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Full Length Research Paper

Combining ability of aphids (*Aphis craccivora* Koch) resistance in cowpea (*Vigna unguiculata* (L.) Walp.)

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General combining ability (GCA) describes the general usefulness of the parental form in terms of the concerned trait, whereas specific combining ability (SCA) indicates importance of the joint action of the genes of parental forms. Such information is useful to identify the best combiners which may be hybridized to build up favourable genes. This present investigation aimed to determine the GCA and SCA effects of cowpea (*Vigna unguiculata* (L.) Walp.) genes resistance to aphids (*Aphis craccivora* Koch). The experimental design consisted of twenty-eight entries comprising of seven parents and their 21 hybrids in a Randomized Complete Block Design with three replications. The study was conducted in two locations: Kamboinse and Farakoba in Burkina Faso. The study focused on plants survival rate (SR) and degree of infestation (DI). Results showed that the survival rate is under control of additive and non-additive genes action. Additive genes are involved in the expression of the degree of infestation. Fourteen crosses capable of producing transgressive segregants were selected. The low values of the narrow sense heritability indicate high influence of environment in the expression of the traits; suggesting the need of improved methods to select in early generation. The results also showed significant genotype by environment interaction (G×E), GCA by environment interaction (GCA×E), and SCA by environment interaction (SCA×E).

Key words: General Combining Ability (GCA), specific combining ability (SCA), additive, non-additive.

INTRODUCTION

Identification of the best performing lines to be used as parents in future crosses is an important step in crop breeding programs (Oakey et al., 2016). When parental plants produce potent offspring, it is an indication of good combining ability. The term general combining ability (GCA) is associated with genes of additive effects; it is

the average performance of a line in hybrid combinations. Based on the average performance of the lines involved, the specific combining ability (SCA) caused by dominance and epistasis, define those cases in which certain combinations do relatively better or worse than expected (Sprague and Tatum, 1942). Such information

may help breeders to identify the best combiners which may be hybridized to build up favourable fixable genes. In cowpea (*Vigna unguiculata* (L.) Walp.), various analysis had been undertaken aiming at selection for several traits among these: yield and yield contributing traits, extra-earliness, physical properties of seed, polyphenols and phytates content, soluble sugar content, resistance to biotic, and abiotic stress (Badhe et al., 2016; Romanus and Hussein, 2008; Oliveira et al., 2016; Nassourou et al., 2017; Maina et al., 2015; Rodrigues et al., 2018; Lima et al., 2017). Diallel in cowpea targeting aphid's (*Aphis craccivora* Koch) resistance has also been undertaken. Thus, cross-reciprocal results indicated no apparent maternal effects on the expression of aphid resistance (Bata et al., 1987; Pathak, 1988). Maternal effects are due to cytoplasmic genetic factors whereas non-maternal effects are due to interactions between the effects of nuclear and cytoplasmic genes (Mukanga et al., 2010). In Burkina, diallel analysis for improvement of cowpea targeted yield improvement, resistance to *Striga* and *Alectra* (Tignegre, 2010; Dieni, 2017).

The present study undertaken in two locations focused on cowpea resistance to aphids. It aimed to determine cowpea genes action in the resistance to aphids (*Aphis craccivora* Koch).

MATERIALS AND METHODS

Plant genetic materials

The genetic materials for this study were seven cowpea inbred lines: SARC1-91-1, KVx295-2-124-99, IT97K-556-6, SARC1-57-2, Tiligre (KVx775-33-2G), NS-Farakoba, and CB27. These lines were selected on the basis of their diverse geographical origin, their morphological characteristics and their ability to thrive well under aphids. F_1 hybrids were developed from 2017 to 2018 using a half diallel cross of 7×7 without reciprocals.

Aphids' strains

The collection took place in September 2018. In each site under study, cowpea plants infested with aphids were collected and placed in cages. The aphids were brought back to the laboratory to be reared on a susceptible variety (KVX 396-4-5-2D). The screening test was done with the descendants of the wild strain.

Field layout

Twenty-eight entries comprising seven parents and their 21 hybrids were sown in a Randomized Complete Block Design (RCBD) with three replications. The experimental plot consisted of four pots. The study was conducted in two locations, Kamboinse in the Sudano-Sahelian climatic zone (12.46N; -01.55W) and Farakoba in the Sudanian zone (11.05N; 04.21W). The Sudanian zone is characterized by an annual average rainfall of 1015.8 mm, an annual average potential evapotranspiration of 2011.1 mm and an annual average temperature of 27.3°C. The Sudano-Sahelian zone has an annual average rainfall of 755.3 mm, an annual average potential evapotranspiration of 2444.0 mm and an annual average temperature of 28.7°C (Pallo and Sawadogo, 2010). The screening

was done with seven days old seedlings. Cowpea plants remained under aphids' infestation during the test. Row data of plants' survival rate (SR) and aphids' degree of infestation (DI) were collected.

Data collection and analysis

The investigation made in this study was focused on plants survival rate (SR) given by Equation 1 and the degree of infestation (DI).

$$SR = \frac{Nb \; of \; plts \; surviving}{Tot.nb \; of \; plts} x100 \tag{1}$$

where SR = survival rate; Nb of plts surviving = number of plants surviving; Tot.nb of plts = total number of plants.

The mean data of each plot was used for statistical analysis. The nature and magnitude of genes action was determined using Plant Breeding Tools (PBTools) for Griffing's (1956) numerical approach and Dial 98 for Hayman's (1954) graphical approach. The Griffing's method for diallel analysis was based on the following model:

$$Xij = u + gi + gj + sij + (1/b) \sum_{k=1}^{b} eijk \tag{2}$$
(i = j =1...p; k = 1...b),

where u = the population mean; g_i = the general combining ability effect of the ith parent; g_j = the general combining ability effect of the jth parent; S_{ij} = the specific combining ability effect of the cross between the ith and j[th] parents; e_{ijk} = the environmental effect associated with ijk[th] observation. The graphical approach (Vr-Wr graph) was used to test the regression of the parental variance (Vr) on the parents-offspring covariance (Wr). With Vr: the variance of the rth array and Wr: the covariance between the parents and their offspring in the rth array. The array refers to the crosses in which a particular parent is common.

RESULTS

Genes action and dentification of genotypes with significant GCA and SCA

For all the traits (SR and DI), genotypes were significantly different in all the two sites (Table 1). At Kamboinse the GCA effects of the lines were significantly different only for the DI (P<0.001). For the SR, the GCA effects were not significant. In the site of Farakoba, the GCA effect was not significant neither for the SR nor for the DI. At Kamboinse, the SCA was not significant neither for the SR nor for the DI. At Farakoba, the SCA effect was significant both for the SR and the DI.

In all the graphs, the data points representing the parental lines are scattered (Figures 1 to 4). For the SR at Kamboinse, the closest to the origin were: CB27, Tiligre, KVx295-2-124-99, and IT97K-556-6. At Farakoba, the closest to the origin was KVx295-2-124-99 and SARC1-91-1. For the DI and in the site of Kamboinse the closest to the origin was Tiligre and CB27. At Farakoba the closest was Tiligre, SARC1-57-2, KVx295-2-124-99 and IT97K-556-6. In both locations and concerning the SR (Figures 1 and 2) the regression line passes above the origin, cutting the Wr axis, respectively at the intercepts equal to 20.7 and 56.8. For the DI the regression line

Table 1. GCA and SCA effects for SR and DI across two locations.

Source	Df	SR		DI	
		Kamboinse	Farakoba	Kamboinse	Farakoba
Rep.	27	3043.15***	74.4378	1.45	0.65
Genotypes	27	699.68**	1120.40**	1.36**	1.25*
GCA	6	394.62	364.55	1.34***	0.44
SCA	21	187.11	376.01*	0.2	0.41*
Error	54	106.46	147.17	0.17	0.23

* P<0.05; ** P<0.01; ***P<0.001. SR=Survival Rate; DI=Degree of Infestation, GCA= General Combining Ability; SCA= Specific Combining Ability.

$$Wr^2 = 308.6Vr$$

$$Wr = 1.0\,Vr + -64.940$$

$$Wr = 0.351Vr + 20.717$$

1= Tiligre

2= CB27

3= Sarc1-57-2

4= NS-Farakoba

5= Sarc1-91-1

6= KVX295-2-124-99

7=IT97K-556-6
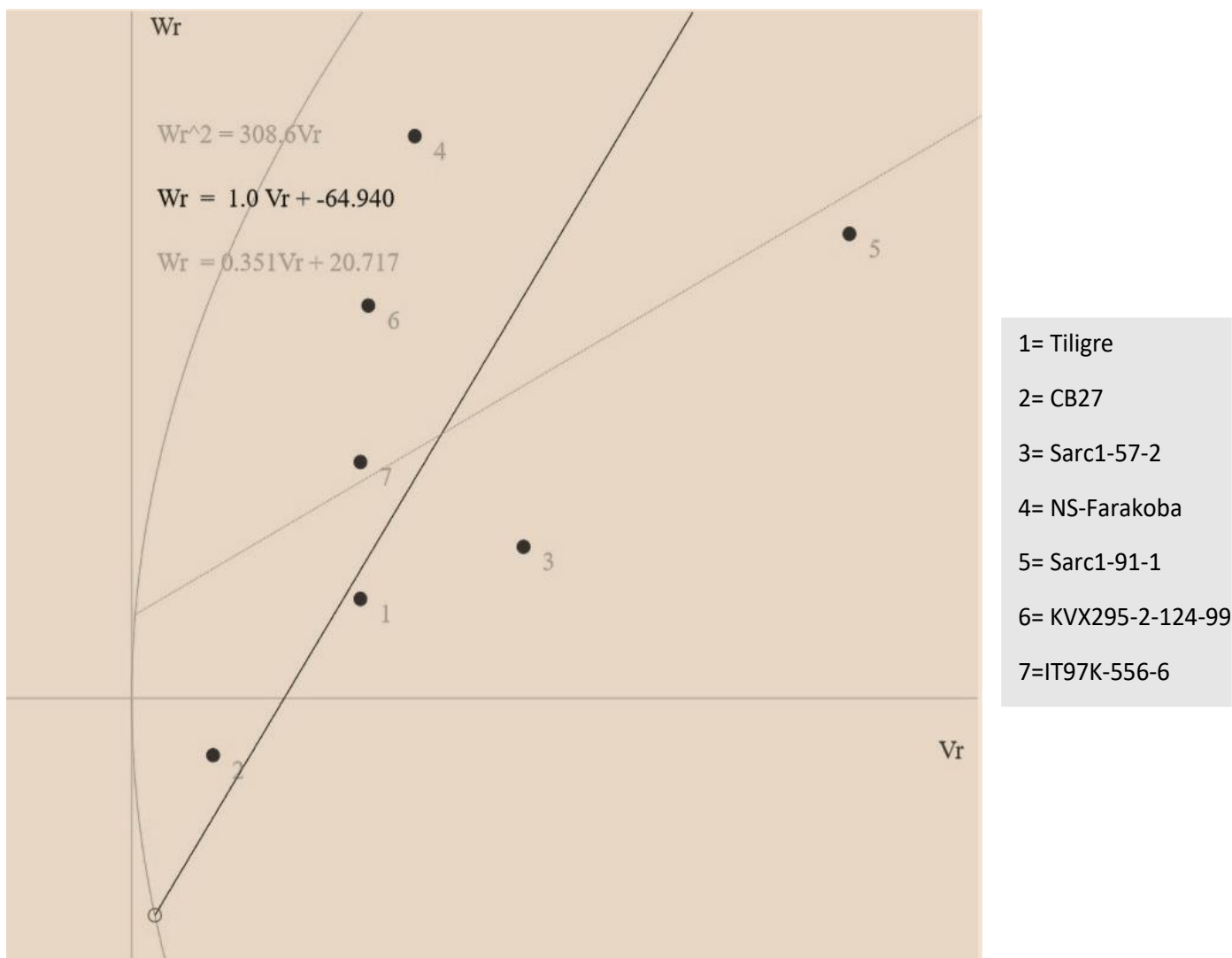
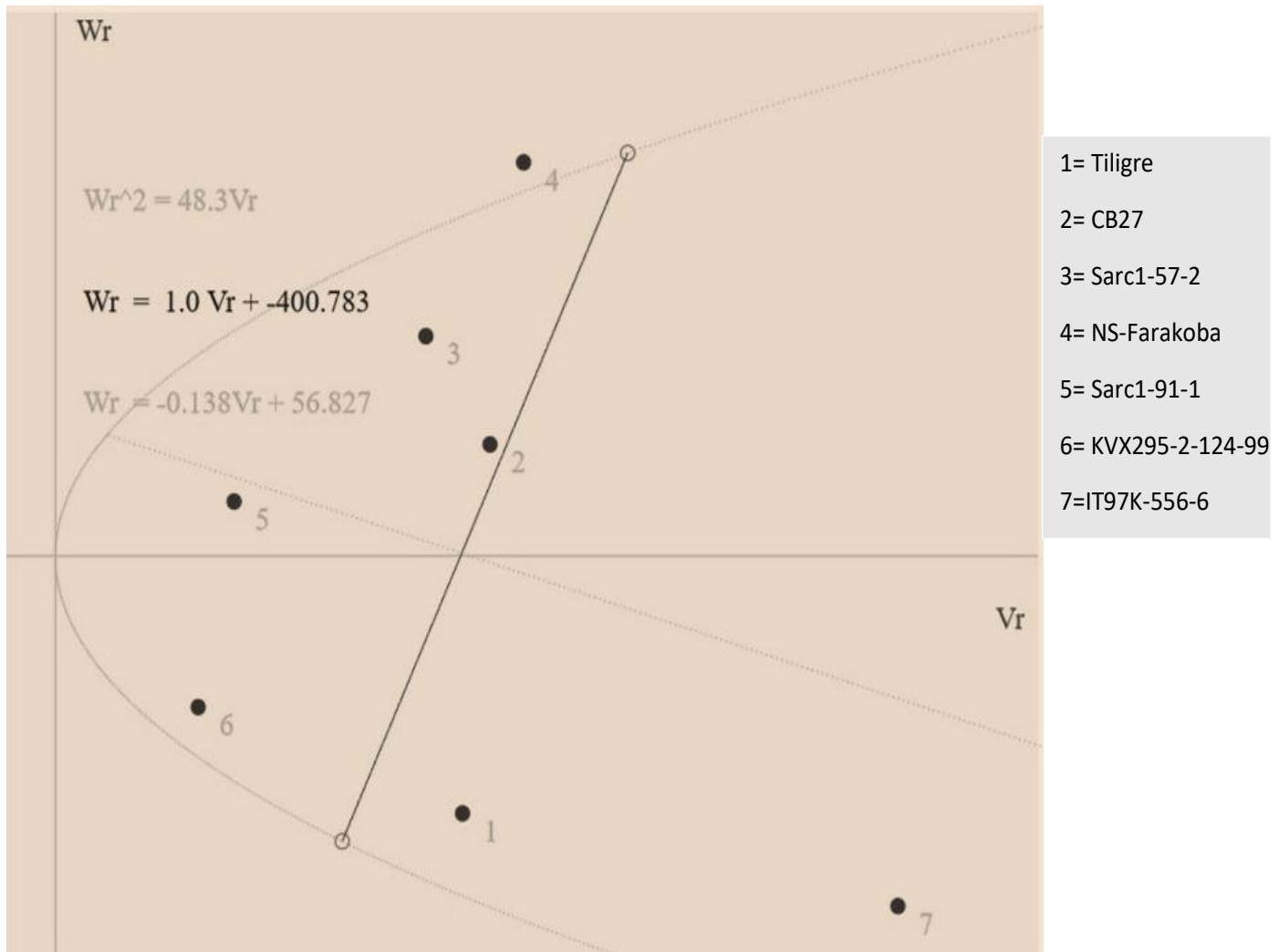**Figure 1.** Regression of parent's variance on parents-offspring covariance for SR (at Kamboinse).

passes below the origin with intercepts equal to -5.39 and -0.059 respectively in both sites.

Lines with significant GCA were few (Table 2). Three lines at Kamboinse recorded significant GCA for the DI. Thus, for the degree of infestation line Sarc1-57-2 recorded the highest GAC of 0.53, then line CB27

Figure 2. Regression of parent's variance on parents-offspring covariance for SR (at Farakoba).

recorded a GCA of 0.39 while line Tiligre recorded a GCA equal to -0.48. Among these lines, Tiligre recorded a negative combining ability while CB27 and Sarc1-57-2 recorded positive GCA. In the site of Farakoba and concerning the SR all of the crosses recorded significant SCA. With respect to the DI at Farakoba, only cross CB27 × NS-Farakoba recorded significant SCA (-1.34).

Assessment of broad and narrow sense heritability

For the SR, broad sense as well as narrow sense heritability was moderate to low (Table 3). Broad sense heritability was 0.62 and narrow sense 0.24 at Kamboinse. These traits were 0.72 and 0.17, respectively at Farakoba. Concerning the DI, broad and narrow sense heritability were moderate to low at Kamboinse with 0.67 and 0.17, respectively and low at Farakoba with 0.4 and 0.09, respectively.

Genotype by environment interaction

The test of homogeneity of the SR and DI's variances in the two sites (Table 4) gives P-values greater than 0.05. The variances were not significantly different. The data at two locations were then pulled together and analysed. The combined means square analysis showed significant differences only for the SR (Table 5). The means square of the two locations for none of the traits (SR and DI) were significantly different. So were the means square of the genotypes, the GCA and the SCA for the same traits. Highly significant difference was found in the genotype by environment (G×E) interaction for the SR (P<0.001). This interaction was not significant for the DI. In the same way the General Combining Ability by environment (GCA×E) interaction was significant for the SR (P<0.05) but not significant for the DI. The Specific Combining Ability by environment (SCA×E) interaction was also highly significant for the SR (P<0.01) but not significant for the DI.
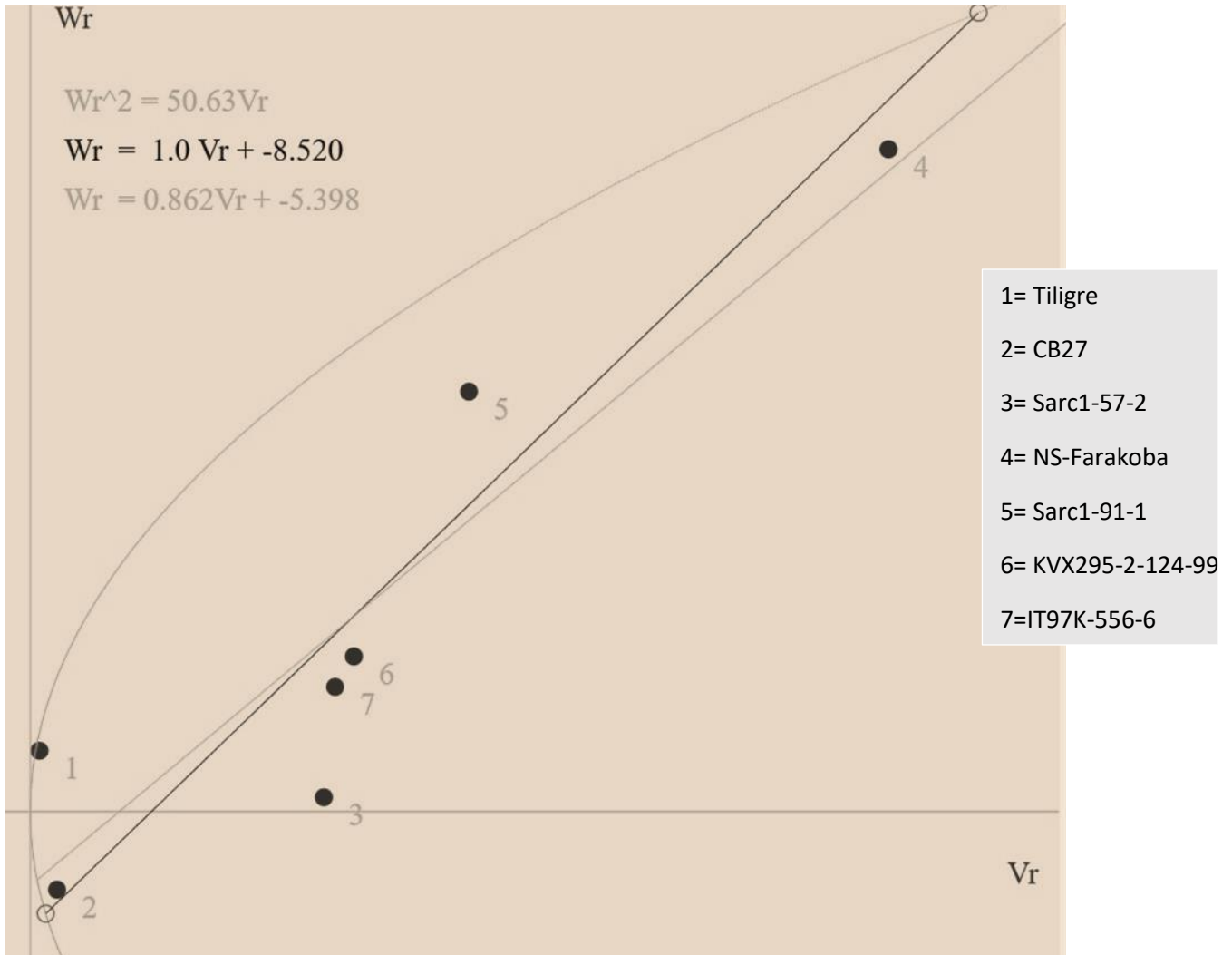
Figure 3. Regression of parent's variance on parents-offspring covariance for DI (at Kamboinse).

DISCUSSION

Gene's action and identification of genotypes with useful GCA and SCA effects

The survival rate assessed at *Kamboinse* is characterized by non-significant GCA and SCA effect, suggesting that epistatic gene(s) play an important role in determining this character (Fehr, 1993). However, the same trait but in another location (Farakoba) recorded a significant SCA suggesting that non-additive nature of genes action is involved in controlling this trait. At Kamboinse and for the DI, the GCA was significant unlike the SCA that was not. This result suggests that additive are involved in the expression of the trait because the GCA variance contains additive effect while SCA contains non-additive (Snehal et al., 2010). Genotypes with high GCA can be used as a basic breeding source for improvement of this crop (Jou-Nteufa and Ceyhan,

2022; Ayo-Vaughan et al., 2013). At Farakoba non-additive genes action was observed for the degree of infestation. These results are in accordance with the work of Fasahat et al. (2016), who found that both additive and non-additive genes effects were found important in governing pest resistance   in crops of greatest commercial interest.

In both locations and for all traits under study, the distribution of genotypes array points (scattered position) suggests a lot of diversity among them. The position of parental points along the regression line indicates the dominance order of the parents. Parents with more dominant genes are located near the origin, while those with more recessive genes fall farther from the origin (Soomro et al., 2015; Nagar et al., 2020). In relation to the Survival Rate (SR), those closest to the origin were Tiligre, CB27, KVx295-2-124-99 and IT97K-556-6 at Kamboinse and KVx295-2-124-99 and SARC1-91-1 at Farakoba. These lines are those with more dominant
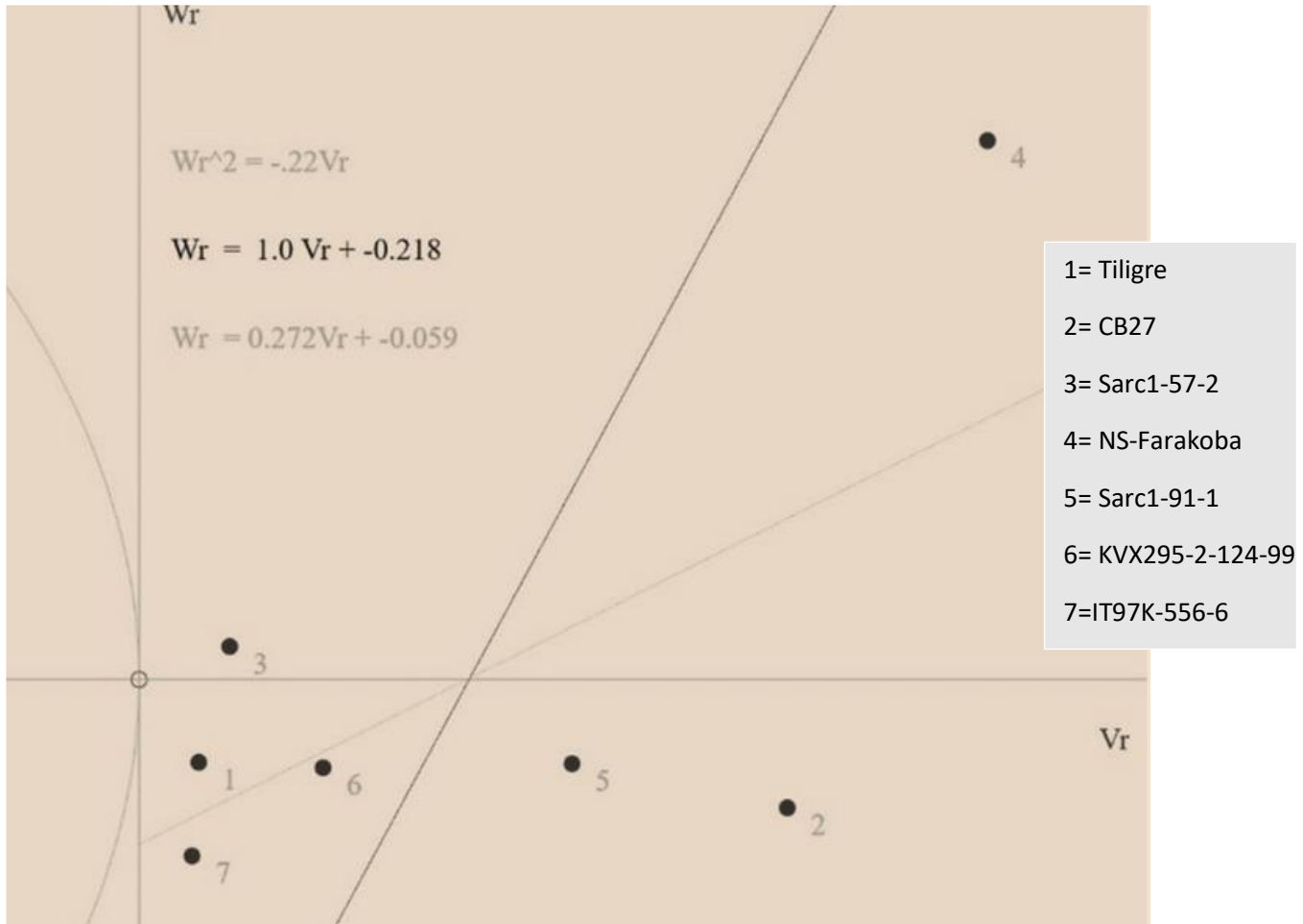
Figure 4. Regression of parent's variance on parents-offspring covariance for DI (at Farakoba).

genes. Regarding the DI, at the Kamboinse site, Tiligre and CB27 exhibit this dominance, while at the Farakoba site, Tiligre, SARC1-57-2, KVx295-2-124-99, and IT97K-556-6 display a higher prevalence of dominant genes. These results show that the expression of resistance is unstable from one location to another suggesting a high influence of the environment in the expression of the traits. The Vr/Wr graph also revealed that the type of gene action includes partial dominance as the regression line intercepted the co-variance (Wr) axis above the origin in Figures 1 and 2. Inversely in Figures 3 and 4, the regression line intercepted the co-variance (Wr) axis below the origin, suggesting an over dominance in the type of gene action.

The study findings thus reveal that the SR is influenced by non-additive genes action, displaying partial dominance and presence of epistasis. In this scenario, improvement can be attained through hybridization. However, hybrid production in cowpea has not been economically viable so far. The utilization of transgressive segregants offers a potential avenue for enhancing this trait. Transgressive segregation has been proposed as a

strategy to enhance various traits in cowpea (Fernandes et al., 2015; Snehal et al., 2010; Tchiagam and Bell, 2011). Additionally, as Fonsecca and Patterson (1968) and Kundu et al. (2023) pointed out, this heterobeltiosis (the superiority of hybrids over better parent) indicates the parental combinations capable of producing high level of transgressive segregants. In the expression of DI, additive and non-additive genes are involved with over dominance. Reciprocal recurrent selection is a good mean to improve this trait. However, even though recurrent selection can be used to improve self-pollinated crops like cowpea, the way the generations are handled in terms of making the crosses (manually) is challenging. In this approach, all the selected individuals need to be crossed in every conceivable combination during each cycle. As a result, recurrent selection can be applied to self-pollinated crops, although this is going to be more expensive compared to cross-pollinated crops like maize. In fact, induced male sterile lines for pollination control using temperature, Gamma ray and chemicals has been reported (Odeigah et al., 1998; Shukla et al., 2017; Sekiguchi et al., 2023). However, in practice only hand

Table 2. Estimates of general and specific combining abilities effects for SR and DI.

Line	Kamboinse		Farakoba	
	GCA (SR)	GCA (DI)	GCA (SR)	GCA (DI)
Tiligre	-	-0.48***	-	-
CB27	-	0.39***	-	-
Sarc1-57-2	-	0.53***	-	-
NS-Farakoba	-	-0.29	-	-
Sarc1-91-1	-	-0.26	-	-
KVX295-2-124-99	-	-0.13	-	-
IT97K-556-6	-	0.23	-	-
SE	-	0.13	-	-

Crosses	Kamboinse		Farakoba	
	SCA (SR)	SCA (DI)	SCA (SR)	SCA (DI)
Tiligre × CB27	-	-	91.67*	0.57
Tiligre × Sarc1-57-2	-	-	44.44*	-0.10
Tiligre × NS-Farakoba	-	-	80.56*	0.16
Tiligre × Sarc1-91-1	-	-	55.56*	0.45
Tiligre × KVX295-2-124-99	-	-	55.56*	-0.33
Tiligre × IT97K-556-6	-	-	41.11*	-0.69
CB27 × Sarc1-57-2	-	-	72.22*	0.38
CB27 × NS-Farakoba	-	-	52.78*	-1.34*
CB27 × Sarc1-91-1	-	-	80.56*	0.65
CB27 × KVX295-2-124-99	-	-	100.00*	0.07
CB27 × IT97K-556-6	-	-	50.00*	0.37
Sarc1-57-2 × NS-Farakoba	-	-	47.22*	0.97
Sarc1-57-2 × Sarc1-91-1	-	-	91.67*	-0.85
Sarc1-57-2 × KVX295-2-124-99	-	-	83.33*	0.09
Sarc1-57-2 × IT97K-556-6	-	-	100.00*	0.53
NS-Farakoba × Sarc1-91-1	-	-	91.67*	0.19
NS-Farakoba × KVX295-2-124-99	-	-	100.00*	0.16
NS-Farakoba × IT97K-556-6	-	-	100.00*	-0.35
Sarc1-91-1 × KVX295-2-124-99	-	-	91.67*	0.98
Sarc1-91-1 × IT97K-556-6	-	-	83.33*	0.50
KVX295-2-124-99 × IT97K-556-6	-	-	88.89*	0.03
SE			10.89	0.43

SR=Survival rate; DI=degree of infestation, GCA= general combining ability; SCA= specific combining ability; SE= standard error.

Table 3. Broad and narrow sense heritability of the SR and the DI at *Kamboinse* and *Farakoba*.

Parameter	Estimate			
	Kamboinse		Farakoba	
	SR	DI	SR	DI
h^2_b	0.62	0.67	0.72	0.4
h^2_n	0.24	0.17	0.17	0.09

h^2_b = Broad sense heritability; h^2_n= narrow sense heritability, SR=survival rate; DI=degree of infestation.

emasculation is being used (Sekiguchi et al., 2023). For the sake of efficiency, the bulk method or the North

Table 4. Comparison of SR and DI's variances across two locations.

Traits	X-squared	df	dfi	p-value
SR	1.43	1	166	0.23
DI	0.09	1	166	0.76

SR=Survival rate; DI=degree of infestation.

Table 5. Combined mean square test of SR and DI.

Source	Df	SR	DI
Env	1	1083.59	108.85
Block (Env)	4	1558.79**	1.05
Genotypes	27	881.54	1.39
G × E	27	938.53***	1.22
Residuals	108	387.24	0.61
GCA	6	1223.81	1.84
SCA	21	783.75	1.26
GCA × E	6	1053.6*	3.49
SCA × E	21	905.63**	0.57
Residuals	108	387.24	0.61

SR=Survival rate; DI=degree of infestation; GCA= general combining ability; SCA= specific combining ability; Env=environment; G×E= genotype by environment interaction; GCA×E= general combining ability by environment interaction; SCA×E = specific combining ability by environment interaction.

Carolina III mating design can be applied instead. By using the bulk method; fixed lines can be selected after about six generations. The number of generations can be reduced by applying markers assisted selection (MAS). Recombinants with many of favourable genes from the parents thus, can be found and they may be more resistant than the most resistant parent. Such plants would be transgressive segregants. In fact, significant SCA effects for a trait suggest the possibility for transgressive segregation that could be linked to the following situations: (i) the joint action of favourable dominant genes dispersed amongst two parents; (ii) the complementary interaction of additive dominant on recessive genes at different loci; (iii) favourable intra or inter locus interactions referred to as over dominance (Mather and Jinks, 1982; Ayo-Vaughan et al., 2013). Based on that, Tchiagam et al. (2011) considered that manifestation of heterobeltiosis that leads to transgressive segregation might also be due to non-additive gene effects in the parents and therefore suggested that SCA performance might be considered as a criterion for selecting the best crosses.

Lines with significant GCA were few. Three lines at Kamboinsé recorded significant GCA for DI. These are: Sarc1-57-2 with 0.53 then CB27 with 0.39 and finally Tiligre with -0.48. Among lines with significant GCA for DI CB27 and Sarc1-57-2 recorded significant but positive GCA. This result suggests that by crossing these lines with other lines the capacity of the offspring to slow down the development of aphids is getting lower. In fact, the DI is a trait that indicates the level of the plant antibiosis (Descamps et al., 2015). Plants with high antibiosis activity are able to produce components against insects. These components reduce the number and the development of that insect. According to MacWilliams et al. (2023), antibiosis functions at the phloem level by blocking sap ingestion, affecting both aphid growth and fecundity.

Tiligre recorded a significant and negative GCA, indicating that its antibiosis ability improves when crossed with other lines. It is a good candidate to use as a parent for the improvement of this trait. The GCA for DI was not significant at either Kamboinse or Farakoba. However, the use of crosses with significant specific combining ability may help improve this trait through the identification of transgressive segregants. Crosses that could generate these genotypes are those with significant and negative SCA for DI. For SR, candidate crosses are those with significant and positive SCA. These crosses demonstrate their ability to produce offspring that express a higher level of tolerance. In fact, SR reflects the plant's ability to withstand insect damage, representing one aspect of plant resistance to insects, also known as tolerance (Descamps et al., 2015; Kamphuis et al., 2016). The results indicate that, although the mode of action of genes has an additive part, non-additive components

play a crucial role in the expression of aphid resistance in cowpea. Selection in this case can be conducted through recombination and fixation of favourable genes in inbred lines. Based on these findings and previous studies on cowpea resistance to aphids (Souleymane et al., 2013; Kusi et al., 2018; Ouédraogo et al., 2018; MacWilliams et al., 2023), crosses capable of producing desirable transgressive segregants are as follows: Tiligre × CB27; Tiligre × Sarc1-57-2; Tiligre × Sarc1-91-1; Tiligre × KVX295-2-124-99; Tiligre × IT97K-556-6; CB27 × Sarc1-91-1; CB27 × KVX295-2-124-99; CB27 × IT97K-556-6; Sarc1-57-2 × Sarc1-91-1; Sarc1-57-2 × KVX295-2-124-99; Sarc1-57-2 × IT97K-556-6; Sarc1-91-1 × KVX295-2-124-99; Sarc1-91-1 × IT97K-556-6; KVX295-2-124-99 × IT97K-556-6.

Assessment of broad and narrow sense heritability

SR and DI recorded moderate to low broad and narrow sense heritability. Broad and narrow sense heritability of SR were moderate to low in both locations, while for DI, the heritability was moderate to low at Kamboinse and low at Farakoba. The low values of narrow-sense heritability underscore the influence of environmental impact on trait expression (Jou-Nteufa and Ceyhan, 2022), indicating that early-stage selection would not be effective (Owusu et al., 2020) unless molecular markers are employed. Hence, Marker-Assisted Selection (MAS) could offer a promising avenue to achieve substantial selection progress in earlier generations.

Genotype by environment interaction

The results indicate that genotype by environment interaction is significant for SR but not significant for DI. This suggests that, for SR, genotypes performing well in the Farakoba site may not perform well at Kamboinse and vice versa. Plant susceptibility to an herbivorous insect is known to depend on the environmental context (Cappuccino and Maddox, 1986; Coffin et al., 2021). Additionally, it shows that for DI, genotypes performing well at one location perform similarly in the other. Similarly, for SR, lines with good GCA and crosses with good SCA before being used as parents for improvement need their performance evaluated in each of the two locations. For DI, lines with good GCA and crosses with good SCA can be used as parents for improvement in both locations. This is feasible because the GCA×E interaction and the SCA×E interaction are significant for SR but not significant for DI.

Conclusion

In the expression of DI, both additive and non-additive

genes are involved, while SR is under the control of non-additive gene action. For SR, the GC) was not significant in either of the two sites. Improvement in this crop for resistance to aphids is achievable through the selection of transgressive segregants. Among the seven lines under study, only Tiligre recorded a significant and exploitable GCA. Considering GCA, SCA, and the level of resistance to aphids of the lines studied, 14 crosses capable of producing transgressive segregants were selected: Tiligre × CB27; Tiligre × Sarc1-57-2; Tiligre × Sarc1-91-1; Tiligre × KVX295-2-124-99; Tiligre × IT97K-556-6; CB27 × Sarc1-91-1; CB27 × KVX295-2-124-99; CB27 × IT97K-556-6; Sarc1-57-2 × Sarc1-91-1; Sarc1-57-2 × KVX295-2-124-99; Sarc1-57-2 × IT97K-556-6; Sarc1-91-1 × KVX295-2-124-99; Sarc1-91-1 × IT97K-556-6; KVX295-2-124-99 × IT97K-556-6. The SR and DI recorded moderate to low broad and narrow sense heritability. The low values of narrow-sense heritability suggest a high influence of the environment in the expression of these traits. This also indicates that selection cannot be effectively made in early generations unless improved methods such as molecular markers are utilized. All interactions, including G×E, GCA×E, and SCA×E, were found to be significant.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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