Research article

Evaluation of the genetic determinism of an F1 generation of barley resulting from a complete diallel cross between autochthones and introduced cultivars

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ABSTRACT

An experimental trial was carried out during two successive crop years, (2015/2016 and 2016/2017). The study focused on an F1 generation of barley (*Hordeum vulgare* L.), composed of twenty hybrids, from a complete diallel cross between autochthones and introduced cultivars.

The aim is to bring together in one combination the maximum of favorable genes existing in local and introduced genotypes. The evaluation of the genetic determinism of parental lines and their descendants, through the measurement of six quantitative variables, is ensured thanks to a detailed genetic analysis according to the model of Griffing (1956) and confirmed by the graphic model of Hayman (1954).

The results obtained reveal the existence of a great genetic variability between the hybrids and between their parents; additive and non-additive genetic effects are involved in the control of the variables evaluated. The variance ratio of general combining ability (GCA) and the specific combining ability (SCA) is less than one unit which explains the preponderance of the dominant genes, with a super dominance involved in the expression of the length of the spike, the number of grains per spike and the productivity per plant; on the other hand, complete and partial dominance respectively control the expression of the height of the plants and the weight of one thousand grains.

1. Introduction

Barley (*Hordeum vulgare* L.) is one of the world's largest cereal crops with an estimated production of 141 Mt (Faostat, 2018), primarily for livestock feed and malt manufacture (Newton et al., 2011), in addition, it can be a valuable complement to whole plant silage for bioenergy production (Bernhard et al., 2018), with barley accounting for 15% of world cereal consumption. This species is cultivated in a wide range of environments; it adapts to very fertile areas with high production but also fits well in environments characterized by a great climatic variability (Dawson Ian et al., 2015). This adaptation is linked to a short development cycle and an appreciable growth rate at the beginning of the cycle (Benmahammed, 2005). This importance of barley is due in part to the improvement of cultural management, but also to genetic progress (Hanifi, 1999).

The improvement of barley requires the exploitation of its genetic variability in order to guarantee the capacity of adaptation, to ensure the possibility of introducing new selection criteria and finally, to allow the increase of the genetic gain during the following generations. According to Gallais (2013), the genetic improvement of barley aims to bring together in the same genotype, the variety, the maximum of favorable genes. Research should focus on the selection of biotic and abiotic stress tolerant varieties; productive and stable in their production (Hanifi, 1999). However, after a certain period, the performance of a given variety may decrease (Bouzerzour and Benmahammed, 1993). Indeed, it is important to regularly renew the existing range of varieties (Khaldoun et al., 2006).

The selection of hybrids more efficient than their parents is very practical (Zhang et al., 2015), therefore, this way takes enough time. But, the prediction of the performances of the hybrids could be analyzed from the first generation F1. Indeed, the general combining ability is considered as a useful indirect criterion for the choice of the parents (Zhang et al.,

2015), the parents having high GCA values could be used in the creation of the improved lines (Mühleisen et al., 2013). The SCA, specific combining ability, makes it possible to select the best favorable alleles (Madić et al., 2014) when a hybrid combines well only in certain crosses, which means that it has a good SCA (Qu et al., 2012). In a F1 generation, the study of agronomic parameters as well as grain yield is very important for the analysis of genetic determinism of hybrids (Zhang et al., 2013) the mode of action of genes provides information on the forms of transgression of characters (Klykov et al., 2018), indeed, the mode of action of genes in F1 hybrids is classified as having an additive and non-additive expression, the additive gene expression is where the level of gene expression of F1 hybrids is equal to the level of gene expression of the average parent. On the other hand, non-additive gene expression occurs when the level of gene expression in F1 hybrids is different from the average parent (Fujimoto et al., 2018). Thanks to the use of DNA chips then, the sequencing of RNAseq, genes potentially involved in the expression of characters have been identified (Swanson-Wagner et al., 2006). Today, many studies focus on trancriptome analysis to compare parental lines with their F1 hybrids. On the other hand, quantitative genetics remains a powerful tool in the study of parental lines and their descendants.

The present research was initiated with the aim of (i) combining in the same combination the maximum of favorable alleles (ii) to select the best genitors and the best hybrids (iii) to have an idea about the mode of action of genes and transgression of characters.

2. Materials and methods

2.1. Experimental protocol

The studied plant material consists of twenty hybrids resulting from a complete diallel cross between five varieties of six-row barley, including two autochthonous genotypes (Saida and Tichedrett) and three other introduced (Plaisant, Bahia and express). The choice of these parents was based on resistance to different types of diseases and the average length of the straw. The experimental tests were carried out during two successive crop season (2015/2016 and 2016/2017). The experimental design adopted was the randomized complete block design with four repetitions. The crosses were made according to a complete diallel plan which includes the P^2 combinations in pairs. The conduct of the tests was followed in a very regular manner where medium plowing and superficial manners were carried out in order to prepare a suitable seedbed for the establishment of the crop. The F1 generation was studied during the second campaign; the weeding and the cover fertilizer were done at the opportune time.

2.2. Methods of study

2.2.1. The measured characters

Measurements and counts were made in the field and in the laboratory for five agronomic parameters: the height of the plants at flowering; the length of the ear; the number of ears per plant; the number of grains per ear; the weight of a thousand grains and the productivity of the plant.

2.2.2. Genetic analysis techniques

The analysis is divided into two parts, for model I the block effect was considered as a random variable and the varieties as a fixed variable. Concerning the diallel analysis of Griffing (1956) and Hayman (1954), the parents; a series of F1 and the reciprocals were used for each treatment separately.

2.2.3. Demonstration of genetic effects

The first part requires the analysis of the crossover effect because before undertaking a detailed analysis of the effects, it makes sense to ensure that this genetic variation is significant by decomposing the following variances: variation related to crosses; variation related to repetitions; repetition-crossover interaction (if possible) and residual variation.

2.2.4. Genetic analysis techniques using the Griffing method (1956)

The second part of the analysis concerns the decomposition of genetic effects (Demarly, 1977).

2.2.5. Genetic analysis techniques using the Hayman graphical method (1954)

The decomposition of genetic effects according to the Hayman model (1954 and 1959), which makes it possible to determine the dominance and the value of the genetic stock of each parent from the point of view of their intended character, and to predict the existence of additive actions of parallel genes determining fixable transgressive combinations in terms of barley improvement. This method is based on the analysis of variances and covariances to deduce the additive and dominance effects involved in the inheritance of the traits studied (Farshadfar et al., 2011).

The progress of the analysis includes not only the search for conclusions but also the verification of certain assumptions related to the model. Before any analysis, it is necessary to know if there is a maternal effect for all the combinations. This verification is done by the STUDENT "T" Test for both averages; one grouping all the values above the diagonal, the other the values of the character below the diagonal. The mean values are obtained by summing the two values of the two reciprocal crossings on 2: that is (xri + xir)/2. From these averages the variance and the covariance associated with each family:

- Variance of parents: $Vp = (1/n - 1) [\sum X_{ii}^2 - (\sum X_{ii})^2 / n]$; (1)

- Variance of r families: $Vr = [\sum X_{ri}^2 - (\sum X_{ri})^2 / n] / (n - 1)$; (2)

- Covariance of r families: $Wr = [\sum X_{ii} . X_{ri} - (\sum X_{ii} . \sum X_{ri}) / n] / (n - 1)$ (3)

For the calculation of W1 we have:

- $nX_{ii}X_{ri} = (X11) 2 + (X22.X12) + (Xrr.X1r) + (Xnn.X1n)$ (4)

- $nX_{ii} = X11 + X22 + ...Xrr .... + Xnn$ (5)

- $nX_{ri} = X12 + X1r + X1n ... .. + Xrn$ (6)

Each line Lr is therefore represented by three values:

- its eigenvalue Yr for the studied character (Xrr);
- its variance Vr of the family formed of all Xri hybrids;
- its covariance Wr between hybrids Xri is self-fertilization.

From these data, we obtained the following genetic components: (i) variations due to an additive effect (D); (ii) the variation components due to the effect of gene dominance (H1); (iii) calculations to predict the proportion of positive and negative genes in parents (H2) the covariance between additive effects and non-additive effects Fr; (iv); (v) dominance effects (as algebraic sum on all heterozygous loci in all crosses) (h_2); (vi) expected environmental components of variation (E); (vii) the average degree of dominance $(H 1/D)^{1/2}$; (viii) the proportion of genes with positive and negative effects in parents (H 2/4H 1); (ix) the proportion of dominant and recessive genes in parents (KD/Kr); (x) the number of gene clusters that control the trait and exhibit dominance (h^2/H_2); (xi) heritability in the broad sense (H^2); (xii) heritability in the narrow sense (h^2).

2.3. Statistical analysis techniques

The results of the experiment were analyzed using software: IBM-SPSS. Statistics, version 20 (Statistics Package for Social Science). The materiality threshold used is 5%; if the probability is greater than or equal to this threshold, the effect is insignificant. On the other hand, if the probability is less than 5%, we admit the existence of a significant overall effect, and when the probability is less than 1% we consider that the effect is very highly significant.

Table 1

Study of parental lines and F1 generation by highlighting the genetic effects of measured variables.

Characters studied	HPF	LE	NE/P	NG/E	WTG	PRO
Parental lines						
Average general	59,652	07,409	07,050	52,300	40,500	15,094
Probability	00,000	00,001	00,024	00,000	00,000	00,005
CV%	17,660	13,780	18,580	24,970	14,440	35,850
The F1 generation						
Average general	55,420	08,690	09,630	58,750	42,730	24,010
Probability	00,000	00,000	00,000	00,000	00,000	00,000
CV%	16,540	21,170	10,700	11,480	10,900	27,690
Average of squares						
Genotypes	203,201***	001,53***	010,87***	129,89***	060,24***	087,99***
Blocks	053,13	003,410	000,517	020,004	001,72	002,13
Interaction	026,30	000,41	001,370	005,78	003,57	024,70

HPF = height of the plant at flowering in (cm), LE = length of the ear in (cm), E/P = number of ears per plant, NG/E = number of grains per ear, WTG = weight of one thousand grains in (g), PRO = productivity per plant in (g), and CV = coefficient of variation, *** highly significant at p $\leq$ 0,001.

3. Results

3.1. Studies of parent lines and F1 generation

Analysis of the variance of the genotype factor reveals a highly significant to significant varietal effect for all the traits measured in the parental lines. In contrast, in the F1 hybrids, the analysis of the variance indicates a very highly significant genotype effect for all parameters tested (Table 1).

Based on (Table 1), the general averages of the traits measured in F1 hybrids are greater than the averages noted in their parents, with the exception of the plant height at flowering parameter for which the mean values of the hybrids are lower. the mean values of their parents (55.42 cm in hybrids and 59.65 cm in broodstock). The coefficient of variation indicates higher variations in hybrids relative to their parents for the parameters HPF and LE respectively (16.54 and 21.17%). However, this coefficient reveals relatively important values in the parents that the hybrids for the rest of the measured characters. The highlighting of genetic effects reveals the performance of each hybrid within its block. Variance analysis shows highly significant differences for all parameters evaluated in F1 hybrids. The F test observed is very high compared to the theoretical F test for a probability of 0.001 and a risk of error of the first α species of 5%.

3.2. Decomposition of genetic effects by the Griffing method (1956)

The detailed decomposition of genetic effects by the Griffing method (1956) reveals highly significant differences in general and specific combining ability, whereas the analysis of the variance indicates non-significant differences for the maternal and specific effects of all the evaluated parameters. The GCA/SCA variance ratio is less than one for all tested parameters except the thousand grain weight (Table 2).

The ranking of parental varieties in descending order of their overall skill suitability values reveals that the Bahia and Plaisant varieties occupy the first position followed by Saida and Tichedrett (Table 3).

Both introduced cultivars (Bahia and Plaisant) expressed better GCA values for the parameters: plant productivity; ear fertility; the length of the ear and the height of the plant at bloom, indeed, the Bahia variety tends to transmit to its descendants a better productivity of the plant and a better fertility of the ear on the other hand, the genotype Plaisant tends to transmit to his descendants a better length of the spike and a low height of the plant (wanted character to decrease the height of the pouring straws). For its part, the autochthon variety, Tichedrett, expresses better GCA values for the number of ears per plant character and for its part; the second autochthon variety, Saida, has a good capacity to transmit to its descendants a better weight of one thousand grains (Table 3).

The high SCA genotypes are: Bahia X Pleasant for the length of the ear; the fertility of the ear and the productivity of the plant; Saida X Bahia for the weight of one thousand grains and Bahia X Saida for the number of tillers ears. In contrast, crosses Bahia X Tichedrett and Plaisant X Bahia expressed low SCA effects for plant height at flowering (Table 4).

3.3. Analysis of genetic effects by the Hayman's method (1954)

The interpretation by Hayman's method can only be realized when certain hypotheses are verified, such as diploid segregation; reciprocity;

Table 2

Analysis of the variances of the diallel cross: Model of Griffing (1956).

Characters studied	Average of squares				GCA/SCA
	GCA	SCA	Maternaleffect	Specific effect	
HPF	022,46***	154,59***	001,57[ns]	000,10[ns]	000,14
LE	000,24***	001,05***	000,11[ns]	000,20[ns]	000,23
NE/P	000,60***	010,05***	000,67[ns]	000,22[ns]	000,06
NG/E	009,08***	041,12***	000,03[ns]	000,20[ns]	000,03
WTG	026,52***	759,52***	000,47[ns]	000,48[ns]	000,25
PRO	007,76***	076,66***	000,04[ns]	001,18[ns]	000,10

*** Highly significant at p $\leq$ 0,001, ns: not significant.

Table 3

General combining ability (GCA) values for each parent.

Parental lines	HPF	LE	NE/P	WTG	NG/E	PRO
Saida	-01,57	00,09	-00,57	02,75	-03,63	-01,71
Bahia	-01,49	00,18	00,09	-00,62	03,92	01,60
Plaisant	-02,07	00,26	-00,11	00,49	-01,24	01,17
Tichedrett	00,59	-00,09	00,68	-01,80	-01,04	-01,74
Express	04,54	-00,45	00,05	-00,79	02,03	00,69

Table 4
Specific combining ability (SCA) values of different hybrids tested.

Genotypes	HPF	LE	NE/P	WTG	NG/E	PRO
Sai × Bah	-08,377	-00,842	-02,508	07,220	-05,702	-05,635
Sai × Plai	-02,215	00,004	-01,632	05,730	-03,165	-05,100
Sai × Tich	-03,757	00,383	-03,093	04,710	-05,042	-07,057
Sai × Exp	-01,707	00,365	-01,802	-01,002	-03,410	-05,350
Bah × Sai	07,950	-00,732	03,492	-04,787	01,675	06,428
Bah × Plai	07,602	01,198	-01,297	01,063	08,880	10,998
Bah × Tich	-19,320	00,158	01,908	00,143	01,980	-05,205
Bah × Exp	00,293	-00,147	-00,467	00,755	08,078	02,768
Plai × Sai	-00,092	-00,210	02,368	-03,657	06,385	05,790
Plai × Bah	-10,082	00,875	-00,297	-03,690	-09,847	-07,545
Plai × Tich	04,875	-00,760	-01,882	03,613	67,600	-00,530
Plai × Exp	-03,498	-00,155	-00,590	01,928	-05,035	-04,160
Tich × Sai	05,417	00,910	00,907	-04,437	01,435	02,010
Tich × Bah	10,413	-00,045	-00,425	-04,687	-02,170	-01,655
Tich × Plai	-01,435	00,013	01,118	00,373	01,540	03,210
Tich × Exp	-01,677	-00,972	02,282	-03,562	-04,412	03,370
Exp × Sai	-00,290	00,328	00,865	01,738	00,503	02,573
Exp × Bah	08,667	-00,047	-00,467	02,688	04,905	03,068
Exp × Plai	00,738	-00,405	01,743	-04,375	-01,225	-00,330
Exp × Tich	06,700	00,185	-01,718	00,225	04,615	-00,517

Sai = Saida, Tich = Tichedrett, Bah = Bahia, Plai = Plaisant, Exp = Express.

effects of independent genes; two alleles per locus; homozygous parents and random distribution of genes between parents. If the fit to a regression of slope +1 is suitable ie the slope of the line Wr/Vr must be not significantly different from 1, in this case, the model will be valid for all the characters studied HPF; THE; NTE; NG/E; WTG and PRO.

3.3.1. Estimates of genetic components

3.3.1.1. Influence of additivety (D) with respect to dominance (H1). Estimates of variation in genetic components reveal significant differences in additive and non-additive effects for all parameters evaluated. An equality of additive and non-additive effects (D = H1) is found for the HPF character which signifies the presence of a complete dominance confirmed by the (Fig. 1a). The additive effects are superior to the dominance effects (D > H1) for the WTG parameter, which shows the importance of the genes acting in a cumulative manner thus suggesting a partial dominance (Fig. 1e) by contrast, the non-additive effects are more important than additive effects (D < H1) for LE characters; NE/P; NG/E and PRO which indicates the presence of a supredominance (Fig. 1.b; c; d; f). The degree of dominance calculation (H1/D) ½ supports the results found by a value equal to one for the HPF character, with values greater than one for the LE parameters; NE/P; NG/E and PRO are respectively (4.43, 1.5, 3.11 and 2.95) and by a value less than one for the character WTG is (-1.16). (Table 5),

3.3.1.2. Gene distribution in parents. The difference between H1 and H2 is an indication of the unequal distribution of dominant and recessive genes. Indeed, there is an asymmetric distribution between the dominant genes and the recessive genes for all the characters studied. This asymmetry of the genes is verified by the ratio H2/4H1 which is different from its maximum value of 0.25, for all the characters tested, (Table 5).

3.3.1.3. Proportion of dominant and recessive genes. The characters LE; NG/E and WTG express frequencies F greater than zero (F > 0) are respectively (0.65, 174.9, and 8.09) which indicates the importance of the dominant alleles in relation to the recessive alleles. This is confirmed by the KD/Kr ratio which gives values greater than one (KD/Kr > 1), that is (1, 4; 3, 18 and 1, 02) in the cited characters suggesting an excess of dominant genes. Regarding HPF parameters; NE/P and PRO, the frequencies of F take values lower than zero (F < 0) are respectively (-191; -3, 66 and -16, 73) which shows that most alleles are recessive, this is verified by KD/Kr values which are less than (KD/Kr < 1) are respectively (0.78, -0.31 and 0.9) thus showing an excess of the recessive genes

(Table 5). These results are confirmed by (Fig. 2).

3.3.1.4. Effect of the environment. Significant differences in the environmental component for all parameters evaluated. High values were found for HPF characters; NG/E; PRO and WTG are respectively (67.5, 43.29, 29.33 and 20.29) as well as low values for the characters LE and NE/P with respectively (0.51 and 3.62).

3.3.1.5. Heritability. Heritability in the broad sense (H²), HPF parameters; NEP; WTG and PRO, expressed as moderate values are respectively (58.9, 57.41, 52.03, 40.14 and 42.37%) which shows that environmental factors have a significant effect on the control of these traits. On the other hand, the LE character expresses a very high value (95.86%) suggesting that the environmental conditions have little effect on the phenotypic variance which is then largely due to the genotypic differences. Concerning heritability in the narrow sense (h²), relatively low values were expressed by the LE parameters; HPF; PRO; NGE and NE/P are respectively (31.20, 22.08, 17.66, 13.95 and 11.03%) which confirms that the dominance variance is greater than the additive variance suggesting that these characters are governed by dominance type genetic effects. On the other hand, the narrow sense heritability for the WTG character is stronger than that of the other traits (87.90%), which show that the additive genetic variance is larger than the dominance variance, (Table 5).

3.3.1.6. Number of genes controlling the characters. From the estimates of the h²/H2 component, the parameters LE; NE/P, NG/E and PRO are under the control of a gene or block of genes to express dominance, (Table 5). The positive values of h²/H2 thus expressing a dominance for the LE and WTG parameters are (4.37 and 0.14) suggest the tendency towards dominance towards the upper parent at the top of the graph (Fig. 1b and e), however, the negative values of h²/H2 for HPF characters; NE/P; NG/E and PRO with respectively (-0.45, -4; -1.21 and -18.89) suggesting the tendency towards dominance towards the lower parent that approaches the point of origin on the graph (Figure 1 a; c; d and f).

3.3.2. Direction and order of dominance by the graphical model of Hayman (1954)

According to (Fig. 1a), the regression line passes through the origin which indicates a complete dominance in the expression of the character (HPF), for the (Fig. 1.b; c; d and f) the regression line intersects the Wr axis below the origin for the parameters (LE; NTE; NG/E and PRO) which means the existence of a superdominance in the expression of these characters; on the other hand, there is an incomplete dominance in the expression of the character (WTG) because the regression line intersects the ordinate axis (Wr) above the origin (Fig. 1e).

The points of the intersection of the parabola with the Wr/Vr regression line characterize genotypes all possessing dominant genes when (Wr and Vr increase) whereas all genotypes are governed by recessive genes when (Wr and Vr decrease).

According to (Fig. 1a), the two genotypes Express and Plaisant contain dominant genes, however, the autochthon variety,Tichedret,t and the introduced cultivar,Bahia, have both recessive and dominant genes. The autochthon Saida variety contains only recessive genes and is located at a distance from the parabola, which indicates that the possibilities for transgression are strong.

According to the (Fig. 1b), both Plaisant and Tichedrett genotypes contain dominant genes, however express and Saida contain recessive and dominant genes. The Bahia genotype has recessive alleles for control of ear length. Possibilities of transgression would be present for the selection of this character.

According to (Fig. 1c), the Bahia variety contains dominant genes; both Tichedrett and Pleasant genotypes contain dominant and recessive alleles for controlling the number of ears per plant; however, both cultivars, Express and Saida, contain only recessive genes. Possibilities of
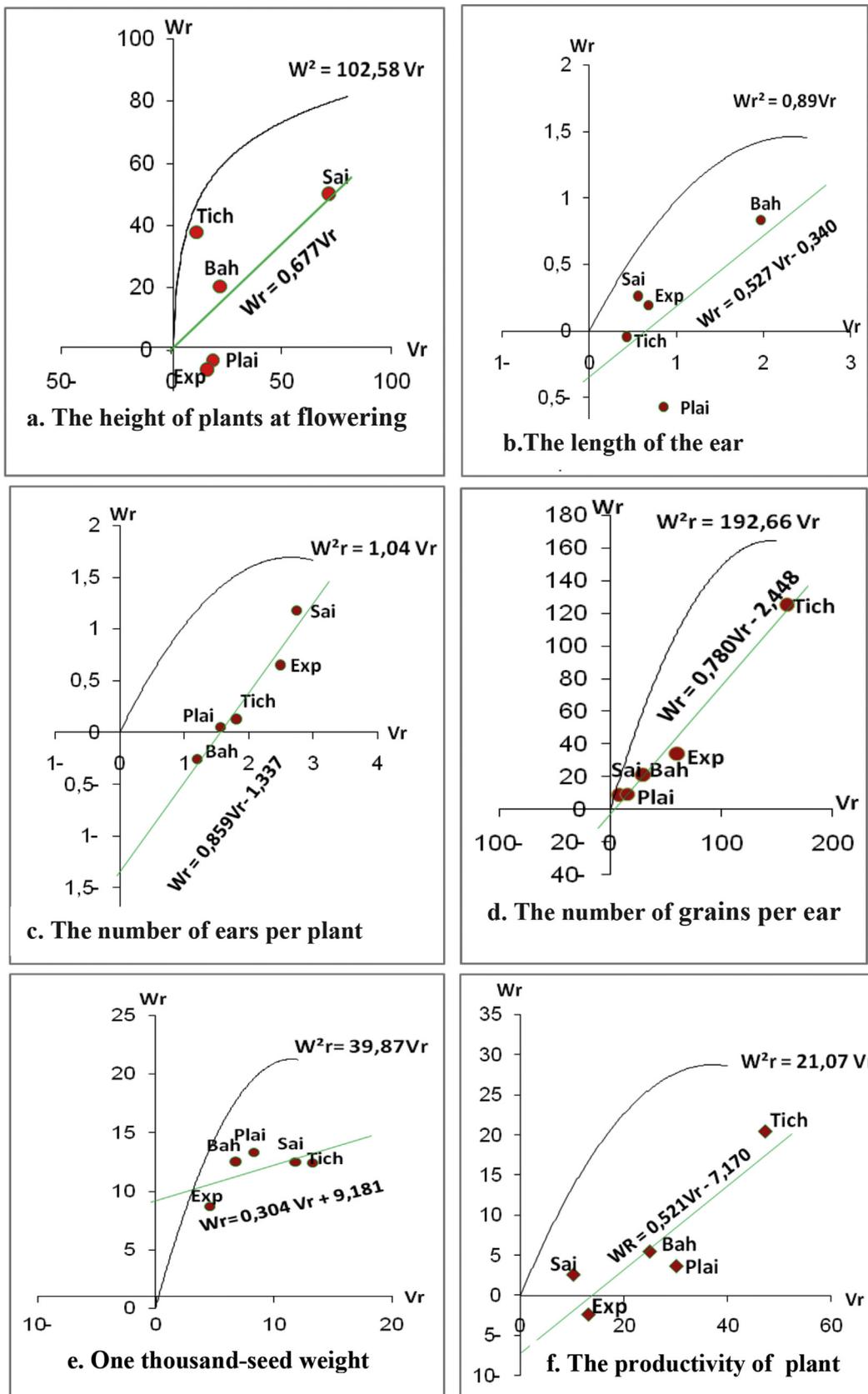
Fig. 1. Graphical representation of Wr as a function of Vr. Wr: covariance between parent r and his descendants; Vr: variance of a parent r and his descendants.

Table 5

Values of the genetic components expressed by the variables measured in F1 hybrids from the complete diallel cross.

Ratio/Parameter	HPF	LE	NE/P	NG/E	WTG	PRO
Additive effect (D)	+014,00***	+00,16***	+00,4***	+17,66***	+6,04***	+5,18***
	±0,09	±0,07	±0,03	±3,75	±0,75	±1,94
Dominance effect (H1)	+014,00***	+03,02***	+00,97***	+171,98***	-8,19***	+45,18***
	±0,21	±0,17	±0,07	±30,04	±1,65	±11,27
Symmetry/asymmetry of allele (H2)	-051,00***	+00,49***	-09,49***	-158,42***	-74,37***	-148,4***
	±0,18	±0,15	±0,05	±25,99	±1,43	±1,42
Mean Fr over arrays (F)	-191,00***	+00,65***	-03,66***	+174,9***	+8,09***	+81,41***
	±0,22	±0,19	±0,02	±17,1	±1,74	±2,46
Environmental component(E)	+067,50***	+00,51***	+03,62***	+43,29***	+20,29***	+29,33***
	±0,12	±0,07	±0,04	±1,42	±0,08	±2,26
Heritability in narrow sense (h^2)	022,08	031,20	011,03	013,95	087,90	017,66
Heritability in the broad sens (H^2)	058,90	095,86	057,41	052,03	040,14	042,37
Average degree of dominance proportion of positive and negative alleles in parents (H2/4H1)	-000,91	+005,91	-002,44	-000,23	+002,27	-000,82
Proportion of dominant and recessive alleles in the parents (KD/Kr)	+060,86	+044,00	-000,65	-001,91	-000,04	-001,41
Number of groups of genes which control the character and exhibit dominance (h^2/H_2)	-000,45	+004,37	-004,00	+061,21	+000,14	-018,89

*** Highly significant at p ≤ 0,001.

transgression would be present for the selection of the number of ears per plant.

According to (Fig. 1d), Plaisant, Saida and Bahia contain dominant genes, however, the genotype Tichedrett all its alleles are recessive to control the number of grains per ear, and the possibility of transgressions could exist.

According to (Fig. 1e), the Bahia and Plaisant varieties contain both recessive and dominant genes for the control of the weight of a thousand grains, however, the two local genotypes, Saida and Ttichedrett contain recessive genes by cons, the Introduced genotype Express has only dominant alleles. Possibilities of transgression would be present for the selection of this character.

According to (Fig. 1f), Express and Saida contain dominant genes, however, Plants and Bahia introduced genotypes have recessive and dominant alleles to control the productivity of the plant, so the local cultivar Tichedrett has only dominant genes. Possibilities of transgressions could exist.

According to (Fig. 2.a; c; f), the correlation between (Wr + Vr) and parental values X is positive, which means that recessive alleles would be favorable for the increase of HPF characters; NT/E and PRO. On the other hand, the correlation between (Wr + Vr) and the parental values of the characters LE; NG/E and WTG is positive indicating that these parameters would be controlled by dominant alleles (Fig. 2.b; c; e).

4. Discussion

The study of parental lines and their descendants by variance analysis shows a significant varietal effect for all parameters measured in autochthons and introduced broodstock; on the other hand, in F1 hybrids, the analysis reveals highly significant genotype effects for all the characters tested. The mean values for all the traits measured in the offspring are close to or greater than the average values recorded in their parents. Oury et al. (1990); Bouchetat and Aissat (2018), find that the maximum values taken by the hybrid are of the same order of magnitude as those measured in the parents, these results are consistent with those of Benmahammed (2005), who found out of thirty-nine hybrids, averages close to those of the parents who generated them.

For the analysis of genetic effects by the Griffing method (1956), the results found indicate that the general and specific combining ability (GCA and SCA) play a significant role in the expression of all the characters tested in the F1 generation whereas, the maternal and reciprocal effects are not significant for all the parameters, these results are in agreement with those of Zerihun et al. (2019). According to Zhan et al. (1996), values of parental lines can be a good indicator of the effects of GCA. A cross between parents of different GCA values (high and low) produces a positive SCA effect (Bhowmik et al., 1990), this genetic

interaction responsible for high SCA values can be additive X additive or additive X dominance. The first is fixable and can be used in the selection, while the second is non-fixable (Falconer, 1974). The GCA/SCA variance ratio is less than one unit for all the characters studied. The nature of the actions of the non-additive genes is more important than the nature of the actions of the additive genes. An GCA/SCA ratio close to unity is suggestive of the predominance of genetic actions of a more additive than non-additive nature (Baker, 1978). Most research on the mode of action of genes in trait transmission, in barley, has indicated that non-additive effects are more important than additive effects, at least for one trait, indicating predominance of dominance-type gene action (Nakhjavan et al., 2009; Patial et al., 2016; Pesaraklu et al., 2016; Yadav, 2016).

These results are confirmed by the Hayman model (1954) which is valid for all evaluated variables. Indeed, the influence of the additivity with respect to the dominance reveals a equality between the two components for the character HPF indicating a complete dominance on the other hand, the non-additive component is more important than the additive component for the characters: LE; NTE; NG/E and PRO which signifies a superdominace controlling the expression of these characters, these results are in agreement with those of Budak (2000); Soylu (2002) and Sharma et al. (2003) for HPF parameters; THE; NTE and PRO and those of Sharma et al. (2003) and Rohman et al. (2006), for the NG/E character. Regarding the weight of thousand seeds, a partial dominance is observed, it is confirmed by the importance of the additive component (D > H1), our results are in agreement with those of Hanifi-Mekliche and Gallais (1999) and which report that this character is under the governance of additive action genes.

For the distribution of genes in the parents, an asymmetric distribution between the dominant genes and the recessive genes was obtained for all the characters studied. These results are affirmed by Bouzerzour and Djakoune (1998). For the proportion of dominant and recessive genes, the characters LE; NG/E and WTG have the dominant alleles more important than the recessive alleles indeed, the dominant alleles would be favorable to the increase of these characters. For HPF; NT/E and PRO an excess of recessive alleles was found indicating that these parameters would be controlled by recessive alleles. A significant difference was found for the environmental component for all parameters evaluated, these results being consistent with those of Rohman et al. (2006); Eshghi and Akhundova (2009); Aghamiri et al. (2012); Metwali et al. (2014) and Pesaraklu et al. (2016), because many quantitative traits are controlled by polygenic determinism with possible environmental influences (Klug et al., 2006). It is weak in heritability in the narrow sense, but the heritability in the broad sense is high, which means that the variance due to dominance and trans epistasis is higher than the variance of additivity. Pal and Kumar (2009) indicate a predominance of dominant genetic effects in the
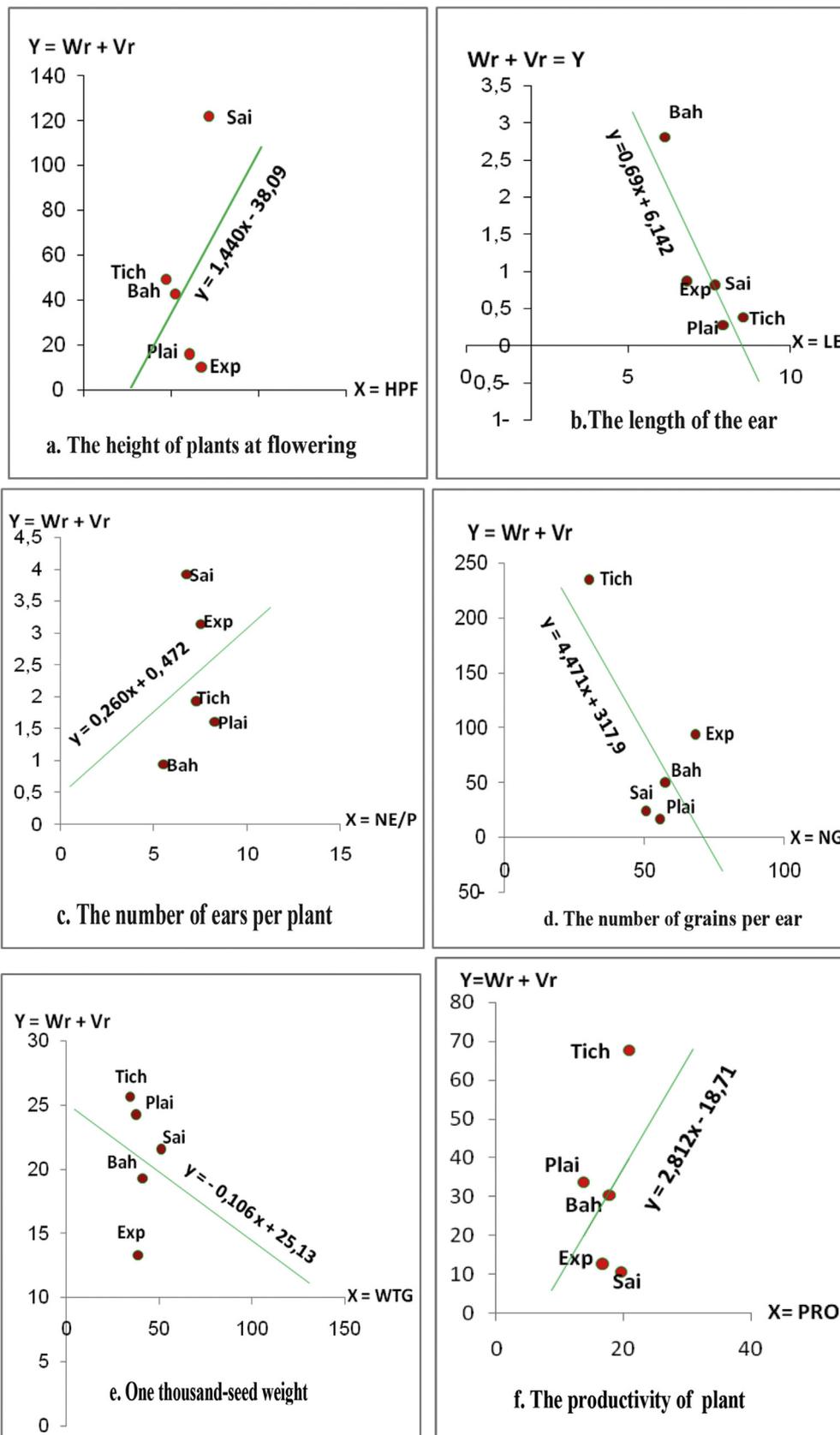
Fig. 2. Graphic representation of the quantity (Wr + Vr) as a function of X: parental values of the characters. Wr + Vr: parental order of dominance.

control of heredity of traits: height of plants; the length of the ear; the number of grains per ear and the productivity of the plant. Sunil et al. (2015), support these results by confirming a low heritability of these traits, while Bargougui (2016) joins these authors in the low rates of heritability he found for these traits. Experimental results show that development-related traits always have fairly high heritability in all environments and populations, indicating high genetic variation, however, other complex traits such as productivity often have low heritability (Gallais, 1990; Khaldoun et al., 2006).

5. Conclusion

The analysis of the nature of genetic actions shows that additive and non-additive effects are involved in the genetic control of the variables studied with the preponderance of non-additive action genes. For strong GCA variances, the choice in parenting formula is effective therefore, Bahia and Pleasant are best for the plant's productivity traits; ear fertility; spike length and height of the plant at bloom, however, the Saida and Tichedrett autochtones genotypes are best for the weight characters of one thousand grains and the number of ears per plant, however, the choice of parents, before hybridization, remains priority for low SCA variances. Possibilities of transgression would be present for the selection of characters tested but it is necessary to wait for future generations. In fact, the low values of heritability indicate that the improvement of these characters by the selection, within the early generations of this complete diallel, would be ineffective. The selection must therefore be delayed until a reasonable degree of homozygosis is obtained.

Declarations

Author contribution statement

Fawzia Bouchetat: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

Abdelkader Aissat: Contributed reagents, materials, analysis tools or data.

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