



CROP SCIENCE

Selecting tropical wheat genotypes through combining ability analysis

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Abstract: The selection of parents to originate promising base populations, as well as the knowledge of the gene effects controlling agronomic traits by means of diallel, are useful to drive genetic gains in Brazilian tropical wheat breeding programs. The goals of this study were to select tropical wheat parents with a high frequency of favorable alleles and segregating populations with high potential to originate superior progenies through partial diallel analysis. Thus, 14 parents were divided in two groups and crossed in a 7×7 partial diallel scheme to originate 49 F_1 combinations. After obtaining F_2 generation, the populations and the parents were evaluated in the field in the summer of 2021. Days for heading, plant height, rust and yellow spot resistance, and grain yield were evaluated. The data were subjected to partial diallel analysis. There were significant effects of general combining ability for all traits. The specific combining ability effect was significant for days for heading and plant height. The additive gene effects were predominant over the non-additive ones. The parents with the highest frequency of favorable alleles for the traits evaluated were selected in each group. Four populations with high genetic potential to originate superior progenies were selected.

Key words: genetic gain, favorable alleles, gene effect, *Triticum aestivum* L.

INTRODUCTION

World wheat production in the 2021/22 crop year is estimated at 771 million tons (USDA 2022). Brazil is expected to produce around 9 million tons, which represents approximately only 1% of world production. Despite the low production, Brazil is a major consumer of wheat, and the country imports large amounts of wheat each year to meet the domestic demand. In 2022, Brazil will import around 6.5 million tons of wheat, which represents almost half of the domestic consumption (CONAB 2022). These estimates reflect the need for significant progress in Brazilian wheat production in order to achieve self-sufficiency in the production of this important cereal.

Wheat breeding programs have a key role on the development of yielding cultivars adapted to environmental conditions and with traits that meet the requirements for industrialization. Thus, targeted crosses are performed between superior cultivars to obtain segregating populations that, subsequently, allow the extraction of superior lines. However, the selection of parents as well as segregating populations with better performance is not a trivial task, requiring a series of specific criteria for breeders, such as analysis of genetic diversity and genetic potential of the parents as a function of the frequency of favorable alleles (Casagrande et al. 2020).

Several methodologies can be used to identify potential crosses; some are based on information from the parents, such as parental average and genetic diversity. However, the breeder must seek information regarding the combining ability between the parents. In this sense, diallel analysis is a suitable methodology for determining the best combinations between parents and selecting the best performing segregating populations in autogamous species breeding programs (Teodoro et al. 2019, Moura et al. 2018, Mulbah et al. 2015). With diallels, it is possible to infer the ability of the parents to transfer favorable alleles to their offspring and to compare the performance of the combinations obtained. In addition, diallel analysis allows the understanding of the nature of the genes that control a given trait (Hei et al. 2016).

Diallel analysis proposed by Griffing (1956) has been used in wheat breeding programs for selecting parents, determining the nature of gene action of traits, identifying potential crosses, and selecting superior segregant populations (Mia et al. 2017, Pagliosa et al. 2017). However, the use of complete diallel is often limited when there is interest in evaluating a significant number of parents. Moreover, the breeder is not always interested in evaluating all possible combinations but rather identifying populations derived from parents of distinct groups. Thus, partial diallel analysis is a promising alternative for studying the combining abilities of a significant number of parents (Pimentel et al. 2013).

The selection of parents and segregating populations based on the combining ability may be hindered by environmental effect, due to its interaction with additive and non-additive gene effects (Gowda et al. 2012). Diallel analyses conducted in more than one environment allow the detection of the combining ability × environment interaction, making the process more efficient as the conclusions regarding the best parents and populations are particularized for each environment (Nardino et al. 2020). However, the low availability of seeds in the F₁ generation in autogamous species limits the investigation of the combining abilities in more than one environment. Diallel analysis in the F₂ generation is an interesting strategy to circumvent this problem, since the availability of seeds in this generation gives the opportunity to evaluate genotypes in two or more environments. Furthermore, the predictions made in F₂ generation provide confidence in the inferences regarding the potential of the parents and segregating populations (Pelegri et al. 2020).

The scarcity of information about the genetic potential of a significant number of tropical wheat parents and segregating populations, associated with the immediate need for genetic progress in Brazilian wheat production, justifies the use of robust biometric methodologies that allow the selection of progenies in segregating populations from crosses between dissimilar parents and with adequate combining ability in order to obtain high yielding and adapted cultivars, and guide the best use of the genetic potential of parents in tropical wheat breeding programs.

The objectives of this work were to select tropical wheat parents with a higher frequency of favorable alleles and segregating populations with greater potential to originate superior progenies through partial diallel analysis.

MATERIALS AND METHODS

Crossings

To obtain the experimental material, 14 parents (Table I) divided in two contrasting groups regarding high grain yield potential and adaptability to tropical climate (Group 1), technological quality and disease resistance (Group 2) were crossed in a partial diallel scheme to obtain 49 F₁ combinations (Table II). The crosses were performed during the summer of 2020 in three sowing seasons in a greenhouse belonged to the Agronomy Department of the Federal University of Viçosa, Minas Gerais, Brazil. After maturation, the spikes were manually trilled to obtain F₁ seeds, and stored in a cold chamber.

Table I. Information about the parents used for obtaining 49 F₁ combinations through partial diallel mating. Group 1: high grain yield potential and adaptability to tropical climate. Group 2: technological quality and disease resistance.

Group 1	Pedigree	Company	Year of release
BRS 264	Buck Buck/Chiroca//Tui	EMBRAPA	2005
BRS 404	MGS Aliança/WT 99172	EMBRAPA	2015
IAC 388	CETTIA / IAC 287/IAC 24	IAC	2014
IAC 389	WBLLI*2 / BRAMBLING	IAC	2016
CD 151	BRS 120/ORL 95282	COODETEC	2012
CD 1303	CD 150/BRS 177	COODETEC	2016
IPR Potyporã	PF 973515/LD 0221	IAPAR	2016
Group 2	Pedigree	Company	Year of release
Aton	Mestre/Fuste// Mestre	Biotrigo	2018
Duque	Toruk#3/Celebra//Noble	Biotrigo	2017
Astro	Toruk/Celebra	Biotrigo	2019
Toruk	Mirante/IBIO 0901//Quartzo	Biotrigo	2014
Madre Pérola	Marfim/Quartzo	OR Sementes	2017
ORS 1403	Inia Tijereta/Alcover//Abalone	OR Sementes	2016
Destak	ORS 1405/3/Marfim/Quartzo//Marfim	OR Sementes	2020

Note. EMBRAPA: Empresa Brasileira de Pesquisa Agropecuária; IAC: Instituto Agrônomo de Campinas; COODETEC: Cooperativa Central de Desenvolvimento Agrícola; IAPAR: Instituto Agrônomo do Paraná.

Table II. Partial diallel crosses scheme of 14 parents divided in two groups, where: Group 1: 1 = BRS 264; 2 = BRS 404; 3 = IAC 388; 4 = IAC 389; 5 = CD 151; 6 = CD 1303; 7 = IPR Potyporã; and Group 2: 1' = Aton; 2' = Duque; 3' = Astro; 4' = Toruk; 5' = Madre Pérola; 6' = 1403; 7' = Destak.

P1/P2	1'	2'	3'	4'	5'	6'	7'	Parents
1	Y _{11'}	Y _{12'}	Y _{13'}	Y _{14'}	Y _{15'}	Y _{16'}	Y _{17'}	Y ₁
2	Y _{21'}	Y _{22'}	Y _{23'}	Y _{24'}	Y _{25'}	Y _{26'}	Y _{27'}	Y ₂
3	Y _{31'}	Y _{32'}	Y _{33'}	Y _{34'}	Y _{35'}	Y _{36'}	Y _{37'}	Y ₃
4	Y _{41'}	Y _{42'}	Y _{43'}	Y _{44'}	Y _{45'}	Y _{46'}	Y _{47'}	Y ₄
5	Y _{51'}	Y _{52'}	Y _{53'}	Y _{54'}	Y _{55'}	Y _{56'}	Y _{57'}	Y ₅
6	Y _{61'}	Y _{62'}	Y _{63'}	Y _{64'}	Y _{65'}	Y _{66'}	Y _{67'}	Y ₆
7	Y _{71'}	Y _{72'}	Y _{73'}	Y _{74'}	Y _{75'}	Y _{76'}	Y _{77'}	Y ₇
Parents	Y _{1'}	Y _{2'}	Y _{3'}	Y _{4'}	Y _{5'}	Y _{6'}	Y _{7'}	

Note. P1: parents from group 1; P2: parents from group 2.

Generation advance

In winter 2021, the F₁ generation was sown in pots in the greenhouse to advance the generation and obtain F₂ seeds. In May 2021, the spikes were harvested, manually trilled, and the seeds were counted and separated for subsequent sowing in June 2021.

Field experiment

Two experiments were conducted in the winter of 2021 in the experimental areas of Professor Diogo Alves de Mello (20° 45' 14" S; 42° 52' 55" W; 648 m altitude), called Environment A (EA), and UEPE Aeroporto (20° 44' 41" S; 42° 50' 31" W; 659 m altitude), called Environment B (EB), both belonged to the Agronomy Department of the Universidade Federal de Viçosa, Minas Gerais, Brazil.

The experiments were designed in an 8 × 8 lattice design with two replications, containing 49 F₂ segregating populations, the 14 parents, and a commercial check used to complete the lattice (BRS 254). Plots consisted of three three-meter-long rows spaced at 0.20 m apart. The sowing density used was ten seeds per linear meter according to the method of conducting segregating populations adopted by McVetty & Evans (1980).

Management

Sowing was performed using a conventional system in Environment A. In environment B, the experiment was conducted in a no-till farming system, under *Urochloa brizantha* straw. At sowing, base fertilization was performed with 300 kg ha⁻¹ of the formula 08-28-16 (nitrogen, phosphorus, and potassium). In the covering fertilization, 90 kg ha⁻¹ of nitrogen in the form of urea (45% N) was distributed, divided in two phases: tillering, phase 20 to 29 of the Zadoks et al. (1974) scale; and booting, phase 40 to 46 of the Zadoks et al. (1974) scale.

The chemical control of weeds was done by applying the active ingredient metsulfurom methyl at a dose of 5 g ha⁻¹ of the commercial product, 20 days after emergence. The chemical control of aphids (*Metopolophium dirhodium* and *Sitobion avenae*) was done by applying the active ingredient acetamiprid at a dose of 375 g ha⁻¹ of the commercial product, in the post-anthesis phase. For diseases, no chemical control was performed, so that the natural reaction of the genotypes to the pathogens was observed. The experiment was conducted with sprinkler irrigation to meet the water needs of the crop.

Traits evaluated

Table III presents the traits evaluated as well as the descriptions of the evaluation methodologies.

Table III. Description and methodology of assessment of five wheat agronomic traits.

Code	Trait	Unit/ Scale	Assessment methodology
DH	Days for heading	days	Days in which 50% of the plants of the plot showed spikes
PH	Plant height	cm	Measured from the ground level to the beginning of the spike (excluding awns)
LR	Leaf rust	note	Notes from 0 to 4 attributed according to McIntosh et al. (1995) scale
TS	Tan spot	note	Notes from 1 to 5 attributed according to Lamari & Bernier (1989) scale
GY	Grain yield	g	Total grain mass from the plants of the plot

Statistical analysis

For each trait, the data were subjected to individual and joint analysis of variance to investigate the significance of the effects and estimate the residual mean square. Then, the general mean and the residual mean square were used to estimate the effects of the general (GCA) and specific (SCA) combining abilities. The diallel analysis proposed by Griffing (1956), adapted for partial diallels (Dhillon 1978, Vencovsky & Barriga 1992), was performed as follows:

$$y_{ijkl} = \mu + (b/e)_{ij} + GCA_{I_k} + GCA_{II_l} + SCA_{kl} + e_j + GCA_{I_k}e_j + GCA_{II_l}e_j + SCA_{kl}e_j + \epsilon_{ijkl}$$

where:

y_{ijkl} is the observed value of the kl -th genotype, in the i -th block, in the j -th environment; μ is the overall mean (fixed effect); $(b/e)_{ij}$ is the effect of the i -th block in the j -th environment (random), $(b/e)_{ij} \sim N(0; \sigma_{b/e}^2)$; GCA_{I_k} is the GCA effect of the k -th parent in group I (fixed); GCA_{II_l} is the GCA effect of the l -th parent of group II (fixed); SCA_{kl} is the SCA effect between the k -th parent of group I and the l -th parent of group II (fixed); e_j is the effect of the j -th environment, $e_j \sim N(0; \sigma_e^2)$; $GCA_{I_k}e_j$ is the interaction between the GCA effect of the k -th parent of group I and the j -th environment, $GCA_{I_k}e_j \sim N(0; \sigma_{GCA_e}^2)$; $GCA_{II_l}e_j$ is the interaction between the GCA parent of the l -th parent of group II and the j -th environment, $GCA_{II_l}e_j \sim N(0; \sigma_{GCA_e}^2)$; $SCA_{kl}e_j$ is the interaction between the SCA effect of parents k and l , from groups I and II, respectively, with the j -th environment, $SCA_{kl}e_j \sim N(0; \sigma_{SCA_e}^2)$; and ϵ_{ijkl} is the mean experimental error, $\epsilon_{ijkl} \sim N(0; \sigma_\epsilon^2)$. The following restrictions were considered: $\sum GCA_{I_k} = 0$; $\sum GCA_{II_l} = 0$; $\sum SCA_{kl} = 0$; $e SCA_{kl} = SCA_{lk}$.

The quadratic variance components of the general and specific combining ability were obtained by the method of moments, based on the mean square expectation, as follows:

$$\hat{\Phi}_{GCA_I} = \frac{MS_{GCA_I} - MSR}{JL}$$

$$\hat{\Phi}_{GCA_{II}} = \frac{MS_{GCA_{II}} - MSR}{JK}$$

$$\hat{\Phi}_{SCA_k} = \frac{MS_{SCA_k} - MSR}{IJ}$$

where:

K is the number of parents in group I; L is the number of parents in group II; I is the number of replications; J is the number of environments; MS_{GCA_I} and $MS_{GCA_{II}}$ are the mean squares of GCA of groups I and II, respectively; MS_{SCA_k} is the mean square of the SCA effect; and MSR is the residual mean square.

The relative importance of additive and dominance effects involved in the control of the traits ($\hat{\theta}$) was provided by the following expression (Baker 1978):

$$\hat{\theta} = \frac{\hat{\Phi}_{GCA_I} + \hat{\Phi}_{GCA_{II}}}{\hat{\Phi}_{GCA_I} + \hat{\Phi}_{GCA_{II}} + \hat{\Phi}_{SCA}}$$

Softwares

Individual and joint analyses of variance, as well as diallel analysis, were performed in GENES software (Cruz 2016). Figures were made in R software, version 4.0.2 (R Core Team 2020), using functions from the ggplot2 (Wickham 2016) and corrplot (Wei & Simko 2021) packages.

RESULTS

Diallel analysis

The analysis of variance of the joint partial diallel is presented in Table IV. The genotype source of variation was significant at 1% probability for all traits. There was a significant effect at 5% probability of the source groups for PH and TS, and at 1% probability for DH. The GCA I effect was significant at 5% probability for DH and TS, and at 1% probability for LR. The GCA II effect was significance at 1% probability only for PH. The mean effects of SCA were significant at 1% probability only for the traits DH and PH.

The interactions of GCA and SCA effects with the environment (Table IV) revealed the significance of GCA I × E at 5% probability for TS and GY, and at 1% probability for PH. The effect of GCA II × E was significant at 5% probability for DH. Finally, there was a significance of SCA × E at 5% probability for TS and at 1% probability for GY.

The estimates of the relative importance of the additive and non-additive effects involved in the control of the traits obtained through the quadratic components of variation were close to unity for DH, PH, LR, and TS, and equal to one for GY (Table IV).

Table IV. Joint diallel analysis for five wheat agronomic traits evaluated on environments A and B.

Source of variation	DF	Mean square				
		DH	PH	LR	TS	GY
Genotype (G)	62	7.99**	123.53**	1.41**	2.07**	12789.92 ^{ns}
Groups	1	180.87**	173.47*	0.16 ^{ns}	2.58*	7181.87 ^{ns}
GCA I	6	12.84*	251.29 ^{ns}	7.11**	8.99*	42414.39 ^{ns}
GCA II	6	5.56 ^{ns}	347.77**	2.38 ^{ns}	2.76 ^{ns}	28346.98 ^{ns}
SCA	49	4.16**	79.41**	0.62 ^{ns}	1.14 ^{ns}	7371.94 ^{ns}
Environment (E)	1	0.27 ^{ns}	6.85 ^{ns}	0.00 ^{ns}	0.02 ^{ns}	10.82 ^{ns}
G × E	62	2.24 ^{ns}	51.67 ^{ns}	0.46 ^{ns}	0.93**	18710.05*
Group × E	1	0.96 ^{ns}	17.47 ^{ns}	0.86 ^{ns}	0.00 ^{ns}	14945.88 ^{ns}
GCA I × E	6	1.65 ^{ns}	199.75**	0.09 ^{ns}	1.39*	23881.71*
GCA II × E	6	5.69**	38.28 ^{ns}	0.69 ^{ns}	0.73 ^{ns}	13871.09 ^{ns}
SCA × E	49	1.92 ^{ns}	35.87 ^{ns}	0.46 ^{ns}	0.93*	18746.12**
Residual	98	1.82	39.81	0.40	0.62	9455.80
ϕ_{GCA_i}		77.14	1480.36	46.97	58.59	230710.13
$\phi_{GCA_{ii}}$		26.18	2155.72	13.86	14.98	132238.26
ϕ_{SCA}		2.34	39.60	0.22	0.52	0.00
θ		0.98	0.99	0.99	0.99	1.00

Note: DF, degrees of freedom; DH, days for heading; PH, plant height; LR, leaf rust; TS, tan spot; GY, grain yield; GCA I, general combining ability of parents from group I; GCA II, general combining ability of parents from group II; SCA, specific combining ability; ϕ_{GCA_i} , quadratic component of variation of the general combining ability of parents from group I; $\phi_{GCA_{ii}}$, quadratic component of variation of the general combining ability of parents from group II; ϕ_{SCA} , quadratic component of variation of the specific combining ability; θ , relative importance of the additive and non-additive effects.

** and * Significant at 5 and 1% probability by the F test.

^{ns} Not significant at 5% probability by the F test.

GCA I effects

The estimates of the mean effects of GCA I are presented in Figure 1. High GCA values, positive or negative, indicate that a given parent differs from the others with respect to the frequency of favorable alleles. Low magnitudes point to the non-significance of the effect. Considering the traits related to cycle and disease, high and negative estimates are desired, whereas for grain yield, high and positive estimates are desired.

For the trait days for heading (Figure 1a), the parents with the lowest GCA estimates were BRS 404 (-0.62) and BRS 264 (-0.45). Considering the trait leaf rust (Figure 1b), the lowest estimates of the GCA effect were observed for CD 1303 (-0.41), IAC 389 (-0.32), and IPR Potyporã (-0.32). The analysis of GCA I in the two environments, as a result of the interaction (Figure 2), shows that the lowest effect estimates for plant height were from BRS 264, with values of -4.48 and -2.44 in EA and EB, respectively, and CD 1303, with a value of -5.60 in EA (Figure 2a). For tan spot (Figure 2b), the lowest values were from the parents IAC 389 (-0.78) and IPR Potyporã (-0.50) in EA, and CD 1303, with values of -0.37 and -0.33 in EA and EB, respectively.

For the trait grain yield, the highest estimate of GCA in EA was for the parent CD 1303 (79.31). The estimates of this effect in EB suggest that it is non-significant because of the low magnitudes.

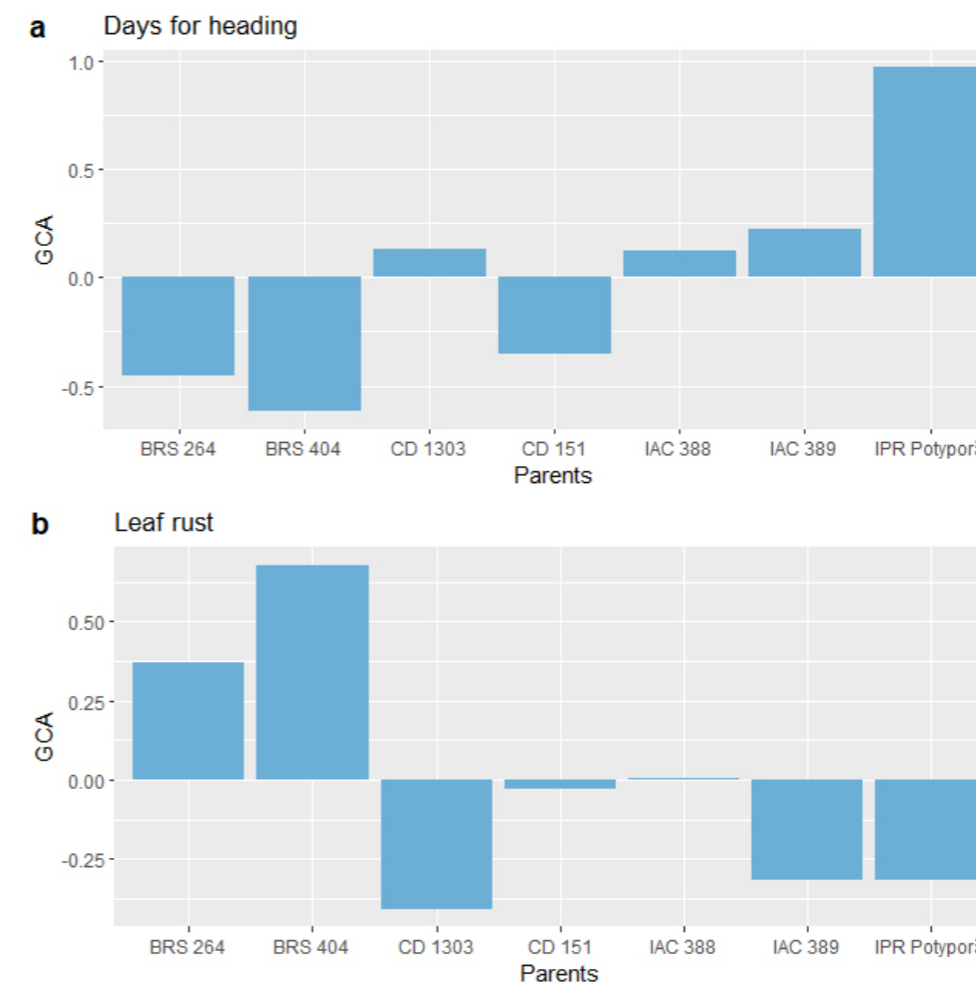


Figure 1. Mean effects of general combining ability of parents from group I for days for heading (a) and leaf rust (b).

GCA II effects

The lowest GCA II estimates for the plant height trait (Figure 3) were from Astro (-3.03) and Toruk (-2.53). The interaction of the effect of GCA II with the environment for the traits days for heading shows that in EA, the lowest effect estimates were presented by Astro (-0.79) and Duke (-0.45), while in EB, the lowest effect estimates were from Aton (-0.32) and Duke (-0.57) (Figure 4).

SCA effects

As with GCA, the interpretation of SCA is relative to its magnitude and direction. Thus, for traits related to cycle, height, and diseases, the major interest resides in high and negative estimates of this effect.

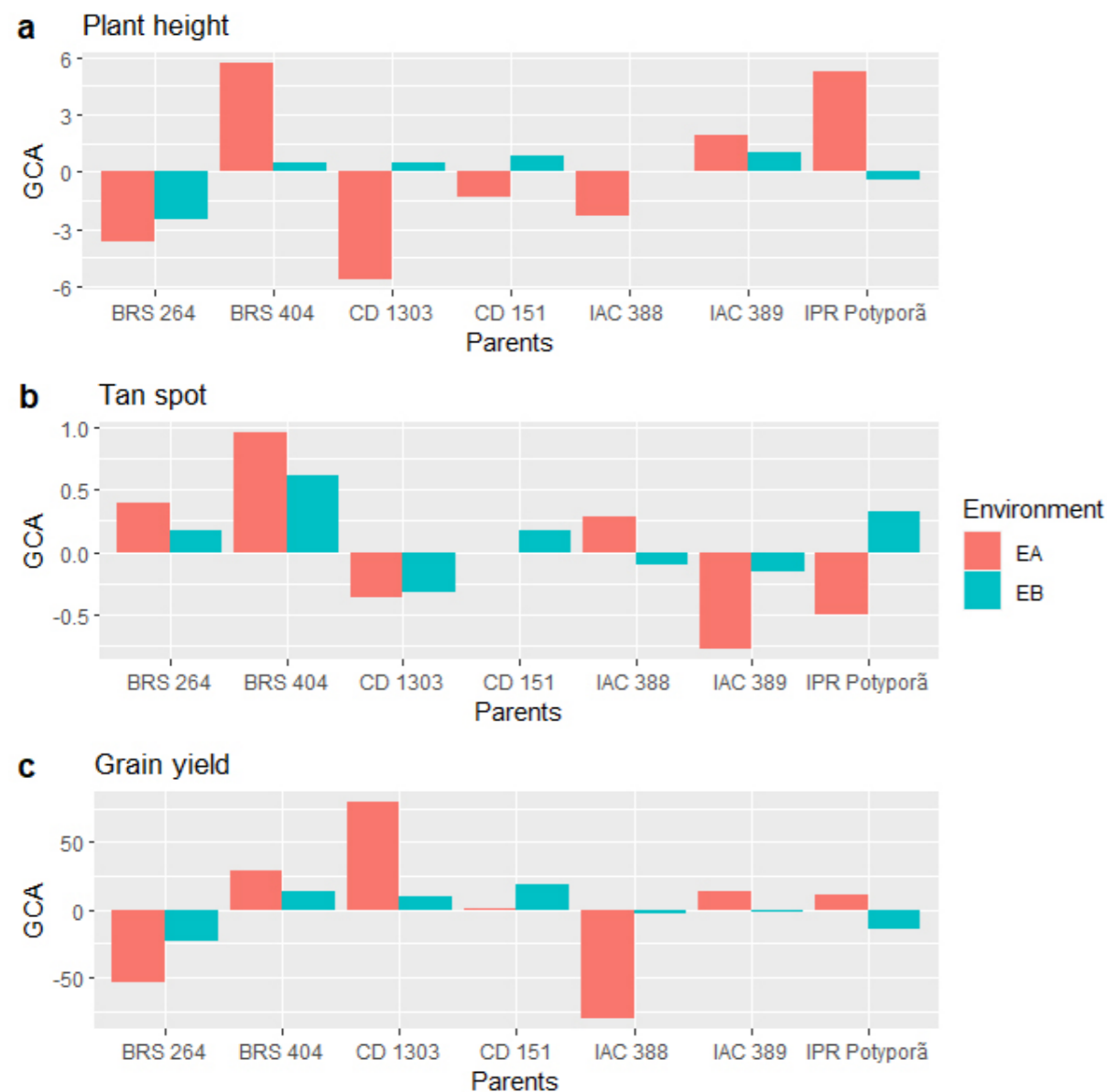


Figure 2. Effects of general combining ability of parents from group I on environments A and B for plant height (a), tan spot (b) and grain yield (c).

For grain yield, high and positive estimates are desired. However, the most important premise for the selection of the best combination is that at least one of the parents involved in the crossing presents high estimates (positive or negative) for GCA.

Given the average effects of SCA on the trait days for heading (Figure 5a), the population BRS 264/Destak (-1.28) should be chosen. Considering the trait plant height (Figure 5b), the best ones were BRS 404/Astro (-2.43) and CD 151/Toruk (-6.01). For the trait tan spot, the lowest SCA estimates in EA were observed for IAC 389/Duque (-0.71) and IPR Potypor/ORS 1403 (-0.98) (Figure 6a), and CD 1303/1403 (-1.05) in EB (Figure 7a).

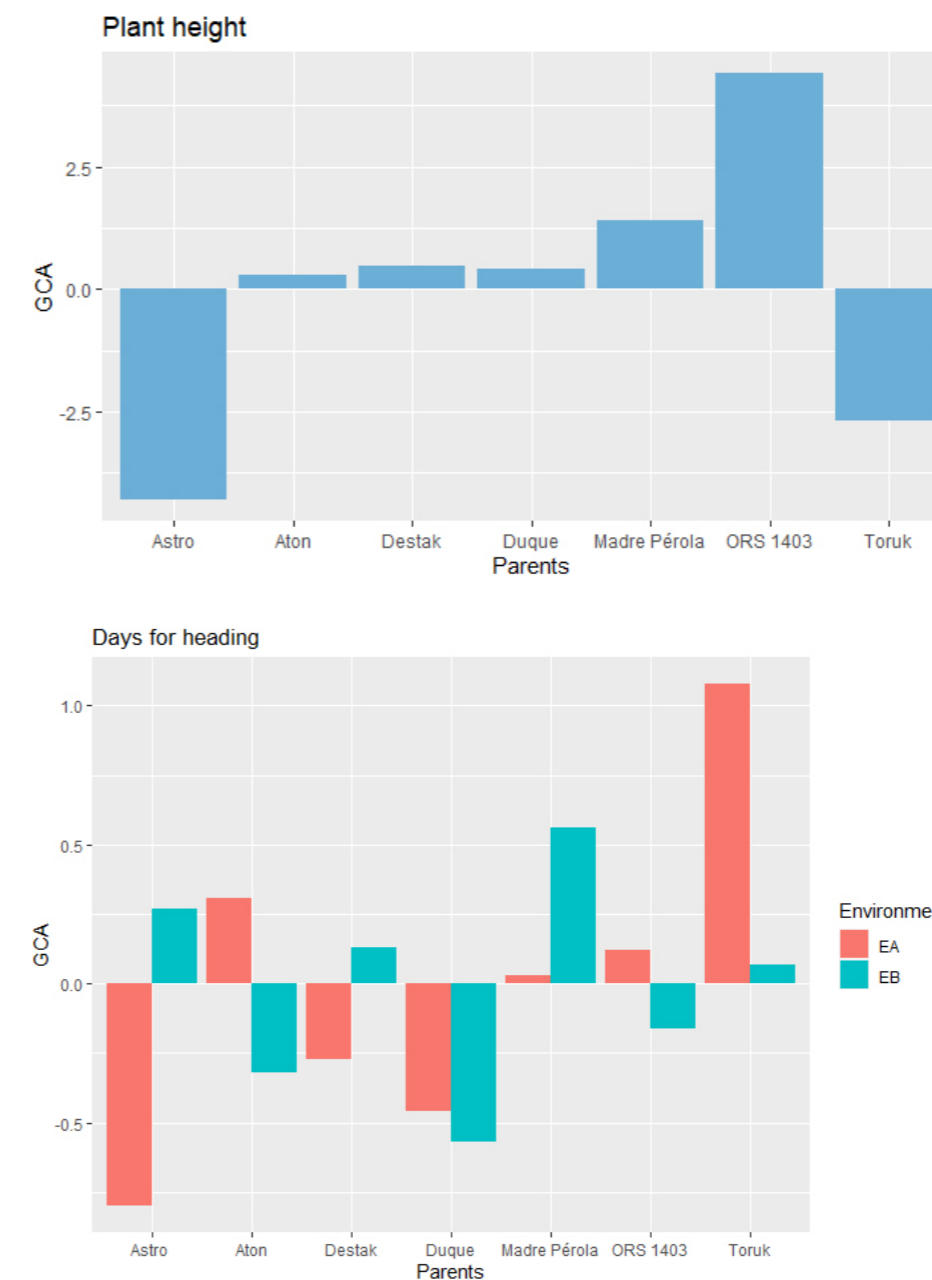


Figure 3. Mean effects of general combining ability of parents from group II for plant height.

Figure 4. Effects of general combining ability of parents from group II on environments A and B for days for heading.

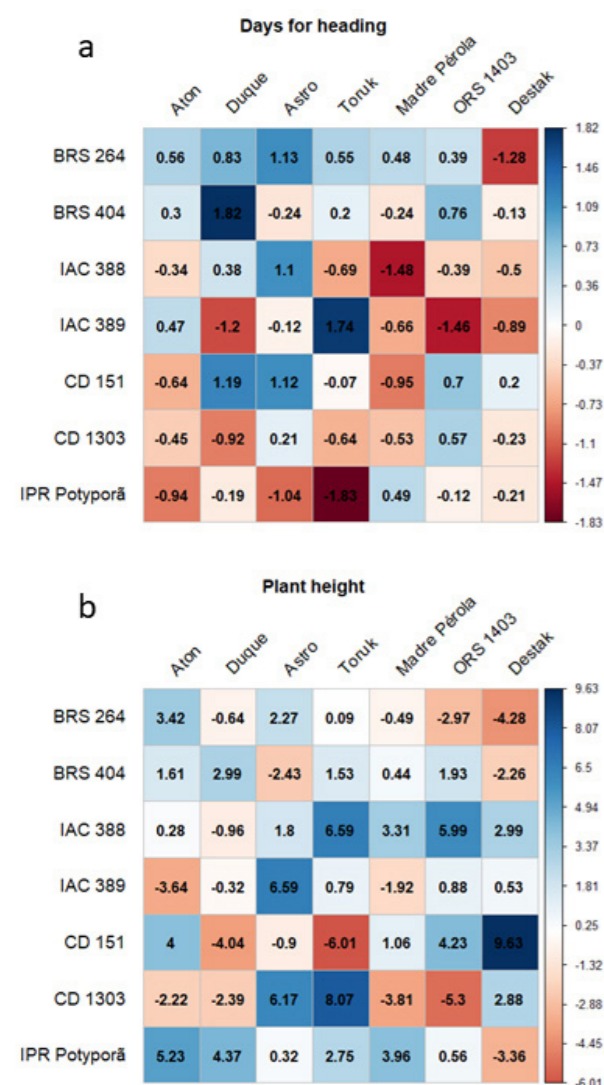


Figure 5. Mean effects of the specific combining ability between 14 parents for the traits days for heading (a) and plant height (b).

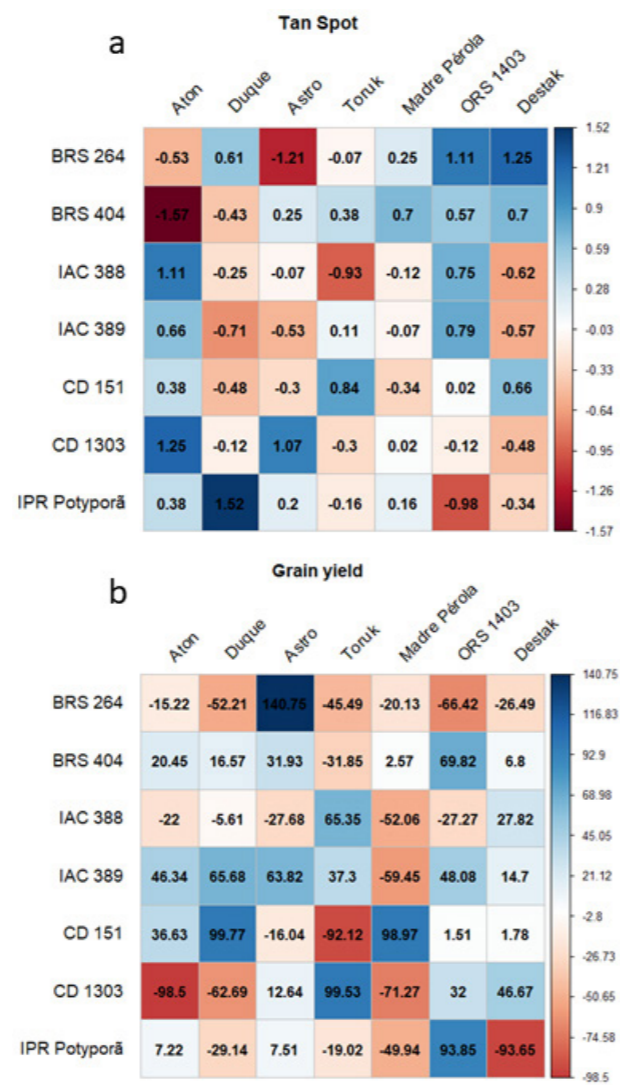


Figure 6. Effects of the specific combining ability between 14 parents for the traits tan spot (a) and grain yield (b) on environment A.

For the trait grain yield, considering EA, the best combination is the one with high SCA and involving the parent CD 1303, in this case, it is the cross CD 1303/Tonuk (99.53) (Figure 6b). The selection of the best population in EB based on SCA would be erroneous since the GCA estimates of the parents in this environment were of low magnitude.

DISCUSSION

The significance of the mean effects of GCA I of the GCA I × E interaction indicates the existence of variability in the general combining ability of the parents of group I. The same occurs with the parents of group II, considering the traits in which the effects of GCA II and GCA II × E were significant. The non-significance of the effect of GCA II and the GCA II × E interaction for diseases can be explained by the

fact that this group consists of parents with high resistance to major pathogens, as demonstrated by Casagrande et al. (2020), which suggests that these parents do not differ from each other with respect to the frequency of favorable alleles for this trait. The significance of the mean effects of SCA and the SCA × E interaction for the traits DH, PH, TS, and GY points to the existence of variability of non-additive gene effects.

It is possible to infer that both additive and non-additive effects are important in controlling traits such as height, cycle, disease resistance and grain yield (Fellahi et al. 2013). Even so, the superiority of the quadratic components of GCA of groups I and II over the quadratic component of SCA evidenced by the relative importance of additive and dominance effects, indicates predominance of additive gene effects over non-additive effects (Hei et al. 2016).

The interactions of GCA and SCA effects with environments show that the effects are not consistent across environments (Kamara et al. 2021). Given that the relative contributions of additive and dominance effects interact with environmental effects, wheat breeding programs should take advantage of information regarding environments and the G × E interaction for optimization of crosses and the choice of evaluation sites.

The general combining ability is a function of the average behavior of a given parent in its hybrid combinations or the frequency of favorable alleles (Cruz et al. 2012). Thus, we can infer that there are parents that contribute differentially to the manifestation of the considered traits in their offspring, increasing or reducing their values. This information is important because, from the identification of promising genotypes regarding the GCA, there is security in the choice of parents to be included in future crossing blocks.

Specific combining ability refers to the behavior of a given parent in specific combinations, or it represents the deviation in the behavior of a given combination compared to what would be expected in the general combining ability of the parent (Teodoro et al. 2019). Therefore, SCA is related to non-additive gene effects, mainly dominance deviations. As such, its significance is a function of the gene complementarity or divergence between the parents involved in a cross. In this experiment, the non-significance of SCA and the SCA × A interaction for LR suggests small complementarity between the parents for this trait.

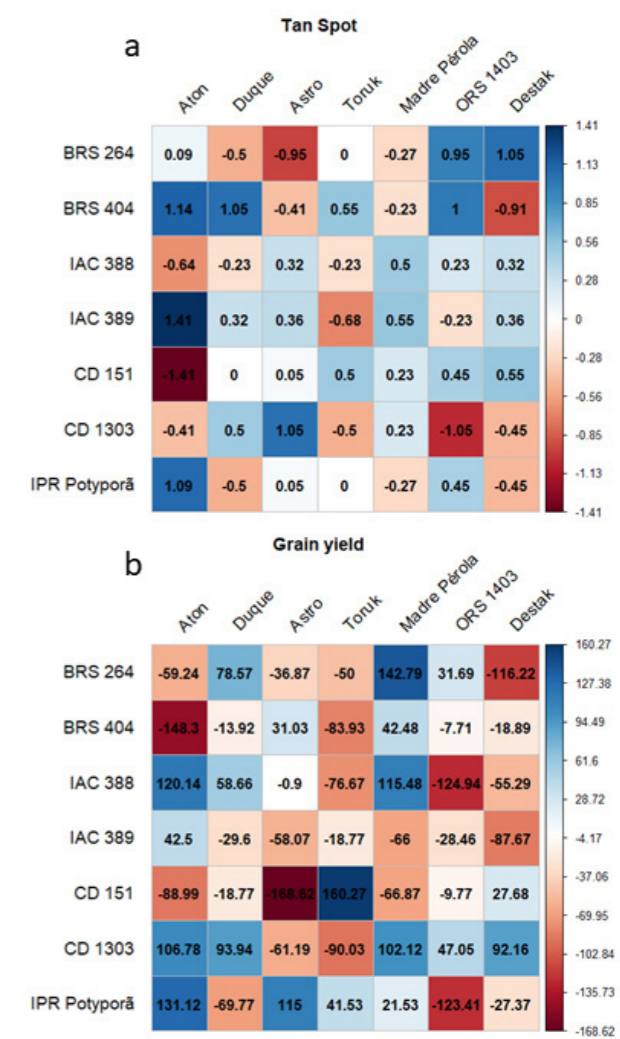


Figure 7. Effects of the specific combining ability between 14 parents for the traits tan spot (a) and grain yield (b) on environment B.

The non-significance of the SCA effect may also result from the small contribution of dominance effects to the expression of a given trait in the F_2 generation. Pimentel et al. (2013) found no significance of specific combining ability for grain yield in F_2 and F_3 generations of wheat. Given that in the F_2 generation there is a decrease in the frequency of loci in heterozygosity, evaluation of SCA in this generation or in more advanced generations may provide biased estimates of this effect. Even so, the low seed availability normally obtained in the F_1 generation in autogamous species, associated with the greater importance of additive effects, justifies the estimation of the specific capacity in the F_2 generation.

Another hypothesis for the non-significance of SCA for leaf rust is a possible insufficient genetic divergence between the parents. Sherlosky et al. (2018) stated that there is a certain genetic similarity between the germplasm of different wheat breeding programs in Brazil, a consequence of Law 9456 of 1997, which allows the exchange of germplasm between institutions.

Partial diallel analysis is an efficient strategy to study the combining abilities of a significant number of parents (Lima et al. 2022). The estimates of GCA and SCA parameters in the F_2 generation allowed inferences to be made regarding the potential of the parents and segregating populations, besides allowing the conduct of trials in two environments.

The predominance of the additive effects over the non-additive ones found in this work corroborates with the results obtained by Valério et al. (2009), Pagliosa et al. (2017), and Hei et al. (2016). Thus, we can infer about the existence of favorable alleles capable to be transmitted to their offspring. When the additive effects are pronounced, greater are the possibilities of expressive gains with selection since these effects are cumulative over generations and are the main source of genetic variability to be exploited by most autogamous breeding programs (Teodoro et al. 2019).

The dominance deviations become of greater importance when the objective of the breeding program is the development of hybrids, in view of the exploitation of the heterosis (Whitford et al. 2013). Heterosis is defined as the average superiority of the F_1 relative to the average of its parents (Shull 1948) and is a function of allelic complementarity, degree of dominance, and epistatic interactions (Melchinger et al. 2007). Although heterosis has been found in wheat for the trait grain yield (Longin et al. 2013, Adhikari et al. 2020), when the main interest lies in obtaining lines, additive effects are considered more important than dominance deviations, which complicate the selection process.

Obtaining GCA estimates can be extremely useful in the initial stages of a breeding program, since inferences regarding the best parents are made through the interpretation of this parameter. Furthermore, in the absence of significant SCA effects, GCA can be used as a predictor of the behavior of a given parent in hybrid combinations (Pimentel et al. 2013). Considering what has been conceptualized so far, the selection of the best parents of each group for the set of evaluated traits can be proceeded.

Regarding the cycle, the combining abilities of the parents BRS 264 and BRS 404 (Group I) and Duque (Group II) should be used. These parents, when involved in a given crossing, contribute to the reduction of the cycle in their offspring. Aiming to reduce plant height, the parents CD 1303 and BRS 264 (Group I), Astro and Toruk (Group II) stand out. Obtaining cultivars with low height is interesting, especially in irrigated production systems that use high amounts of nitrogen fertilization. In addition, the reduction in the height of wheat plants may be associated with greater responsiveness to

environments with water stress (Tahmasebi et al. 2014), which makes it interesting to include these parents in crossing blocks aiming the development of cultivars adapted to regions characterized by frequent incidence of water shortages (Pasinato et al. 2018).

The development of cultivars resistant to major diseases in wheat should evaluate the use of the combining abilities of the parents CD 1303 and IAC 389, both from Group I, for resistance to rust and yellow spot. The parents of Group II should also be included in future crossing blocks aiming at the development of genotypes resistant to major diseases since they do not differ regarding the high frequency of favorable alleles for this trait.

For the grain yield trait, CD 1303 stood out in relation to all other parents regarding its combining ability, suggesting a high frequency of favorable alleles for this trait and the potential use of this parent in breeding programs. Mezzomo et al. (2021) performed a prediction of the genetic potential of 56 segregating populations of tropical wheat using the methodology of Jinks & Pooni (1976) and concluded that, from seven populations with the greatest potential for obtaining superior lines for grain yield, four had the CD 1303 cultivar as a parent.

For the development of superior lines, the inclusion of the parents described above in crossing blocks should be evaluated due their general combining abilities. In addition, the information coming from the specific combining abilities should also be considered, considering the traits governed by genes whose loci exhibit some dominance deviation. In this case, the major interest is to obtain superior segregants capable to originate superior lines in relation to the desired traits (Joshi et al. 2004). Thus, the crosses that had the lowest SCA estimates for cycle, plant height, and yellow spot were BRS 264/Destak, CD 151/Toruk, and CD 1303/1403, respectively. Considering grain production, the CD 1303/Toruk cross outperformed.

In this work, the superiority of the additive effects in relation to the non-additive ones indicates the possibility of using the Single Seed Descent (SSD) method to conduct the segregating populations (Kamaluddin et al. 2007). One of the advantages of using the SSD method is that it provides the maximum additive genetic variance between populations, so that selection in advanced generations will benefit from the greater existing additive genetic variance (Borém & Miranda 2013). The predominance of additive effects also provides security in the selection of superior populations already in early generations (Pimentel et al. 2013). As a reflection of this, there is optimization of time and resources in breeding programs, focusing efforts on the evaluation of really promising populations. Modifications in the methods of conducting segregating populations can be introduced depending on the objectives of the breeder.

As for the specific combining ability, the best crosses can be selected, as previously discussed, to originate superior segregants in relation to the considered traits. Besides this, crossings between selected populations can be an interesting strategy in view of obtaining superior recombinants, being applicable, for example, in a recurrent selection program. This strategy would allow the breaking of possible existing links between genes, promotion of recombination, and concentration of favorable alleles in the gene pool (Joshi et al. 2004), allowing the continuous improvement of the traits with simultaneous maintenance of the existing genetic variability. After successive cycles of selection, we may include new parents for the expansion of variability, concomitant to the displacement of the average in the desired direction.

CONCLUSIONS

The parents with the highest frequency of favorable alleles are: BRS 264 and BRS 404 (group I), Astro and Duque (group II) for cycle; CD 1303 and BRS 264 (group I), Astro and Toruk (group II) for plant height; CD 1303 and IAC 389 (group I) and all seven parents in group II for disease resistance; and CD 1303 (group I) for grain yield. The populations with the greatest potential to originate superior progenies are: BRS 264/Destak, CD 151/Toruk, CD 1303/1403, and CD 1303/Toruk for cycle, plant height, yellow spot, and grain yield, respectively.

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