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Diallel analysis of cowpea [*Vigna unguiculata* (L.) Walp.] for seed size, and resistance to *Alectra vogelii* Benth.

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ABSTRACT

Cowpea production is hampered by several abiotic and biotic constraints. Parasitic weed *Alectra vogelii* is a formidable biotic constraint in cowpea production. This study was implemented to determine gene actions involved in cowpea seed size and its resistance to *Alectra* in order to determine the appropriate breeding approach to develop resistant cowpea varieties to *Alectra vogelii*. For this purpose, a half diallel of 9 parents was developed at Kamboinse in 2016. The F_1 and their parents were screened in screen house with *Alectra vogelii* seed collected from *Alectra* infested field in Koupela in centre east Burkina Faso. Data were collected on dates to cowpea flowering, cowpea hundred seeds weight and the severity of *Alectra* 70 days after planting and analysed with Diall 98 software. Both additive and non-additive gene actions were operative for the investigated characters. Additive gene effects were more important, resulting in high narrow sense heritability, inferring that breeding progress can be achieved through backcross or single seed descent method.
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Keywords: additive, Burkina Faso, dominance, general combining ability, gene action, heritability.

INTRODUCTION

Cowpea (*Vigna unguiculata*) is an important grain legume crop in Sub-Saharan Africa. The crop is an excellent source of protein for both human and animal nutrition (Ouattara et al., 2014; Enyiukwu et al., 2018; Jayathilake et al., 2018). It also serves as a cash crop in the largest production areas (Horn et al., 2015). In Burkina Faso, cowpea is one of the major crop in the agricultural system. It is the leading grain legume crop and the fourth most important staple crop produced (DGPER, 2018). However, cowpea production encounters several abiotic and biotic constraints among which drought, insect pests, parasitic weeds and virus (Tignegre, 2010; Batieno, 2014; Issoufou et al., 2017; Salifou et al., 2017; Neya et al., 2019). Such constraints are responsible of drastic yield loss (Issoufou et al., 2017; Neya et al., 2019). The most important parasitic weeds in cowpea production are *Alectra vogelii* and *Striga gesnerioides* (Li et al., 2009). *Alectra vogelii* is a hemiparasitic weed responsible for several negative effects on cowpea production. Remarkable (50%-100%)

yield losses are not uncommon in *Alectra* infested fields (Karanja et al., 2013). In addition, *Alectra* effects affect the mineral composition of cowpea grain (Alonge et al., 2001).

Management strategies including cultural practices, chemical control and genetic resistance, have been proposed (Magani et al., 2009; Karaya et al., 2012; Yunusa et al., 2013; Kwaga, 2014). From these methods, genetic resistance is the most efficient and most affordable from both breeders and farmers view (Rubiales et al., 2006). *Alectra* resistant cowpea varieties have been identified in Burkina Faso through both field and screen house screening (Dieni et al., 2018). However, some of these lines do not possess most farmers' preferred traits. Large size, rough texture and white colour seed are widely adopted (Tignegre, 2010; Horn et al., 2015). Therefore, the creation of genetic variability which is the basis for plant improvement is necessary. The genetic variability required can be created through hybridization. For the sake of creating useful genetic variability, a judicious choice of parents to be crossed and the breeding approach is crucial. Therefore, it was necessary to determine the appropriate breeding strategy to settle down a sustainable breeding programme and provide high valuable information to breeders in making decision for the breeding method as well as selecting the genetic material to be used (Chukwu et al., 2016). The diallel method II is more effective if reciprocal effect are negligible (Chukwu et al., 2016). It provides maximum information about the genetic structure of a character, the parents as well as allelic frequencies (El-Maghraby et al., 2005; Iqbal et al., 2007). Therefore, a study of the combining abilities of a set of genotypes, through diallel analysis, will undoubtedly contribute to the achievement of the research objectives. The combining ability studies cover: (i) the general combining ability (GCA), which is the average performance of a line in a series of crosses, and (ii) the specific combining ability (SCA), which is the deviation from the performance predicted on the basis of the GCA. The objective of this study was to determine (i) the general combining ability (GCA) of cowpea for seed size and resistance to *Alectra vogelii* and (ii) the gene actions involved in the expression of the aforementioned parameters.

MATERIALS AND METHODS
Genetic material

In this study, nine cowpea lines: Moussa Local, KVx30-309-6G, IT82D-849, Nafi, Tiligre, Komcalle-P5, IT98K-205-8, IT81D-994, and B301 were selected based on their reaction to *Alectra vogelii* and their varietal characteristics showed in Table 1. The genotypes B301 and IT98K-205-8 were highly resistant. The lines IT81D-994, Komcalle-P5, Tiligre, Nafi, KVx30-309-6G, Moussa local, and IT82D-849 were moderately resistant to highly susceptible in that order. Tiligre, Nafi and Komcalle-P5 are improved lines possessing farmers' and consumers' preferred characteristics. Moussa local is one of the most accepted local cowpea varieties but susceptible to numerous constraints (*Alectra*, *Striga*, Cowpea aphid born mosaic virus: CABMV, drought, etc.). The other lines were selected for their good level of resistance (B301, IT81D-994, and IT98K-205-8), their high susceptibility (IT82D-849 and KVx30-309-6G), and their contrasting seed characteristics.

The selected parents were hand crossed (Rachie et al., 1994) in a 9x9 half diallel mating design in a screen house at the Institut de l'Environnement et de Recherches Agricoles (INERA) Kamboinse research station in Burkina Faso from June 2015 to March 2016. The parents (9) and their F_1 progenies (36) were evaluated under artificial infestation. *Alectra vogelii* seeds used for the infestation originated from Koupela. The seeds were collected in infested cowpea field at the end of the 2014 rainy season and kept at room temperature until use.

Experimental design and data collection

The experiment was conducted in screen house at INERA in Kamboinsé research station in Burkina Faso from April to June 2016 in Randomized Complete Block Design (RCBD) with three replications. Each

block comprised 45 pots of 12 L representing the experimental unit. The pots were filled with a sterilized substrate composed of three volumes of sand for one volume of clay (3v:1v) and infested with about 1000 *Alectra* seeds. The seeds were thoroughly mixed with sterile sand before the infestation. The infested pots were watered for 14 days in order to break *Alectra* seeds dormancy to enable their optimal germination. Thereafter, a single cowpea seed was planted per pot. NPK fertilizer (14-23-14) was applied a day before planting cowpea at a rate of five grams (g) per pot. Two insecticide sprays were done as recommended in cowpea production in Burkina Faso.

Data collected were as follows
1. Number of days to cowpea first flowering (DTF);
2. Severity of *Alectra vogelii* attack 70 days after planting (SEV) using a scale of 5 classes where : 1: highly resistant, no emergence of *Alectra* shoots; 2: resistant, one to three shoots of *Alectra* emerged above ground which can die few days later; 3: moderately resistant, presence of some fertile shoots of *Alectra*; 4: susceptible, presence of many shoots of *Alectra* with moderate damages (leaf discoloration and browning), and 5: highly susceptible, severe damages with sometimes death of the cowpea plant.
3. Cowpea 100 seed weight (HSW).

Data analysis

The diallel analysis software DIAL win 98 Ukai (1998) reviewed in 2002 was used for data analysis. The data were analysed according to Griffing's (1956) and Walters & Morton's (1978) methods.

Griffing's method II was used to determine general combining ability (GCA) effects of the parents and specific combining abilities (SCA) effects of specific crosses as follows: $X_{ij} = \mu + g_i + g_j + s_{ij}$

Where, μ= 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 i^{th} and j^{th} parents.

The estimate of general combining ability (GCA) effects of and the significance of the GCA effects of each genotype were determined using the formula described by Dabholkar (1999):

$$G_i = \frac{1}{p+2}[(Y_{i.} + Y_{ii}) - \frac{2}{p}Y_{..}] \quad \text{and}$$

$$t_{cal} = \frac{G_i}{S.E._{Gi}} \quad \text{where} \quad S.E._{Gi} = \sqrt{\frac{p-1}{p(p+2)}\sigma^2}$$

Where:
G_i: general combining ability effect of the ith parent, $Y_{i.}$: mean of the i_{th} parent, $Y_{..}$: grand mean, $S.E._{Gi}$: standared error, σ^2: error mean square, p: number of parents.

Walters and Morton's (1978) method allowed to determine the gene actions involved the expression of the different parameters and estimate the genetic parameters as well. The mathematical equation of the model is written as:

$y_{ij} = m + g_i + g_j + l + l_i + l_j$ for off-diagonal elements and $y_{ii} = m + 2g_i$ for elements along the diagonal.

Additive and dominance gene effects in Walters and Morton's model were estimated as in Hayman (1954) where: a = g_i=additive effects of genes; b = dominance effects of genes. The b factor is divided into b_1 = 1 = mean dominance effects; $b_2 = l_i$ = additional dominance deviation due to the parents, b_3 (l_{ij}) = residual dominance effects (effects of epistasis and failure of assumptions).

The genetic parameters were estimated by the software and broad sense (H^2) and narrow sense (h^2) heritabilities were calculated as a proportion of genotypic variance (σ^2_g) on phenotypic variance (σ^2_p) and additive variance (σ^2_A) on phenotypic variance (σ^2_p) respectively. To determine the relative importance of the GCA and SCA in the gene actions involved in the expression of the studied parameters, the Baker's ratio $2\sigma^2_{GCA}$ / ($2\sigma^2_{GCA}$ + σ^2_{SCA}) was computed (Baker, 1978).

Table 1: Characteristics of the nine (9) cowpea genotypes used in the half diallel crosses.

Number	Varieties	Types of varieties	Seed size	Seed colour	*Alectra vogelii*
1	Moussa Local	Local	Medium	White	S
2	KVx30-309-6G	Improved	Big	White	S
3	IT82D-849	Improved	Big	Red	S
4	Nafi	Improved	Big	White	MR
5e	Tiligre	Improved	Big	White	MR
6	Komcalle-P5	Improved	Medium	White	MR
7	IT98K-205-8	Improved	Medium	White	R
8	IT81D-994	Improved	Big	White	MR
9	B301	Local	Small	Brown	R

S= susceptible, MR= moderately resistance, R= resistant.

RESULTS

Combining ability effects

The results of the significance of general and specific combining abilities effects are presented in Table 2. The general combining ability (GCA) effects were significant (P<0.01) for all the traits. However, the specific combining ability effects were significant (P<0.01) for only days to flowering (DTF) and severity of *Alectra* (SEV). The SCA effects were not significant (P>0.05) cowpea 100 seed weight (HSW). The ratio of the GCA variance over the SCA variance was greater than 1 for SEV and HSW except DTF (0.341) meaning that the GCA components were more important than the SCA for these two parameters; on the other hand, the SCA was higher than the GCA for DTF.

The general combining ability (GCA) effects of the nine varieties for the studied parameters are presented in Table 3. For DTF the highest GCA (4.29) was observed with the variety IT81D-994 whereas IT82D-849 presented the lowest GCA (-5.59). The highest value of GCA for SEV was exhibited by IT82D-849 (1.06) whilst B301 (-1.12) showed the lowest GCA for the same parameter. B301 (-6.73) also had the lower

value of GCA for HSW. The greater GCA were observed with Tiligre (2.31) and KVx30-309-6G (2.38).

Gene actions study

The results of analysis of variance (ANOVA) with Walters and Morton's (1978) method are presented Table 4. Both the additive effects of genes (a) and the dominance effects of genes (b) were significant (P<0.01) for all the traits. Within b, b_1 was significant (P<0.05) for SEV; b_2 and b_3 were both significant (P<0.01) for DTF and HSW. On the other hand, for SEV b_2 and b_3 were significant at P<0.05 and P<0.01 respectively.

Narrow sense heritability (h^2) was high for SEV (0.78) and HSW (0.82). A low narrow sense heritability was detected for DTF (0.26) (Table 5). The average degree of dominance ranged from 0.82 to 1.81. It was less than one for SEV and HSW. In contrast, the average degree of dominance was greater than one for DTF. The average direction of dominance was negative for all the parameters with medium to high proportion of dominant genes (Table 5).

The graphical representations of the regression of Wr (covariance between a parent

r and his offspring) on Vr (variance of a relative r and his offspring) for DTF, SEV and HSW are presented in Figure 1, 2, and 3 respectively. The regression coefficient of Wr on Vr for the different traits investigated varied from 0.297 (DTF) to 0.893 (SEV). The regression slope to the parabola passed below the origin for DTF, but for SEV and HSW it passed above the origin. The Wr/Vr graphs showed that for the parameters days to cowpea flowering (DTF), varieties Moussa local, KVx30-309-6G and Nafi were nearest to the origin. Komcalle-P5, IT98K-205-8 and B301 were farthest from the origin whilst IT82D-849 and IT81D-994 were in medium position. In this graph the variety Tiligre was completely separate from the rest. For the severity of Alectra, the varieties B301 and IT98K-205-8 were closest to the origin, three varieties Tiligre, Komcalle-P5 and IT81D-994 were intermediate, and the remaining four were far from the origin. The graph of Wr on Vr for 100 seeds weight presented only B301 associated with its origin, Moussa local, Nafi, Komcalle-P5 and IT98-205-8 were intermediate and the others on the other hand were farthest from the origin.

Table 2: Mean squares of GCA and SCA of 9x9 half diallel for the studied parameters.

Sources	df	DTF	SEV	HSW
Rep	2	79.7^{ns}	0.86^{ns}	3.75^{ns}
GCA	8	299.57**	2.02**	204.76**
SCA	27	125.58**	4.77**	5.15^{ns}
Error	70	61.43	0.28	5.15
Total	107			

**: significant (p<0.01), ns: not significant, df: degree of freedom, DTF: days to cowpea flowering, SEV: severity of Alectra, HSW: 100 seeds weight.

Table 3: General combining ability effects of the nine cowpea genotypes.

Genotype	DTF	SEV	HSW
Moussa local	1.41^{ns}	0.7*	0.36^{ns}
KVx30-309-6G	-1.04^{ns}	0.73**	2.38**
IT82D-849	-5.59*	1.06**	-0.45^{ns}
Nafi	-2.07^{ns}	0.21^{ns}	-0.52^{ns}
Tiligre	-1.98^{ns}	0.1^{ns}	2.31**
Komcalle-P5	-0.35^{ns}	0.12^{ns}	1.34*
IT98K-205-8	-0.71^{ns}	-0.91**	0.09^{ns}
IT81D-994	4.29*	-0.21^{ns}	1.67*
B301	3.08^{ns}	-1.12**	-6.73**

**: significant (p<0.01), *: significant (p<0.05) ns: not significant, DTF: days to cowpea flowering, SEV: severity of Alectra, HSW: 100 seeds weight.

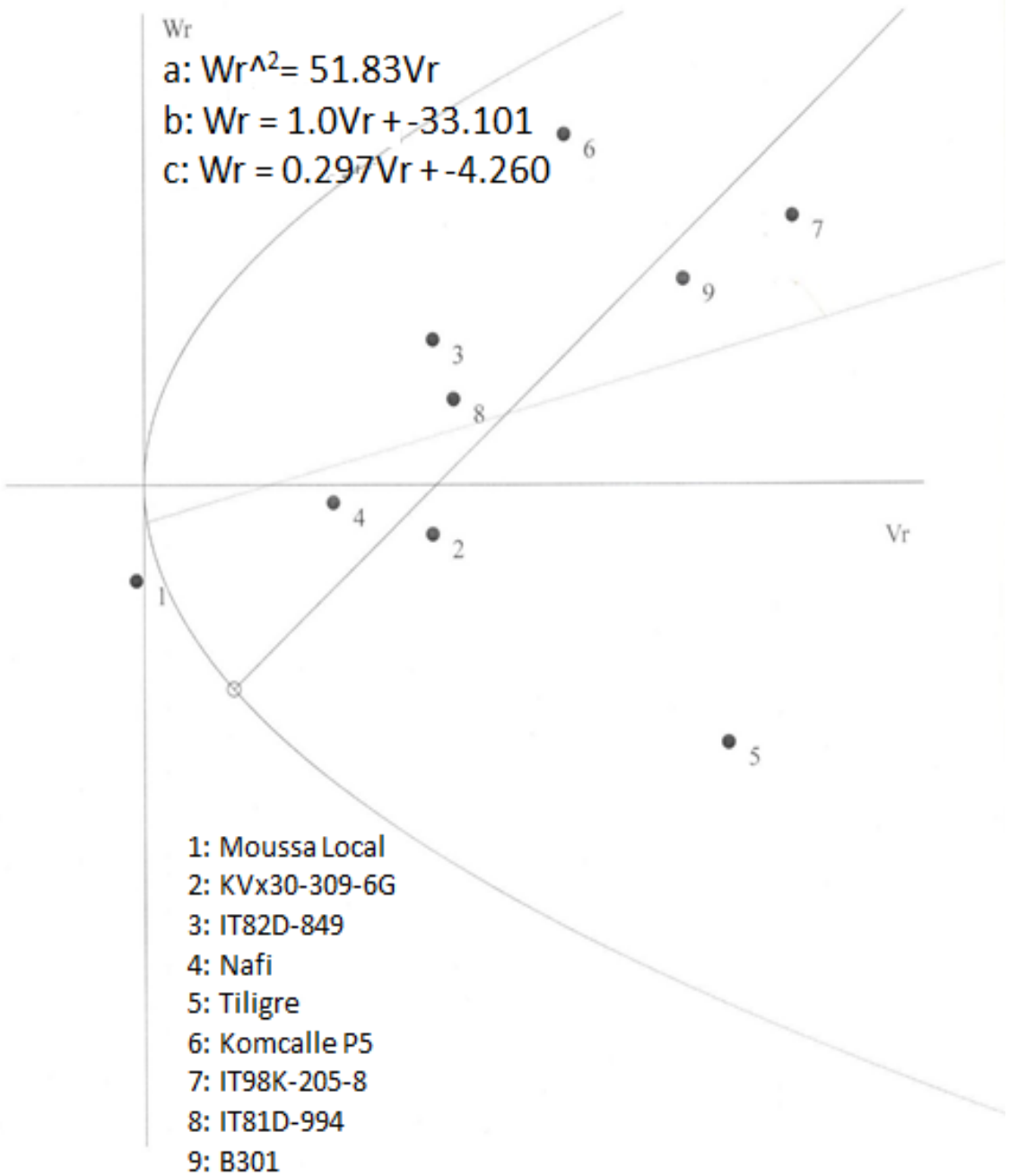**Table 4**: Mean squares of 9x9 half diallel for the studied parameters.

Sources	df	DTF	SEV	HSW
Rep	2	88.01^{ns}	0.14^{ns}	4.24^{ns}
a	8	289.04**	5.42**	79.03**
b	36	143.67**	4.19**	49.38**
b_1	1	2.96^{ns}	8.82**	0.57^{ns}
b_2	8	222.29**	0.56*	34.49**
b_3	27	125.59**	5.09**	55.6**
Error	88	53.43	0.22	4.76
Total	134			

**: highly significant (p<0.01), * significant (p<0.05), ns: not significant. df: degree of freedom, DTF: days to cowpea flowering, SEV: severity, HSW: hundred seeds weight. a: additive effects of genes, b: dominant effects of genes. b_1: mean dominance effects; b_2: additional dominance deviation due to the parents, b_3: residual dominance effects
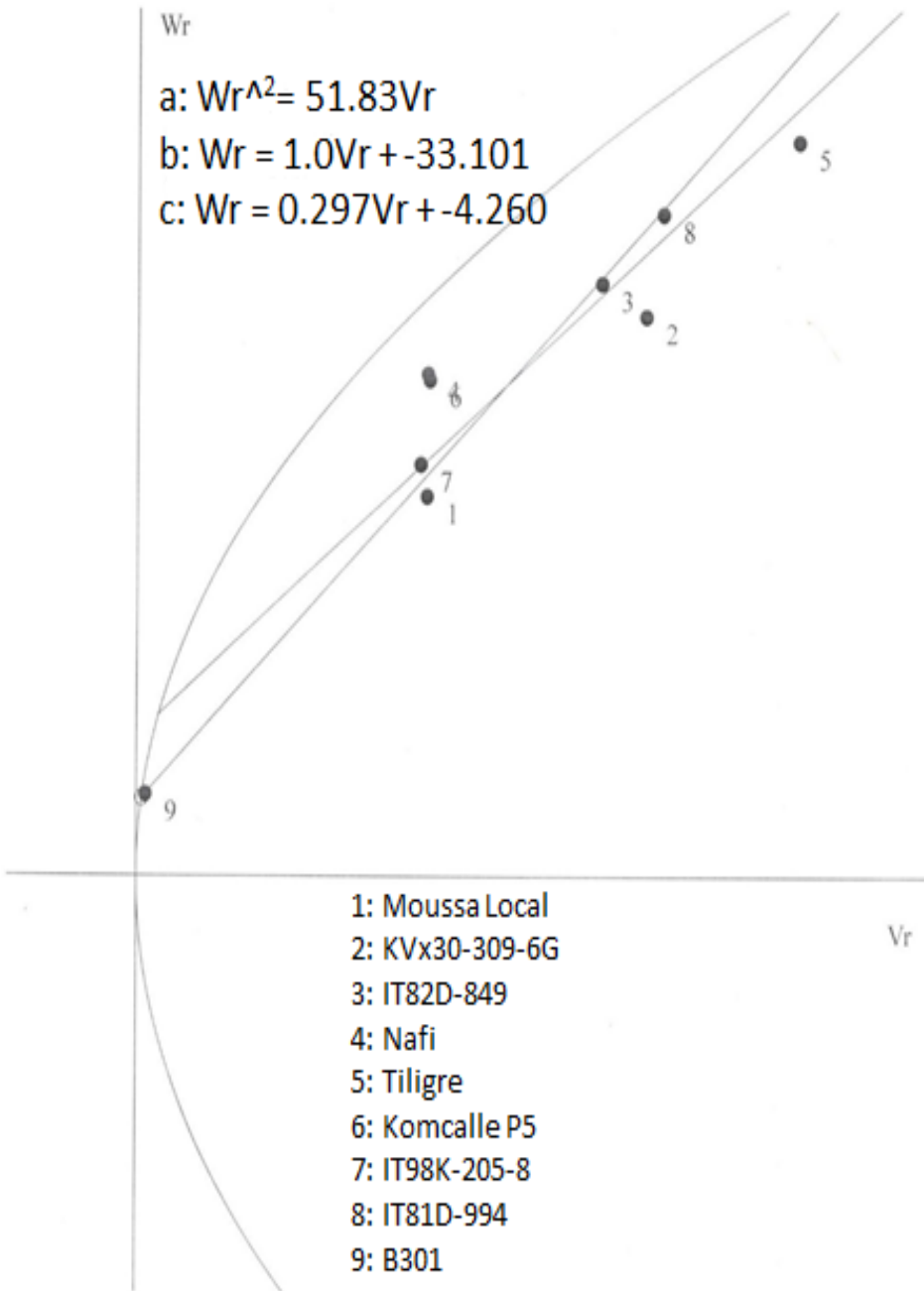
Table 5: Genetic variation and heritability for the studied parameters.

Genetic parameters	DTF	SEV	HSW
Additive variance (D)	51.83	1.72	24.67
Dominance variance (H1)	184.24	1.15	17.76
Dominance variance (H2)	128.84	1.01	8.16
Environment variance (E)	18.75	0.08	1.64
Average degree of dominance $(H1/D)^{1/2}$	1.81	0.82	0.85
Proportion of dominant genes (kd)	0.68	0.39	0.52
Average direction of dominance (h)	-0.66	-1.28	-0.29
Balance of positive and negative alleles (uv)	0.175	0.22	0.12
Broad sense heritability (H^2)	0.73	0.95	0.92
Narrow sense heritability (h^2)	0.26	0.79	0.82

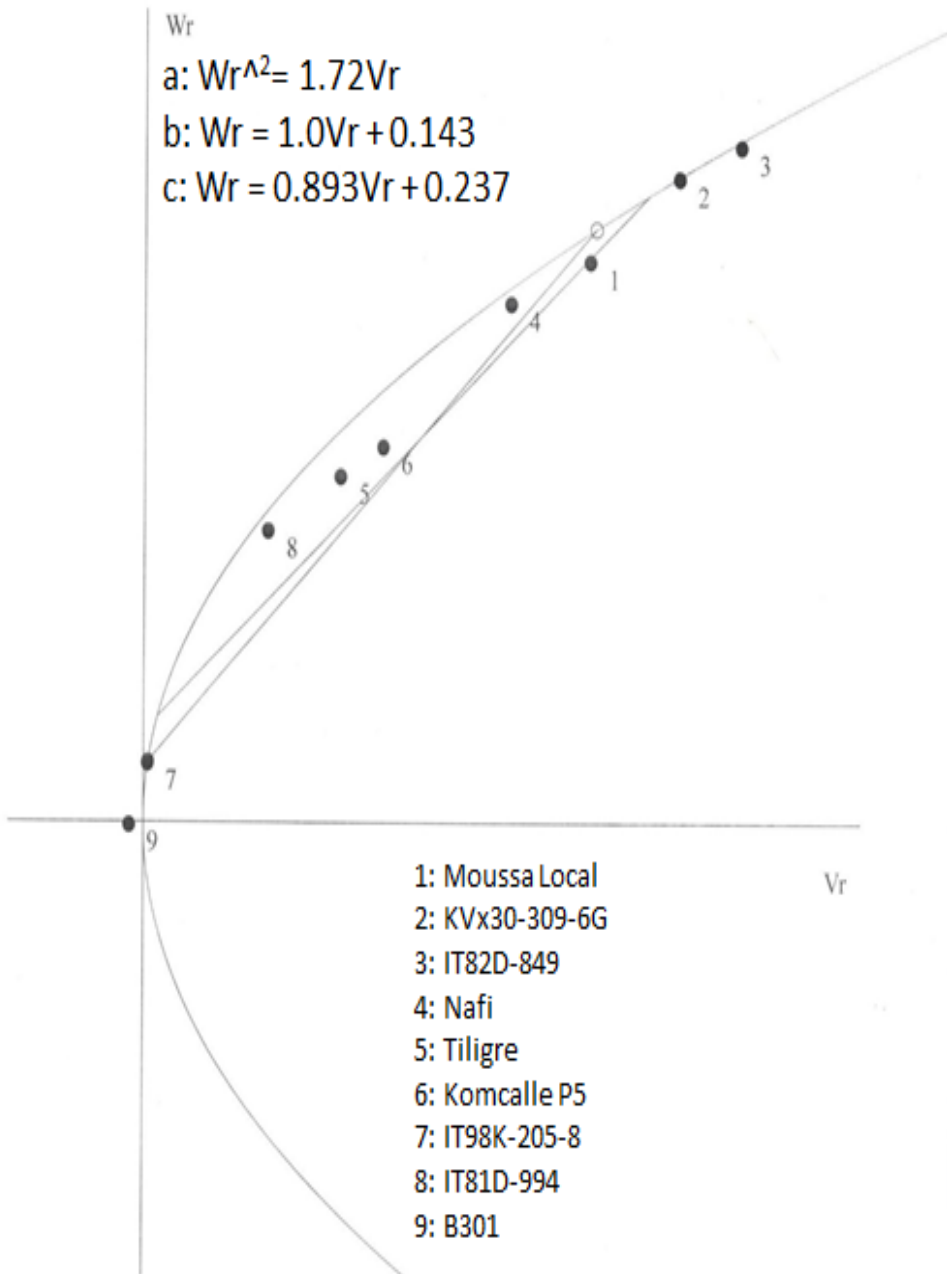*DTF: days to cowpea flowering, SEV: severity, HSW: 100 seeds weight.*

Figure 1: Wr/Vr graph of number of days to cowpea flowering (DTF) of 9x9 half diallel.

a: $Wr^2 = 51.83Vr$
b: $Wr = 1.0Vr + -33.101$
c: $Wr = 0.297Vr + -4.260$

1: Moussa Local
2: KVx30-309-6G
3: IT82D-849
4: Nafi
5: Tiligre
6: Komcalle P5
7: IT98K-205-8
8: IT81D-994
9: B301

Figure 2: Wr/Vr graph of *Alectra vogelii* severity (SEV) of 9x9 half diallel.

Figure 3: Wr/Vr graph of cowpea hundred seed weight (HSW) of 9x9 half diallel.

DISCUSSION

The results showed that both additive or/and non-additive genes effects were involved in the expression of all the investigated traits. Mbwando et al. (2016) also claimed the existence of additive and non-additive gene actions in cowpea resistance to *Alectra* parameters. The proportion of additive gene effects was more important for SEV and HSW with $2\sigma^2_{GCA} / (2\sigma^2_{GCA} +\sigma^2_{SCA})$ values more than unity. However, for DTF the ratio was less than unity indicating the predominant influence of non-additive genes effects (Tchiagam et al., 2011; Eldessouky et al., 2016). Idahosa & Alika (2013) asserted that DTF was mostly under non-additive components control. The relative importance of additive and non-additive gene effects was confirmed by the proportion of dominant genes which were low when additive effects were more important and high (0.68) when it was the opposite. Non-additive gene effects are composed of dominance and epistasis. The significance of b_2 observed implies that there was not uniform distribution of dominant genes among the parents; therefore, some parents were carrying more dominant genes than others. In addition, the significance of b_3 indicated the presence of specific combining ability for some crosses.

Non-additive gene effects including epistasis were present in all the characters, so it could be difficult to predict the outcome of the breeding since non-additive effects are not heritable for self-pollinating crops like cowpea. Similar conclusion was reported by Tignegre (2010) for some cowpea resistance to *Striga gesnerioides*, a closely related parasitic weed to *Alectra vogelii*. However, the narrow sense heritability which is the actual breeding value passed on from parents to offspring was high for all the parameters (74%-82%) except for the parameter days to flowering (26%) indicating the predominance of additive gene effects for these parameters (SEV and HSW).

Very few studies have been undertaken to investigate gene actions involved in cowpea resistance to *Alectra vogelii*. Mbwando et al. (2016) studied the genetic factors involved in cowpea resistance to *Alectra* for two parameters (number of *Alectra* shoots emerged and number of cowpea plant infested). The outcome of this study showed medium narrow sense heritability for each trait, 41.28% and 44.39% respectively. The same range of narrow sense heritability was reported by Tignegre (2010) for cowpea resistance to *Striga gesnerioides*. In addition, high narrow sense heritability (60%) was observed for cowpea resistance to the *cowpea aphid-born mosaic virus* disease in Burkina Faso (Barro et al., 2017).

The high narrow sense heritability for 100 seeds weight reported in this study is in agreement with the findings of previous studies where medium to high narrow sense heritability effects were reported (Lopes et al., 2003; Idahosa et al., 2010; Tignegre, 2010; Egbadzor et al., 2013; Ameen et al., 2014). However, predominant non-additive effects indicating low heritability was also reported for this character (Raut et al., 2017).

The high narrow sense heritability effects detected confirmed that these characters were largely controlled by additive factors. The narrow sense heritability enable a breeder to quantify the progress rate that can be made during the selection process. In addition, the high broad sense heritability (73%-95%) means that these traits are mainly under genetic factors control. Therefore, it is possible to improve for such characters through bulk, pedigree, single seed descent or back-cross selection.

The graphical representation showed that the regression coefficient of the slope was not significantly different from unity for all the parameters and the regression coefficients were high for two of them meaning that the additive-dominance model was satisfied (Lopes et al., 2003; Wu et al., 2006). Although, a low regression coefficient was observed for DTF (0.297) synonymous of a failure of the model for this trait and then suggesting that non-allelic interactions were predominantly involved in the expression of the character (Tchiagam et al., 2011). Therefore, epistasis could be operative for some specific crosses.

The Wr on Vr graph showed that the varieties were scattered along the regression line for all the characters, indicating genetic variability among the parents (Dubey & Ram, 2007). The regression line passed below the origin of the graph, then over-dominance was operative for DTF. Average dominance values $(H_1/D)^{1/2}$ for this trait was greater than 1 (1.81) confirming the over-dominance genes effects revealed from the graphical analysis. Partial dominance genes action was rather present for SEV and HSW with the regression line crossing above the origin. These results were also in agreement with the average dominance values.

For each of the graphs varieties which were closer to the origin carried large proportion of dominant alleles and those that were in extreme position from the origin possessed recessive ones. For instance, for SEV, varieties B301 and IT98K-205-8 accumulated large frequency of dominant alleles as they were nearest to the origin. The recessive alleles were mostly found in IT82D-849, KVx30-309-6G, Moussa local and Nafi. The varieties at mid-distance were those with balanced frequencies of both dominant and recessive alleles. Hence, it could be inferred that partial resistance pattern is operative in IT81D-994, Komcalle-P5 and Tiligre. Varieties B301 and IT98K-205-8 possess vertical resistance.

For 100 seed weight only variety B301 possessed a maximum frequency of dominant alleles and recessives alleles were found in varieties such as IT82D-849, KVx30-309-6G, IT81D-994 and Tiligre. The later varieties, as opposed to B301, had large sized grains. Therefore, it can be deduced that recessive alleles are responsible for big seed size in these varieties. This statement is in agreement with the findings of Noubissié et al. (2011) who mentioned that yield components were mostly controlled by recessive genes. Moreover, the present results corroborate those of (Egbadzor et al., 2013). These authors asserted that small grain size was partially dominant over large grain size.

The varieties KVx30-309-6G and Tiligre had higher general combining ability (GCA) effects for HSW followed by IT81D-994 and Komcalle-P5. Parents exhibiting high

GCA effects for yield component traits are the best combiners which are valuable in breeding (Machida et al., 2010; Machikowa et al., 2011). KVx30-309-6G had the highest GCA for HSW; however, it is *Alectra* susceptible and exhibited positive significant (GCA) for SEV. Therefore, it is not a good recurent parent in breeding for *Alectra* resistance. The varieties Tiligre, Komcalle-P5 and IT81D-994 did not exhibit significant GCA effects for SEV and therefore these varieties offer advantage in both *Alectra* control and seed size increase. In addition, the varieties Tiligre and Komcalle-P5 are farmers' preferred varieties with medium to large seed size and *Striga* tolerance (Tignegre, 2010). Therefore, they can be good combiners to be used to improve cowpea for yield and resistance to both *Alectra* and *Striga*. The landrace B301 confers resistance to both parasitic weeds, as such it could be a good donor parent. However, the dominance gene action (not heritable) involved in the resistance coupled with the recessive inheritance for seed weight (lower GCA) render difficult selection in early generations when B301 is used as donor parent. The variety IT98K-205-8 could be the best donor since it possesses resistance and balanced allele frequencies for grain size. With regard to the high narrow sense heritability for *Alectra* resistance as well as for seed size, a good selection progress can be achieved through backcross or single seed descent breeding method.

Conclusion

Additive gene effects were more important in the inheritance of cowpea HSW and cowpea resistance to *Alectra vogelii* (SEV). Non-additive gene interactions including non-allelic interaction were predominantly operative in the inheritance of DTF. Dominant and recessive alleles were unharmoniously distributed among the parents for all the parameters. Cowpea resistance to *Alectra* was conferred by dominant alleles. In contrast, recessive alleles are responsible for large seed size. The varieties Tiligre and Komcalle-P5 were the best combiners for HSW with regards to breeding progress for resistance to *Alectra vogelii*. High narrow sense heritability was observed for HSW, and

SEV. Therefore, breeding progress can be achieved through single seed descent or backcross selection using Tiligre or Komcalle-P5 as recurrent parents.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

ZD wrote the first draft and all the co-authors read and approved the final version.

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