaraj *et al.*, 2011). Nass (1979) in spring wheat, suggested that heterotic F_1's gave high-yielding F_4's compared to low-yielding F_1's. Therefore, instead of continuing a large number of F_1 crosses in F_2 generation usually non-heterotic ones are discarded. Fasoulas (1988) suggested the evaluation of F_1 and F_2 in low plant density. Roupakias *et al.* (1997) showed in "faba" bean (*Vicia faba*) that heterotic F_1's which exhibited low inbreeding depression in F_2 were promising material for developing lines. Furthermore, Singh *et al.* (2004) used heterosis over mid-parent and heterosis over best parent (heterobeltiosis) as criteria, for identifying parental combinations capable of producing the highest level of transgressive segregants. Kotzamanidis *et al.* (2008) proposed the criterion of combined yield of the F_1 and F_2 for effective identification of superior crosses from the early stages. In the aforementioned breeding schemes information from the evaluation criteria of the F_1 generation as well as from heterotic crosses that continue to be promising in F_2 were used especially when the breeder deals with a vast amount of crosses.

In the present study the F_2 generation preceded F_1 in order to decipher the possible benefits of a controversial experimentation procedure. The study included the evaluation of a number of F_2 bread wheat populations under the common experimentation of Research Centers (i.e., the plot) followed by the evaluation of F_1 generation in isolation environment (i.e., the single plant), using the same criteria, as an attempt to estimate the promising crosses through both generations.

MATERIALS AND METHODS

Six bread wheat cultivars (Acheron, Yecora-E, Nestos, Orfeas, Oropos and Acheloos) were crossed to produce 10 F_2's. The six cultivars were developed at the farm of Cereal Institute of Thessaloniki-Hellas, except Yecora-E which was derived via intra-cultivar selection within Cimmyt's Yecora-70. These varieties were chosen owing to their productivity and stability under Mediterranean environment.

Evaluation of F_2 generation: During 2006-2007 the 10 F_2's and the six parental cultivars were established at the Farm of Cereal Institute at Thermi-Thessaloniki (40, 32N, 23E) in a Randomized Complete Block Design (RCBD) with three replications. The plots consisted of seven rows, 0.60 m long, spaced 25 cm apart (a total area of 1 m^2 per plot) from which only the central five rows were harvested. For each plot 18 g of seed were used and appropriate agronomic practices were done timely to achieve good crop stand. The plants from each plot were harvested and weighed (g $plot^{-1}$).

Besides the same year, a second experiment was established with the aim to produce enough F_1 seed from the diallel crossing of the six parental cultivars.

Evaluation of F_1 generation: During 2007-2008 F_1 seeds were planted at the Farm of the Cereal Institute of Thessaloniki in isolation environment i.e., in honeycomb design (Fasoulas and Fasoula, 1995). The 10 F_1's and their 6 parents were arranged according to the replicated sixteen (R-16) honeycomb design. An interplant spacing of 1 m was used in order to eliminate the masking effects of competition and to maximize phenotypic expression and differentiation (plant density 1.16 plants m^{-2}). Three kernels per plant position were shown to ensure equal germination. Five weeks after sowing, all positions were thinned to a single plant. A few days before thressing, all plants were tagged for identification. Harvesting occurred in the field and individual plant yield (g $plant^{-1}$) was recorded. All experiments were subjected to growing conditions promoting high yields.

Data analysis: The data were subjected to analysis with the Model II analysis of variance and the expected mean squares were estimated for both experiments (Steel and Torrie, 1980). The honeycomb design was analyzed as a completely randomized design. In the RCB design of F_2 generation the stability of each treatment was estimated by partitioning the experimental error while the student's t-test was used for mean comparisons. In the honeycomb design experiment of F_1 generation for mean comparisons the t-test for independent samples from populations with different standard deviations was applied with application of Cochran's approximatation.

Heterosis was estimated over the best parent (heterobeltiosis) and over mid parent (relative heterosis) (Fonseca and Patterson, 1968). Standard heterosis refers to the comparison of a hybrid with a standard variety (Virmani, 1994). At the present study the mean yield of the six parents was used for the expression of standard heterosis. For the evaluation of F_2's the following criteria was applied concerning superiority/inferiority over: (a) The best parent value (BP), (b) The mid parent value $(\overline{MP})$ and (c) the mean yield of the six parental cultivars. The significance of superiority/inferiority over $(\overline{MP})$ and six parental cultivars average was checked with one degree of freedom comparisons.

The same criteria of heterosis were used for evaluating the 10 F_1's. Additionally an experimental criterion suitable for the isolation environment of experimentation was used. This criterion named as Line Crop Yield Potential (LCYP), simulates the isolation environment with the dense stand and was proposed by Fasoula (2008). LCYP combines the stability via the standardized mean of each treatment ($CH = (\bar{x}_t/s)^2$ where, $\bar{x}_t$ is the mean of each treatment and s is the standard deviation) and the productivity of each line via the square of the mean yield of each treatment divided by the grand mean ($CLR = (\bar{x}_t/\bar{x})^2$ where, $\bar{x}$ is the grand mean), according to the author. Additionally, for both generations CLR in total was calculated (i.e., the square of the mean yield of the F_1's divided by the grand mean and the square of the mean yield of the F_2's divided by the grand mean).

Each of the varieties was crossed with the rest, but reciprocal crosses were not made. The General Combining Ability (GCA) was estimated for the incomplete diallel according to Griffing (1956) diallel analysis. Analysis of variance for general and specific combining abilities was made for both generations and the genetic components were estimated for grain yield.

RESULTS

The analysis of variance for grain yield revealed significant differences for both experiments (Table 1). In the F_2 generation experiment, variance due to treatments (i.e., genotypic variance) explained most of the phenotypic variance (Table 1). In the F_1 experiment variance between the genotypes explained most of the phenotypic variance while variance within the genotypes was lower. Since, the genotypes were F_1's and cultivars (i.e., pure lines) there can be no variance within them, constituting σ_w^2 variance due to error and σ_b^2 genotypic variance.

Evaluating the F_2, heterosis for grain yield ranged from -4.89-35.18% for the BP value, from -4.81-38.59% for the $\overline{\text{MP}}$ value and from 0.87-46.57% for standard check heterosis value (Table 2). None of the F_2's managed to significantly outyield the best parent however, three F_2's (Orfeas*Oropos, Oropos*Acheloos, Yecora-E*Oropos) exhibited significantly positive relative and standard heterosis and one F_2 Nestos*Acheloos surpassed significantly in standard heterosis (Table 2). On the contrary in F_1 Nestos *Acheloos showed significant positive heterobeltiosis and relative heterosis but insignificant standard heterosis (Table 3). Three F_1's (Acheron*Yecora-E, Yecora-E*Acheloos, Yecora-E*Oropos) surpassed significantly the mean yield of the six parents while one of them (Yecora-E*Acheloos) outyielded $\overline{\text{MP}}$ value as well (Table 3). Many researchers reported positive heterosis and significant heterobeltiosis in wheat F_1 (Subhani *et al*., 2000; Akhter *et al*., 2003; Farooq and Khaliq, 2004; Hussain *et al*., 2004; Abdel-Moneam, 2009). Yecora-E*Oropos was the common cross that was distinguished in F_1 and F_2 generations. Many researchers reported positive heterosis and significant heterobeltiosis.

Table 1: Mean squares of analysis of variance for grain yield measured in F_2 and F_1 generation with the variance due to genotypes (σ_t^2) and between them (σ_b^2), the variance due to error (σ_ε^2) and within the genotypes (σ_w^2) and the coefficient of variance (CV)

F_2			F_1		
Source of variance	df	Grain yield	Source of variance	df	Grain yield
Genotypes	15	9926.04*	Between	15	1714.22*
Error	47	4874.86	Within	324	709.22
σ_t^2		50.89%	σ_b^2		58.63%
σ_ε^2		49.11%	σ_w^2		41.37%
CV		19.38%	CV		56.26%

*Significant at $p \leq 5\%$

Table 2: Evaluation of F_2 generation with the criteria of heterosis

Genotype	Heterobeltiosis (%)	Relative heterosis (%)	Standard check heterosis (%)	Average (%)
Acheron*Yecora-E	0.19	9.54	0.87	9.42
Nestos*Acheloos	12.99	27.05	29.79*	62.06
Nestos*Orfeas	3.73	16.73	19.37	35.40
Nestos*Oropos	28.66	33.50	24.07	76.64
Orfeas*Acheloos	-4.89	-4.81	9.45	-0.22
Orfeas*Oropos	27.36	38.59*	46.57*	100.00
Oropos*Acheloos	20.27	30.76*	38.15*	79.26
Yecora-E*Acheloos	11.88	19.24	28.51	53.00
Yecora-E*Orfeas	9.53	16.84	26.05	46.59
Yecora-E*Oropos	35.18	38.09*	36.10*	97.20
Range of heterosis	-4.89-35.18	-4.81-38.59	0.87-46.57	

*Significant at $p \leq 5\%$

Table 3: Evaluation of F_1 generation with the criteria of heterosis

Genotype	Heterobeltiosis (%)	Relative heterosis (%)	Standard check heterosis (%)	Average (%)
Acheron*Yecora-E	22.84	25.30	45.20*	70.55
Nestos*Acheloos	46.83*	56.09*	29.38	100.00
Nestos*Orfeas	24.68	28.78	17.33	53.50
Nestos*Oropos	13.31	24.98	22.78	46.16
Orfeas*Acheloos	18.05	7.34	11.09	27.57
Orfeas*Oropos	-7.47	-0.24	0.27	-5.62
Oropos*Acheloos	7.91	25.71	16.93	38.21
Yecora-E*Acheloos	18.38	42.87*	39.92*	76.47
Yecora-E*Orfeas	2.55	14.19	21.21	28.68
Yecora-E*Oropos	15.83	20.86	36.91*	55.63
Range of heterosis	-7.47-46.83	-0.24-56.09	0.27-45.2	

*Significant at $p \leq 5\%$

Table 4: Ranking of F_2's in grain yield (g $plot^{-1}$), the apportionment of experimental error and the stability (Coefficient of Homeostasis CH) of F_2's

F_2's	Mean	Mean (%)	Error (%)	CH	CH (%)
Acheron*Yecora-E	312.80	68.82^{bcde}	1.34	11.35	7.40
Nestos*Acheloos	402.47	88.55^{abc}	3.04	17.90	11.67
Nestos*Orfeas	370.17	81.44^{abcde}	8.42	153.35	100.00
Nestos*Oropos	384.73	84.65^{abcd}	2.39	34.33	22.39
Orfeas*Acheloos	339.40	74.68^{abcde}	7.81	24.92	16.25
Orfeas*Oropos	454.50	100.00^{a*}	8.80	6.53	4.26
Oropos*Acheloos	428.40	94.26^{ab}	6.09	11.15	7.27
Yecora-E*Acheloos	398.50	87.68^{abc}	1.49	9.98	6.51
Yecora-E*Orfeas	390.87	86.00^{abcd}	1.92	7.73	5.04
Yecora-E*Oropos	422.03	92.86^{ab}	1.20	21.44	13.98
Parents	**Mean**	**Mean (%)**	**Error (%)**	**CH**	**CH (%)**
Acheloos	356.20	78.37^{abcde}	4.060	4.900	3.20
Acheron	258.93	56.97^{e}	5.390	33.12	21.60
Nestos	277.37	61.03^{de}	4.340	3.130	2.04
Orfeas	356.87	78.52^{abcde}	1.580	6.730	4.39
Oropos	299.03	65.79^{cde}	5.880	3.540	2.31
Yecora-E	312.20	68.69^{bcde}	36.27	2.340	1.53

*Means followed by different letters are significantly different at 0.05

Mean separation for both generations revealed significant differences between the crosses and the cultivars. The highest yielding F_2 Orfeas*Oropos outyielded significantly four cultivars (Acheron, Nestos, Oropos, Yecora-E) and the lowest yielding F_2 (Acheron*Yecora-E) (Table 4). The opposite results were observed in F_1 i.e., Acheron*Yecora-E became the cross that outyield significantly three cultivars (Acheloos, Nestos, Orfeas) and the lowest yielding cross was Orfeas*Oropos (Table 5). Significant Spearman's rank correlation (67.27%) was found between stability (CH) of F_2 and F_1 grain yield. Additionally, productivity (CLR) in total (as determined in materials and methods) was approximately the same for the crosses (1.16 in F_1 and 1.17 in F_2). No correlation was found for grain yield between the F_2's and the F_1's.

Mean squares for GCA were highly significant for both generations while mean squares for SCA in F_2 generation compared to F_1 were not significant (Table 6). The variance of GCA (V_{GCA}) was

Table 5: Ranking of F_1's in grain yield (g $plant^{-1}$), in productivity Coefficient of Line Record (CLR), in stability Coefficient of Homeostasis (CH) and in yield potential Line Crop Yield Potential (LCYP)

Genotype	Yield	Yield (%)	CLR	CLR (%)	CH	CH (%)	LCYP	LCYP (%)
Acheron*Yecora-E	59.7^{a}	100.00	1.59	100.00	2.98	41.49	4.74	69.56
Nestos*Acheloos	53.2^{ab}	89.11	1.26	79.40	2.89	40.21	3.64	53.52
Nestos*Orfeas	48.2^{abc}	80.80	1.04	65.29	3.79	52.81	3.94	57.80
Nestos*Oropos	50.5^{abc}	84.56	1.14	71.50	4.21	58.67	4.79	70.32
Orfeas*Acheloos	45.7^{abcd}	76.51	0.93	58.53	7.18	100.00	6.68	98.13
Orfeas*Oropos	41.2^{bcd}	69.06	0.76	47.69	1.86	25.85	1.41	20.66
Oropos*Acheloos	48.1^{abcd}	80.53	1.03	64.85	6.61	91.98	6.81	100.00
Yecora-E*Acheloos	57.5^{ab}	96.37	1.48	92.86	2.74	38.19	4.05	59.46
Yecora-E*Orfeas	49.8^{abc}	83.48	1.11	69.69	2.10	29.25	2.33	34.17
Yecora-E*Oropos	56.3^{ab}	94.29	1.41	88.90	4.27	59.46	6.03	88.63
Acheloos	31.9^{d}	53.49	0.45	28.61	1.43	19.90	0.65	9.55
Acheron	46.7^{abcd}	78.21	0.97	61.17	2.51	34.99	2.44	35.88
Nestos	36.2^{cd}	60.68	0.59	36.82	4.53	63.11	2.65	38.96
Orfeas	38.7^{bcd}	64.81	0.67	42.00	3.93	54.72	2.62	38.52
Oropos	44.5^{abcd}	74.63	0.89	55.69	3.61	50.28	3.20	46.94
Yecora-E	48.6^{abc}	81.40	1.05	66.27	2.57	35.76	2.70	39.73

*Means followed by different letters are significantly different at 0.05

Table 6: Mean squares of General Combining Ability (GCA), Specific Combining Ability (SCA) and the variance components for F_1 and F_2 grain yield

Source	df F_1	MS F_1	df F_2	MS F_2
GCA	5	1640.09**	5	22463.23**
SCA	9	991.89**	9	3241.64
Error	14	60.78	28	3467.76
Generation		F_1		F_2
Var GCA		205.011		1871.921
Var SCA		495.946		1080.578

**Significant at $p \leq 0.01$

Table 7: General Combining Ability (GCA) of the parents in F_1 and F_2

Parent	Acheron	Yecora-E	Nestos	Orfeas	Oropos	Acheloos
GCA F_1	-26.72	13.95	-4.2	4.66	5.36	6.95
GCA F_2	-78.17	13.67	-9.0	21.47	50.18	1.86

greater than the variance of SCA (V_{SCA}) in F_2 while the values were revered in F_1 (Table 6). In both experiments GCA of Acheloos and Nestos were found negative constituting them, poor combiners (Table 7). From the diallel analysis it was found that the proportion of the additive genetic component (D) compared to the dominance genetic components (H1, H2) was higher in F_2, resulting in a positive value for the product of additive by dominance effects (F) in F_1 (i.e., excess of dominant genes) in contrast to F_2 where it was negative (Table 8). Moreover, the proportion of dominant genes reduces drastically in F_2 generation [kd/(kd+kr) kd-dominant genes, kr-recessive genes] while the average direction of dominance becomes positive from negative in F_1 (Table 8). Finally broad sense heritability (h_b^2) was higher in F_1 while narrow sense heritability (h_n^2) was higher in F_2 (Table 8).

Table 8: The genetic components of diallel analysis of F_1 and F_2 for grain yield

Genetic component	F_1	F_2
D(1)	25.7411	255.8911
H1(2)	1972.1870	5396.6550
H2(3)	1571.2950	4055.9130
F(4)	92.2659	-2235.6900
kd/(kd+kr)(5)	0.6024	0.0244
H(6)	-11.5000	86.2407
H_b^2(7)	0.9550	0.6810
H_n^2(8)	0.2850	0.4450

(1) Additive variance, (2) Dominance variance 1, (3) Dominance variance 2, (4) Product of additive by dominance effects, (5) Proportion of dominant genes (6) Average direction of dominance, (7) Heritability for diallel in a broad sense and (8) Heritability for diallel in a narrow sense

DISCUSSION

The criteria that were used to determine the promising crosses may be distinguished in the following groups: (a) The criteria of heterosis of F_1 and F_2 according to their parents, (b) The criteria of productivity and stability *per se* of F_1 and F_2 and (c) The criterion of general/specific combining ability of parents.

The first group showed no correlation between the two generations and heterosis and heterobeltiosis in F_1 proved of little significance in determining promising crosses. However, the standard checks heterosis, although was not significantly correlated in the two generations, may act as an indication assisting the selection of promising crosses. It is based on the following data. Firstly, four F_2's outyielded significantly the yield of all the checks, meaning that they surpassed the yield of well adapted cultivars constituting promising populations for selection procedure to set off. Furthermore, three of them (Orfeas*Oropos, Oropos*Acheloos, Yecora-E*Oropos) exhibited significantly positive relative heterosis. Many researchers (Nass, 1979; Cox and Murphy, 1990; Kotzamanidis *et al*., 2008) proposed the F_2 productivity and the $\overline{MP}$ value as selection criteria for promising crosses. According to Crow (1948) a heterotic F_2 that showed resistance to inbreeding in a quantitative trait, has mainly additive genetic action. Secondly, genetic variability among families in F_2 generation after selfing is equal to $\sigma^2_A+\sigma_D^2/2$ (where, $\sigma^2_A\rightarrow$ additive genetic variance plus a component that is mainly a function of degree of dominance and $\sigma^2_D\rightarrow$ dominance variance) (Empig *et al*., 1972) which means that the expression of heterosis in F_2 is more meaningful in breeding procedure than F_1. Superiority of F_2 over the check cultivars as a criterion for selecting elite crosses in wheat has been used in previous studies (Gouli-Vardinoudi and Koutsika-Sotiriou, 1999; Singh *et al*., 2004) and from a practical point of view it is most important because it is aimed at developing desired hybrids superior to the existing high yielding commercial varieties (Alam *et al*., 2004). If we take under consideration that the experiments were conducted at a Mediterranean region which is characterized by drought during winter with low temperatures as well as terminal drought associated with above-optimal temperatures, we may conclude that the aforementioned three F_2's have better performance in abiotic stress conditions.

Evaluating the F_1, it revealed contradictory results to the preceding F_2. The F_1 of Orfeas*Oropos was the only one with negative heterosis and heterobeltiosis. According to Nass (1979), heterotic F_1's resulted in higher yielding F_4's than non heterotic F_1's. Many researchers report the significance of heterosis in wheat breeding (Briggle *et al*., 1967; Gyawali *et al*., 1968; Yadav and Murty, 1976; Singh and Sharma, 1989; Prasad *et al*., 1998; Singh *et al*., 2004; Kotzamanidis *et al*., 2008). A wheat breeder dealing with a large number of crosses would probably exclude non heterotic ones thus preventing them from continuing in F_2. The data indicated that the use of more criteria rather than heterosis/heterobeltiosis can succeed in a more efficient prediction of high-yielding genotypes. In particular Nestos*Acheloos was a highly heterotic F_1, whereas, in F_2 was equal to BP, MP and standard check heterosis. However, the prementioned cross Orfeas*Oropos in F_2 received the highest values (Table 2) and if it was discarded in F_1, promising material would have been lost. The data reveals that a common criterion of evaluation for both F_1 and F_2 may be the superiority over a standard mean yield than the other heterotic patterns. An example may be the case of Nestos*Acheloos with the F_2 alone playing the higher role in the identification of promising material. As additive variance in F_2 is twice as dominance variance, heterotic genotypes such as Orfeas*Oropos, Oropos*Acheloos and Yecora-E*Oropos might prove promising populations.

The second group that was referred to the performance *per se* of F_1 and F_2 showed significant correlation between the stability and the productivity in total, criteria that could be used to link the performance of both generations safely. The fact that total productivity of both generations was higher than the unit (>1), according to Fasoula (2008) indicated promising material. On the contrary, lack of correlation between mean yields of the crosses could be explained from the different behavior of the materials due to resistance to abiotic stresses such as plant density being one of them (Tani *et al.*, 2005). Hence, comparing the two groups of criteria i.e., heterosis and productivity, we may assume that the different sowing system that was used, plot for F_2 (approximately 350 plants m^{-2}) and isolation environment for F_1 (1.16 plants m^{-2}) conducted to discriminate the crosses under an indirect index which was the resistance to density.

A diallel analysis for grain yield for both generations revealed the importance of F_2 generation. Variance of GCA (V_{GCA}) was found higher compared to the variance due to SCA (V_{SCA}) in the F_2 generation. On the contrary V_{SCA} was greater in F_1 than V_{GCA} results that were expected since heterotic effects in F_1 are due to dominant effects. The GCA:SCA ratio tilted in favor of GCA in F_2 but not in F_1 indicating the preponderance of additive gene effects in the genetic control of grain yield in F_2 and the dominance effects action in F_1. The importance of additive gene action for various economic traits in bread wheat has been reported by many researchers (Singh and Rana, 1987; Singh, 1988; Pokhrel *et al.*, 1993; Joshi *et al.*, 2004). However, due to the quantitative inheritance of grain yield other researchers (Mann *et al.*, 1995; Dhayal and Sastry, 2003; Ahmad *et al.*, 2011) reported non additive gene action for grain yield. According to Bernardo (2002), if epistasis is assumed negligible or absent, V_{GCA} is a function of the additive variance (V_A) while V_{SCA} is equal to the variance component due to dominance variance (V_D). Therefore, heterotic expression in F_1 may prove a quick prediction criterion as absence of significant additive gene action inhibits heritable progress. The genetic parameters of the diallel analysis further revealed the advantages of F_2 versus F_1 in the selection procedure. The excess of dominant genes in F_1 compared to the negative value of the product of additive by dominance effects (F) in F_2 revealed that non additive gene action played a predominant role in the inheritance of grain yield in F_1 where, the opposite happened in F_2. Similar results for F_1 grain yield were reported by Ahmad *et al.* (2011). The reduction of dominant genes in F_2 generation compared to the F_1 constituted another parameter which promoted the selection efficiency in F_2. Moreover, since the average direction of dominance was found positive in F_2 and negative in F_1, a negative direction of dominance indicated that dominant genes will inhibit the increase of the characteristic under study. Finally, narrow sense heritability in F_1 was very low compared to broad sense heritability which indicated the importance of dominant variation in the total inherited variation. On the contrary in F_2 the difference between the two heritability values was lower indicating an increase of additive gene action in F_2 thus a higher chance for successful selection.

The indications resulted from F_2 generation are far more valuable than the ones provided on F_1. Heterosis alone, due to lack of additive gene action, cannot determine the promising crosses, resulting in possible loss of valuable genetic material. Moreover, the application of various criteria may be proved helpful in the identification of promising crosses during the breeding procedure. The diallel analysis for grain yield showed for both generations that Acheron and Nestos were poor combiners (negative GCA) outlining the importance of F_2 in the selection procedure. As an assessment criterion GCA seemed to be able to evaluate parents whereas, the genetic components simply described the inheritance of a quantitatively expressed characteristic, rendering the predictions more subjective. Conclusively in a wheat breeding program, skipping information of F_1 might give a "Trojan horse" for an otherwise non heterotic genotype to express its favorable genes in the following generations while the combined use of the three groups of evaluation consists a powerful tool for breeder's use.

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