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Genetic variability studies of Valencia groundnut varieties for late leaf spot (*Phaeoisariopsis personata*) resistance

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The study was initiated to determine the genetic variability of late leaf spot (LLS) resistance among segregating generations of Valencia groundnut varieties. Crosses were made between NuMex-M_3 × ICGV-SM 02501, Valencia C × ICGV-SM 02501, Redbeauty × ICGV-SM 03590 and Valencia C × SGV-07009 parental lines and the resulting generations (F_1, F_2, BC_1P_1 and BC_1P_2,), along with parents for each cross, were evaluated for LLS resistance on a 1-9 scale under natural conditions in a randomized complete block design (RCBD) with three replications. Analysis of variance was performed for generations of each cross, coefficients of variation and heritability were estimated for all crosses except for the Valencia C × SGV-07009 cross. Three crosses showed highly significant differences among generations for LLS resistance (P≤ 0.05). The three crosses exhibited moderate to high levels of genotypic coefficient of variation (GCV) (15.43 to 23.13 %) and phenotypic coefficient of variation (PCV) (16.89 to 28.82%). The exception was the Redbeauty × ICGV-SM 03590 cross which showed low (9.50%) GCV. Broad-sense heritability (h^2_b) estimates for LLS disease scores were moderate to high (32 to 64%) for the three crosses. The results reveal substantial variation for LLS resistance in generations of these crosses indicating that the trait under study was heritable.

Key words: Valencia groundnut, *Arachis hypogeae,* late leaf spot, resistance, genetic variability.

INTRODUCTION

In Uganda, groundnut (*Arachis hypogeae* L) is the second most important legume crop after common beans (*Phaseolus vulgaris* L.) (UBOS, 2010) grown in all parts of the country (UBOS, 2010; Okello et al., 2013). The production volume gradually increased from about 130,000 tons on 216,000 ha in 2003 to over 185,000 tons

on 253,000 ha in 2009 (FAO, 2009). As a legume, groundnut improves soil fertility by fixing nitrogen (Janila et al., 2013), and therefore, requires fewer inputs making it ideal for cultivation by resource poor farmers (Smartt, 1994). In addition it is well adapted to the hot, semi-arid conditions of Uganda (Okello et al., 2010; UBOS, 2010). As a cash crop, groundnut gives relatively high returns for limited land area. Nutritionally, groundnut kernels are a rich source of energy and a principal source of protein (Asibuo et al., 2008; Jambunathan, 1991; Shilpa et al., 2013). Groundnut is also a very good source of minerals (calcium, magnesium and iron) and vitamins (B1, B2 and Niacin) (Sigh and Diwakar, 1993). In addition, in many countries groundnut hay is used for fodder (Ozyigit and Bilgen, 2013), and the shells used for fuel (Janila et al., 2013).

The low productivity of the crop is ascribed mainly to foliar diseases of which late leaf spot (LLS) caused by *Phaeoisariopsis personata* (Berk. and Curtis) is said to be the most devastating fungal disease accounting for over 60% yield loss of Valencia groundnut in Uganda (Mugisha et al., 2004). According to Kalule et al. (2010), all Valencia varieties in Uganda are susceptible to LLS disease, and yet they are preferred by farmers for their early maturity attribute (Okello et al., 2010; 2013), by consumers for their sweet taste (Pattee et al., 2001) and by traders for their high oil content (Kaaya and Warren, 2005). Effective chemical control is heavily reliant on multiple fungicide applications (Jordan et al., 2012), which is costly for our resource poor farmers and may not be economical in our rain-fed agriculture (Page et al., 2002). The deployment of resistant cultivars is the most viable option to control LLS disease in groundnut, which could be effective in decreasing the production costs, improving product quality and reducing detrimental effects of fungicides on ecosystems. It is for these reasons that breeders choose to exploit the available genetic resources through plant genetic improvement techniques. However, little has been achieved due the lack of adequate information on genetic variability of LLS resistance on the available Valencia breeding materials, which makes genetic improvement of the crop difficult. In addition, the quantitative nature of LLS resistance (Dwivedi et al., 2002; Upadhyay et al., 2009; Khedikar et al., 2010), suggests that resistance is rather complicated, which could make direct selection for LLS resistance challenging in the breeding program. Information on the coefficients of variation and heritability helps to know whether the observed variability in the available material is due to genotype or environmental factors. Moderate PCV and GCV have been reported for LLS resistance in 28 F2 populations involving eight parents by Vishnuvardhan et al. (2012). In 2008 Khedikar reported high PCV (21.71 to 33.55) and moderate to high GCV (14.46 to 24.76) for LLS disease scores under natural conditions. Kumari (2008) observed high PCV (29.96 to 36.07) and GCV (27.71 to 32.96) for LLS resistance. Anderson et al. (1991) observed low to high broad sense heritability estimates for components of resistance to LLS disease. Vishnuvardhan et al. (2012) reported high and Khedikar et al. (2010) also reported high to very high (40.87 to 82.81%) h^2_b of LLS resistance in groundnut. However, Falconer and Mackay (1996) concluded that heritability values depend on the structure of the population and environmental conditions where the materials are evaluated. In this study, GCV, PCV and broad-sense heritability (h^2_b) for LLS resistance were estimated using Valencia breeding populations to generate more information to be used in suggesting a breeding program strategy for developing LLS resistant groundnut genotypes.

MATERIALS AND METHODS

The research was conducted at the National Semi-Arid Resources Research Institute (NaSARRI) of the National Agricultural Research Organization (NARO) located 01^0 30' 00" N and 33^0 33' 00" E in Serere district, Uganda. This location represents a humid and hot climate that receives an annual rainfall of 1,000-1,200 mm. In the study, groundnut genotypes with varying levels of resistance to LLS were used (Table 1). The genotypes had been characterized for resistance to LLS by the Groundnut Improvement Program at NaSARRI.

Generation of first filial generations (F_1 progenies)

Valencia lines Valencia C, NuMex-M_3 and Redbeauty were used as female (susceptible lines) while SGV- 07009, ICVG-SM 03590 and ICGV-SM 02501 were the male parents (resistant lines). In July 2011, three seeds from each of the parents were planted in plastic pots of diameter 45 cm and height 15 cm containing garden soil. The parental lines were grown in a glass house. Staggered planting of parents was done where the male parents were planted one week earlier than the female parents in order to synchronize flowering and to ensure continuous availability of flowers and floral buds for making crosses. Plants were watered every two days until they reached physiological maturity.

At flowering, the female parents were emasculated with forceps in the evening, and crossings were made the following morning. Bi-parental mating design was employed where four crosses were made between NuMex-M_3 × ICGV-SM 02501, Valencia C × ICGV-SM 02501, Redbeauty × ICGV-SM 03590 and Valencia C × SGV-07009 parental lines. In each cross 15 female flowers were pollinated. At physiological maturity the pods of the parental lines and crosses (F_1s) were harvested separately, dried, and packed in labeled envelops, and stored.

Generation of F_1, F_2, BC_1P_1 and BC_1P_2 populations

In December 2011, 15 F_1 seeds generated from each

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Table 1. Botanical names, origin, pedigree, and response to late leaf spot (LLS) of six groundnut lines.

Genotype	Botanical Name	Pedigree	Country of origin	Response to LLS
Redbeauty	Valencia	Landrace	Uganda	Susceptible
Valencia C	Valencia	Selection from Colorado Manfredi	USA	Susceptible
NuMex-M_3	Valencia	Valencia C × ICGV 87157	USA	Susceptible
JL 24	Spanish	Selection from Taiwan EC94943	India	Highly susceptible
ICVG-SM O3590	Virginia	-	Malawi	Resistant
ICGV-SM 02501	Spanish	-	Malawi	Resistant
SGV 07009	Virginia	SGV 91707× Serenut 1	Uganda	Resistant

cross described above, along with their respective parents were grown in a glass house. The F_1 seed were planted alongside their respective parents to identify the successful crosses. The parents were also used to generate more F_1 seeds as described above. At flowering, five F_1 plants were selfed to generate F_2 seeds while five plants were backcrossed to susceptible parents (P_1) and five plants backcrossed to donor plants (P_2) to produce $BC_1P_1$and BC_1P_2 seeds, respectively. The parents of the respective crosses were used as male parents, and the F_1 generation as female parents in generation of BC_1P_1 and BC_1P_2 seeds.

Evaluation of the six generations of the four crosses

Field lay out

The generations of the four crosses were evaluated in the experimental field at NaSARRI, a hot spot for LLS disease. Six generations P_1, P_2, F_1, F_2 and BC_1P_1 and BC_1P_2 of each of the four crosses: NuMex-M_3 × ICGV-SM 02501, Valencia C × ICGV-SM 02501, Redbeauty × ICGV-SM 03590 and Valencia C × SGV-07009, were set in a RCBD in three replicates with 2-row-plots of ten plants each. The populations and parental lines were planted in the field at a spacing of 45 × 15 cm in June 2012, and the experiment was kept free of weeds throughout the cropping season.

Inoculation

To maximize LLS inoculum pressure under natural conditions, the spreader row technique was used. The groundnut line JL 24, which is highly susceptible to LLS was used as a source of inoculum. Spreader rows were planted after every two rows of test materials and at the border of the experiments to maintain the effective inoculum load. These rows were planted two weeks before planting the experimental materials.

Data collection

LLS disease severity scoring was done at 115 days after planting using a modified nine point scale (Subrahmanyam et al., 1995), where a score of 1 was rated as highly resistant (HR), 2-4 as resistant (R), 5-6 as moderately resistant (MR), 7-8 as susceptible (S), and 9 as highly susceptible (HS).

Statistical analysis

Analysis of variance

Data taken on the generations of each cross were subjected to ANOVA using GenStat version 13 software to test for the significance of the differences between the generations' means of each cross for the LLS disease scores. The ANOVA was based on the linear mathematical model: $Y_{ij}= \mu + r_i + g_j + e_{ij}$; where Yij= observed effect for i^{th} replication and j^{th} genotype, μ = grand mean of the experiment, r_i = effect of the i^{th} replication, g_i = effect of the j^{th} genotype, e_{ij} = residual effect. The generation means were compared using Fisher's protected least significant difference test at 5% level of probability (Payne et al., 2010).

Estimation of PCV, GCV, heritability and genetic advance

In order to determine PCV, GCV, heritability and genetic advance for LLS resistance, variance components (environmental and genotypic variances) were obtained following the method of Kearsey and Pooni (1996) for the three crosses (NuMeX-M_3 × ICGV-SM 02501, Valencia C × ICGV-SM 02501, and RB × ICGV-SM 03590).

Estimation of PCV and GCV: Both PCV (i) and GCV (ii) were estimated following the method suggested by Singh and Chaudhury (1985) and classified as described by Sivasubramanian and Menon (1973) as; low (0-10), medium (10-20) and high (20 and above).

(i) Phenotypic coefficient variation (PCV) = $(\sqrt{V_P})/\overline{X})*100$

(ii) Genotypic coefficient variation (GCV) = $(\sqrt{V_G})/\overline{X})*100$

Where, V_P= Phenotypic variance, V_G=Genotypic variance and $\overline{X}$=Grand mean of the character.

Estimation of broad-sense heritability: Variance components (environmental and genotypic) obtained above were used to determine broad sense heritability (h^2_b) (Kearsey and Pooni, 1996) in the three crosses NuMex-M_3 × ICGV-SM 02501, Valencia C × ICGV-SM 02501, andRB × ICGV-SM 03590 as detailed below.

Broad-sense (h^2_b) = $100[\sigma^2G(F_2)/V_{F2}]$

Where; $\sigma^2G(F_2)$= Genotypic variance in F_2 and V_{F2}= variance of F_2 generation.

Genetic advance (GA): Genetic advance (GA) was estimated following Singh and Chaudhury (1985) method as;

$GA = h^2_b \times k \times \sigma^2_p$

Where, h^2_b = broad sense heritability estimate, σ^2_p = Phenotypic standard deviation, K = Selection intensity at 5 % is equal to 2.06.

Genetic advance as percent of mean (GAM) was then determined as:

GAM % = $(GA/\overline{X})*100$

Where, $\overline{X}$= Grand mean of the trait, GA = Genetic advance.

Table 2. Results of LLS mean score for the six generations of the 4 crosses.

Generation	NuMeX-M_3 × ICGV-SM 02501	Valencia C × ICGV-SM 02501	Valencia C × SGV 07009	Redbeauty × ICGV-SM 03590
P_1 (S)	6.79±0.25^{c}	7.44±0.38^{d}	7.29±0.61^{b}	7.00±0.41^{c}
P_2(R)	3.42±0.18^{a}	3.40±0.16^{a}	8.36±0.31^{b}	3.50±0.50^{a}
F_1	3.50±0.50^{ab}	3.83±0.40^{ab}	7.52±0.78^{b}	4.50±0.50^{a}
F_2	5.33±0.88^{b}	5.22±0.40^{c}	5.00±0.38^{a}	4.60±0.40^{a}
BC_1P_1	5.25±0.75^{b}	4.75±0.48^{bc}	8.17±0.65^{b}	5.00±0.58^{ab}
BC_1P_2	4.75±0.63^{ab}	4.25±0.63^{abc}	5.25±0.37^{a}	4.50±0.50^{a}
MS	27.32	20.14	21.20	4.03
F	19.93**	20.80**	13.66**	4.35**
CV %	22.1	20.6	18.2	18.1

**=significant at P<0.01, S = susceptible, R = resistant, F_1= first filial generations F_2 = Second filial generations and $BC_1P_1$and BC_1P_2 backcrossed to susceptible parents (P_1) and donor parents (P_2), CV%=Coefficient of variation, F = Variation ratio, MS=Mean sum of square.

Table 3. Genetic parameters for resistance to LLS in groundnut.

CROSS	NuMex-M_3 × ICGV-SM 02501	Valencia C × ICGV-SM 02501	Redbeauty × ICGV-SM 03590
V_E	0.83	0.90	0.54
V_G	1.50	0.54	0.25
PCV	28.82	25.21	16.89
GCV	23.13	15.43	9.50
h^2_b(%)	64.00	37.00	32.00
$\overline{X}$	5.30	4.77	5.30
GA	1.13	0.67	0.22
GAM%	21.37	13.63	4.17

V_E=Environmental variance,V_G=Genotypic variance, PCV and GCV=Phenotypic and Genotypic Coefficient of Variation respectively,$h2_b$=Broad heritability, $\overline{X}$=Grand mean of all generations for each cross, GA=Genetic advance and GAM%=Genetic advance as percent of mean.

The Genetic Advance as percent of Mean (GAM %) was categorized following the procedure of Johnson et al. (1955) as low (0-10), medium (10-20) and high (20 and above).

RESULTS

Analysis of variance

The results of ANOVA and Fisher's protected least significant difference tests are shown in Table 2. The four crosses NuMex-M_3 × ICGV-SM 02501, Valencia C × ICGV-SM 02501, Redbeauty × ICGV-SM 03590, and Valencia C × SGV-07009 showed significant differences among generations for LLS scores (P≤0.01). The mean disease scores of the donor parents ICGV-SM 02501 and ICGV-SM 03590 were low while SGV-07009 had very high disease scores, which were similar to the susceptible parents: NuMex-M_3, Redbeauty and Valencia C. In all crosses except Valencia C × SGV-07009, the means of the parents (P_1 and P_2) showed a tendency to be more extreme and contrasting for LLS resistance. Therefore, the later cross was excluded for further analysis. Moderate to high levels of LLS resistance were observed in all populations of the crosses. In general, the backcrosses, BC_1P_1 and BC_1P_2 showed the mean LLS disease score close to their respective recurrent parents Table 2. The segregants in the F_2 generation of the crosses Valencia C × SGV-07009 , Valencia C × ICGV-SM 02501 and M3 × ICGV-SM 02501 showed moderate severity for LLS disease scores, while that of Redbeauty × ICGV-SM 03590 were highly resistant to LLS.

Estimation of PCV, GCV and heritability

The results demonstrating PCV and GCV, heritability and genetic advance estimates for resistance to LLS are presented in Table 3. The PCV estimates were high in NuMex-M_3 × ICGV-SM 02501(28.82 %) and Valencia C ×

ICGV-SM 02501 (24.51 %) crosses and moderate in Redbeauty× ICGV-SM 03590 (16.89 %). The genetic coefficient of variation (GCV) estimates were high in cross NuMex-M_3× ICGV-SM 02501(23.13 %), moderate in Valencia C × ICGV-SM 02501(15.87 %) and low in cross Redbeauty × ICGV-SM 03590 (9.50 %). Broad-sense heritability estimates for LLS disease score were 32, 37 and 64%, respectively, for Redbeauty × ICGV-SM 03590, Valencia C × ICGV-SM 02501 and NuMex-M_3 × ICGV-SM 02501. Genetic Advance as percentage of Mean (GAM) were low in the cross between Redbeauty × ICGV-SM 03590 (10.93%), moderate in Valencia C × ICGV-SM 02501 (19.43%) and high in NuMex-M_3× ICGV-SM 02501 (38.19%).

DISCUSSION

The ANOVA for the 4 crosses showed highly significant differences (P≤ 0.01) among generations for late leaf spot resistance (Table 2), suggesting presence of genetic variability for LLS disease score in the generations. Variability for LLS resistance was also reported by Vishnuvardhan et al. (2012) in experimental materials that comprised of 28 F2 populations. In the present study genotypes ICVG-SM 02501 and ICGV-SM 03590 showed high resistance to LLS and are recommended for use in breeding program as sources of resistance to late leaf spot. An earlier report by Kalule et al. (2010) demonstrated that these lines were the best parents for LLS resistance. Moderate to high levels of LLS resistance was observed in the populations of the 4 crosses (Table 2), indicating that the trait under study was heritable. The results partly agree with that of John et al. (2008) who reported moderate incidence of LLS in F2 population of the Kadiri-3 × ICGV-88083. Kornegay et al. (1980) also observed minimal leaf defoliation in F1 and F2 generations of the cultivated Virginia.

The mean of F_1s of NuMex-M_3 × ICGV-SM 02501, Valencia C × ICGV-SM 02501 and Redbeauty × ICGV-SM 03590 crosses tended towards the mean of the ICGV-SM 02501 and ICGV-SM 03590 resistant parents, respectively (Table 2), indicating mid-parent heterosis in these crosses. In groundnut however, commercial production of F_1 seed is not feasible since it's predominately self-pollinated. According to John et al. (2012), heterotic crosses in self-pollinated crops help breeders to select appropriate crosses that could lead to desirable transgressive segregants in advanced generations. Therefore, breeding methods such as recurrent selection may be used in exploitation of such heterosis in future breeding programs for these crosses.

Several reports indicate that resistance to LLS in groundnut is controlled by several recessive genes (Nevill 1982; Dwivedi et al., 2002; Upadhyay et al., 2009; Khedikar et al., 2010), though, the F_1's in the present study exhibited partial resistance. Walls and Wynne (1985) concluded that partial resistance in F_1 could not be explained solely by completely recessive genes. They suggested that modifier genes were affecting the phenotypic expression of genes at loci controlling resistance. Anderson et al. (1990) also reported that recessive as well as modifier genes may be involved in resistance to LLS disease in groundnut.

The donor line SGV-07009 was highly susceptible to LLS, in spite of the fact that segregating populations F_2 and BC_1P_1 of the cross Valencia C × SGV-07009 were moderately resistant (Table 2). Natarajan et al. (2001) reported that crosses involving susceptible parents may tend to produce resistant progenies with stable resistance due to additive genetic action. Babu (2010) recommended that such transgressive segregants that arise from the susceptible parents on both sides can also be used as potential genetic stocks in resistance breeding programs. However, this cross was excluded for further analysis.

Moderate to high levels of genetic coefficients of variability **(**GCV) (15.43 to 23.13) and phenotypic coefficients of variability **(**PCV)(16.89 to 28.82) were noticed for LLS resistance in all the three crosses, except for the cross Redbeauty× ICGV-SM 03590 which showed low GCV (9.50) Table 3. The results are comparable with Vishnuvardhan et al. (2012) observation of moderate PCV (19.04) and GCV (16.48). The results of the study also partly agree with those of Khedikar et al. (2010) which indicated high (21.71 to 33.55) PCV, Khedikar, (2008) which indicated moderate to high (14.46 to 24.76) GCV and Kumari (2008) which indicated high PCV (29.96 to 36.07) and GCV(27.71 to 32.96) for late leaf spot resistance. High PCV and moderate to high levels of GCV revealed high magnitude of heritable variation for LLS resistance in these crosses.

In the current study, high GCV (23.13) was exhibited in the cross NuMex-M3 × ICGV-SM 02501. A high GCV indicated that the character had high variability which can be attributed to genotype and with very little effect of the environment. According to Oyiga and Iguru (2011), when the magnitude of GCV is higher, it indicates that the genetic component is the major contributor to the total variance of the trait under study. High PCV and GCV of a trait may result in high heritability which suggests that the improvement of this trait by simple selection method could be possible. Vishnuvardhan et al. (2012) concluded that high GCV may indicate a predominant role of additive gene actions and amenability for phenotypic selection in early generations.

Although the GCV values revealed the extent of genetic variability present in the genotypes for LLS resistance, GCV values are not enough to assess the level of genetic variability among the genotypes. Genetic variation could further be explored with help of heritability estimates, which measures the heritable portion of the total variation. In the present study moderate to high h^2_b revealed the existence of inherent variability among the

genotypes, which is more useful for exploitation in selection and hybridization programs. All the three crosses in the present study showed moderate to high h^2_b (32-64%) and low to high GAM (4.17-21.37%). Moderate to very high h^2_b (40.87 to 82.81) estimates were also reported for leaf spot disease severity in groundnut Khedikar et al. (2010) and Kumari (2008) also report very high h^2_b (83.50 to 85.50). Vishnuvardhan et al. (2012) reported moderate GCV (16.48), high h^2_b (74.91) and GAM (29.38) while Kumari (2008) observed high GCV (27.71 to 32.96), h^2_b (83.50 to 85.50) and GAM (52.78 to 62.05) for late leaf spot severity. The discrepancy of the results is not unexpected because such quantitative traits are often affected by several environmental factors and the genetic background of the parental materials. Falconer and Mackay (1996) concluded that heritability values depend on the population and environmental conditions in which the materials are evaluated.

High h^2_b (64.41 %) estimates were observed in the cross NuMex-M_3 × ICGV-SM 02501 indicating a high response to selection due to reduced environment influence thereby validating the results obtained with the high GCV value for this cross. Anderson et al. (1986) also observed high heritability for LLS resistance and concluded that individual plant selection for LLS would be effective in early generations. Moderate h^2_b estimates were observed in Redbeauty × ICGV-SM 03590 (32 %) and Valencia C × ICGV-SM 02501 (37 %) crosses suggesting a high influence of the environment on the trait in these crosses. The high environmental variation could have been a result of variation in relative humidity within the micro-climates. Thus, selection of genotypes from initial generations by LLS disease scores in these crosses may be difficult. Singh (1993) concluded that low to moderate heritability estimates makes selection considerably difficult or virtually impractical due to the masking effect of the environment on the genotypic effect. Furthermore, LLS resistance is polygenically controlled, and cumulative environmental effects on this polygenically controlled trait could have given poor heritabilities for this trait. In such cases simple selection may not be rewarding. Breeding efforts to increase resistance will require good control over environmental variance. Adequate experimental design, accurate phenotyping are key interventions that could increase the heritability of such a polygenic trait.

Heritability estimates when coupled with genetic advance provides a better prediction of expected gain under selection instead of heritability alone. The estimates of genetic advance help in understanding the type of gene action involved in the expression of various polygenic characters (Singh and Narayanan, 1993). High heritability (h^2_b) (64%) coupled with high (21.27) genetic advance was observed for LLS resistance in the NuMex-M_3 X ICGV-SM 02501 cross, indicating significant role of additive gene action for its inheritance. Therefore, simple selection methods would be effective for improvement of LLS resistance from this cross. The results are comparable with reports of Vishnuvardhan et al. (2012), which indicated high GA for LLS resistance. Moderate (32 to 37%) heritability (h^2_b) estimates along with low to moderate (4.17 to 13.63%) genetic advance was observed in Valencia C × ICGV-SM 02501 and Redbeauty × ICGV-SM 03590 crosses, which indicated that additive and non-additive gene actions had a role in the inheritance. The successful breeding methods will be the ones, which exploit additive and non-additive gene effect such as recurrent selection (Nidagundi et al., 2012) and use of biparental mating (Dabholkar, 1992; Soomro et al., 2010).

Conclusions

Based on the observed results, it can be concluded that a considerable amount of genetic variation for LLS resistance existed among the segregating generations of the Valencia groundnut varieties, which can guarantee substantial improvement through selection. However, the amount of variation depended on the genetic back-grounds of the parents that were used in the study. The best strategy for obtaining LLS resistant genotypes is for selection to be carried out in initial inbreeding generations for the cross between NuMex-M3× ICGV-SM 02501, followed by selection in the following generations with higher inbreeding levels in other crosses.

Conflict of Interest

The authors have not declared any conflict of interest.

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