African Crop Science Journal, Vol. 22, No. 4, pp. 327 - 336
ISSN 1021-9730/2014 $4.00

NARROW SENSE HERITABILITY AND GENE EFFECTS FOR LATE LEAF SPOT RESISTANCE IN VALENCIA GROUNDNUTS

W. WAMBI, P. TUKAMUHABWA, N. PUPPALA[1], D.K. OKELLO[2], R.G. NALUGO and N.A. KAAYA[3]
Department of Agricultural Production, School of Agricultural Sciences, Makerere University, P. O. Box 7062, Kampala, Uganda
[1]New Mexico State University - Agricultural Science Center at Clovis, 2346 SR 288, Clovis, New Mexico, USA
[2]National Semi-Arid Resources Research Institute, P. O. Box Private Bag Soroti, Uganda
[3]Department of Food Technology and Nutrition, School of Food Technology, Nutrition and Bio-systems Engineering, Makerere University, P. O. Box 7062, Kampala, Uganda
Corresponding author: tphinehas@caes.mak.ac.ug

(Received 25 July, 2014; accepted 21 November, 2014)

ABSTRACT

Late leaf spot (LLS), *Phaeoisariopsis personata* (Berk. and Curtis) Deighton, is one of the most important foliar diseases of groundnut (*Arachis hypogaea* L.) worldwide. Effective chemical control is heavily reliant upon multiple fungicide applications which are costly for resource poor farmers in Sub-Saharan Africa. The deployment of resistant cultivars is a better option to control this disease in groundnut. A study was conducted to determine narrow sense heritability and gene action controlling LLS resistance in Valencia groundnut materials. The materials used included six generations; F_1, F_2, F_1 backcrosses to the susceptible BC_1P_1 and resistant BC_1P_2 parents, and their respective parental lines of crosses between NuMex-M_3× ICGV-SM 02501, Valencia C × ICGV-SM 02501and Redbeauty × ICGV-SM 03590. All the test materials were evaluated at the National Semi-Arid Resources Research Institute (NaSARRI) at Serere in Uganda. Narrow-sense heritability estimates were 12, 27 and 36%, for Redbeauty × ICGV-SM 03590, Valencia C × ICGV-SM 02501 and NuMex-M_3 × ICGV-SM 02501 crosses, respectively. Both additive and dominance gene effects contributed significantly to the inheritance of LLS resistance in all the crosses, except in Redbeauty × ICGV-SM 02501 where the effects of dominance were not significant.

Key Words: *Arachis hypogaea,* narrow sense heritability, *Phaeoisariopsis personata*

RÉSUMÉ

La tache fusarienne tardive (LLS), *Phaeoisariopsis personata* (Berk. and Curtis) Deighton, est l'une des plus importantes maladies foliaires à l'échelle mondiale au niveau de l'arachide (*Arachis hypogaea* L.). Une lutte chimique efficace contre cette maladie nécessite l'utilisation en quantité importante de plusieurs types de fongicides. Cette approche est très coûteuse pour être adoptée par les petits paysans de l'Afrique Sub-Saharienne. Le développement de variétés résistantes est une meilleure option pour lutter contre cette maladie dont est sujette l'arachide. Une étude a été réalisée afin de déterminer l'héritabilité au sens strict et l'action des gènes contrôlant la résistance à LLS dans la variété d'arachide Valencia. Les matériels génétiques utilisées comprennent six générations; F1, F2, F1 croisée en retour avec les parents susceptible BC1P1 et celui résistant BC1P2 ; ainsi que les parents respectifs des croisements effectués entre NuMex-M3× ICGV-SM 02501, Valencia C × ICGV-SM 02501 et Redbeauty × ICGV-SM 03590. Toutes ces variétés ont été évaluées dans l'institut de recherche des ressources nationales semi-arides (NaSARRI) à Serere en Ouganda. L'héritabilité au sens strict était estimée à 12, 27 et 36%, respectivement pour les croisements entre Redbeauty × ICGV-SM 03590, Valencia C × ICGV-SM 02501 et

NuMex-M3 × ICGV-SM 02501. Dans tous les croisements, la résistance à LLS est sous le control aussi bien de l'action dominante que de l'action additive des gènes ; sauf dans le cas de Redbeauty × ICGV-SM 02501 où les effets dominants des gènes ne sont pas significatifs.

Mots Clés: *Arachis hypogaea,* héritabilité au sens strict, *Phaeoisariopsis personata*

INTRODUCTION

Groundnut (*Arachis hypogaea* L.) is the second most important legume in Uganda, after common beans (*Phaseolus vulgaris* L.) (UBOS, 2010). Groundnuts thrive under relatively low rainfall and is well adapted to hot, semi-arid conditions. Groundnuts improve soil fertility by fixing atmospheric nitrogen (Janila *et al.,* 2013a), and is appropriate for cultivation in low-input agriculture by smallholder farmers (Smartt, 1994). Nutritionally, groundnuts are rich source of oil (33-55%) and protein (19- 31%) (Jambunathan, 1991; Shilpa *et al*., 2013), minerals (calcium, magnesium and iron) and vitamins (B1, B2 and Niacin) (Singh and Diwakar, 1993; Savage and Keenan, 1994). Groundnut haulms, too are very nutritious fodder for animals (Singh and Diwakar, 1993; Janila *et al*., 2013a; Ozyigit and Bilgen, 2013) and can as well be used as compost (Janila *et al*., 2013a).

Production of groundnuts is limited by mainly diseases, of which late leaf spots (LLS) is the most devastating foliar fungal disease, accounting for the major economic yield loss, especially of Valencia groundnuts in Uganda (Okello *et al*., 2010; 2013). Valencia varieties are most preferred for their sweet taste, high number of seeds per pod, early maturity (Patte *et al*., 2001) and high oil content (Kaaya and Warren, 2005) when compared with other groundnut sub species.

The disease occurs wherever Valencia groundnuts are grown, and has been reported to cause over 60% yield losses in susceptible cultivars when environmental conditions are conducive for disease development (Mugisha *et al*., 2004). Effective chemical control is heavily reliant on multiple fungicide applications (Jordan *et al*., 2012), which are costly for resource poor famers, and raise environmental and health concerns.

The deployment of resistant cultivars against LLS disease in Valencia groundnut could be effective in decreasing the production costs, improving production quality and reducing detrimental effects of the chemicals on ecosystems. There is need for breeders to exploit the available genetic resources through genetic improvement techniques. However, such exploitations are limited due to lack of information on heritability of LLS resistance and gene effects controlling LLS resistance in the available Valencia germplasm. Furthermore, it has been reported that LLS resistance is quantitatively inherited (Motagi, 2001; Dwivedi *et al*., 2002; Upadhyay *et al*., 2009; Khedikar *et al*., 2010); signifying the need for information about the genetic effects and heritability of LLS resistance in Valencia groundnuts populations to guide Valencia groundnut improvement process. Good knowledge of narrow sense heritability and the genetic systems controlling expression of such quantitative traits would facilitate choice of the most efficient breeding and selection procedure.

Though information on heritability of LLS resistance has been provided by many authors, Dabholkar (1992) and Falconer and Mackay (1996) concluded that heritability is a property of a population being studied and the environmental circumstances to which the individuals are subjected. According to Anderson *et al*. (1991), estimates of narrow sense heritability of LLS resistance have been inconsistent, ranging from low (0.18) to high (0.74). In addition to additive and dominance variation, it has been suggested that epistasis may also be involved in the inheritance of LLS resistance in Valencia groundnut (Shoba *et al*., 2010), however such information on non-allelic interactions for LLS resistance in Valencia groundnut is very limited. While variation due to dominance effects and their interactions cannot be exploited effectively in Valencia groundnut, additive x additive epistatic variation is potentially useful, as it can be fixed in homozygous cultivars (Singh and Oswalt, 1991). Additive gene actions of LLS resistance have been predominantly reported in

the control of LLS resistance (Anderson *et al*., 1986a and 1986b; Walls and Wynne, 1985). The objective of this study was to determine narrow-sense heritability (h^2_n) of LLS resistance and type of gene actions controlling LLS resistance using Valencia groundnut genotypes.

MATERIALS AND METHODS

The research was conducted at the National Semi-Arid Resources Research Institute (NaSARRI), located 01° 30 00N and 33° 33 00E in Serere district, Uganda. This location represents a humid and hot climate that receives an annual rainfall 1,000 - 1,200 mm and at an elevation of 1085 m above sea level. Six Valencia groundnut genotypes (Table 1), with varying levels of response to LLS were used. The genotypes were characterised for resistance to LLS by Kalule *et al.* (2010).

First filial generations (F_1 progenies). Valencia C, NuMex-M_3 and Redbeauty were used as female (susceptible lines), while ICVG-SM 03590 and ICGV-SM 02501 were the resistant male parents. 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 from NaSARRI experimental field. Parents were grown in a glasshouse and later thinned to two. Staggered planting of parents was done where the male parents were planted one week earlier than the female parents in order to synchronise flowering, and to ensure continuous availability of flowers and floral buds for making crosses. Plants were watered after every two days, using one litre of water per pot until they reached physiological maturity.

At flowering, the female parents were emasculated with forceps in the evening (4.00 - 6.00 pm) and crossed the following morning (between 8.00 and 10.00 a.m.) by rubbing the pollen from donor parents on the stigma of the emasculated plants carefully by hand. The nodes of the flowers that were crossed were tagged with labels, whereby the female parent was written first followed by the male parent. The Bi parental mating design was employed, where three crosses were made between NuMex-M_3 × ICGV-SM 02501, Valencia C × ICGV-SM 02501and Redbeauty × ICGV-SM 03590 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 at NaSARRI at room temperature.

First filial, F_2, BC_1P_1 and BC_1P_2 populations. In December 2011, 15 F_1 seeds generated above from each cross, along with their respective parents, were planted in plastic pots containing garden soil and set up in a glasshouse. The F_1 seed were planted alongside their respective parents, to confirm the successful crosses. These 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 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. Emasculation and hybridisation were done as described for generation of F_1 above.

Evaluation of the six generations of each cross. The generations of the three crosses were evaluated in the experimental field at NaSARRI, a known hot spot for LLS disease. Six generations, namely P_1, P_2, F_1, F_2 and $BC_1P_1$and BC_1P_2 of each cross (NuMex-M_3 × ICGV-SM 02501, Valencia C × ICGV-SM 02501 and Redbeauty × ICGV-SM 03590) were set up in a randomised complete block design (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 cm x15 cm in June 2012. The experiment was manually kept free of weeds throughout the cropping season.

Inoculation. To maximise leaf spot inoculum pressure under natural conditions, the spreader row technique was used. Valencia groundnut, line JL 24, which is highly susceptible to LLS was used as a spreader row. 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 and analysis. Late leaf spot disease severity was scored using a modified nine point scale (1-9) of Subrahmanyam *et al*. (1995) at maturity stage. Visual scores from each of the six generations (P_1, P_2, F_1, F_2, BC_1P_1 and BC_1P_2) were used to calculate the generation means and variances.

Narrow sense heritability estimates for LLS resistance were determined following Kearsey and Pooni (1996) method using variance components as follows:

Narrow-sense heritability (h^2n) = $100[\sigma^2A(F_2)/V_{F2}]$.

Where:

$\sigma^2A(F_2)$ = Additive variance in F_2 and V_{F2} = variance of F_2 generation

The means and variances of the six generations of each cross were subjected to scaling tests A, B and C (Mather and Jinks, 1982) to assess for the adequacy of additive-dominance model. The scales were tested for significance by *t*-test at 5% level of significance as;

$t_A = A\text{-}0/SE_A$, $t_B = B\text{-}0/SE_B$ and $t_C = C\text{-}0/SE_C$

Where:

SE_A, SE_B and SE_C are standard errors of A,B and C scaling tests, respectively.

The null hypothesis for test of significance (H_o) was that A = 0 or B and C in place of A of the scaling test. The additive-dominance model was considered adequate when the *t*-test of any one of the three scales was found not significant. The following assumptions were made while performing the scaling test: (i) all generations have been raised in the same environment, (ii) only autosomal inheritance is considered; (iii) non-allelic interaction is absent; and (iv) no differential fertility and viability.

To estimate the gene effects, a joint scaling test was performed following the method described by Kearsey and Pooni (1996), which uses the weighted least squares analysis, whereby the weighting factor is the inverted ratio of the variance of the means for each generation evaluated and the inverse of the matrix of the parameters. The variance of the means of the generations was obtained by dividing the treatment mean variances by their respective number of individuals on which observations were recorded in each generation. The weighted analysis was used due to the fact that the estimates of the means are obtained with distinct precision among the different generations (Dabholkar, 1992; Kearsey and Pooni, 1996). Genetic models were adjusted to means of the parent lines P_1 and P_2, F_1 and their F_2 segregating generations and the respective backcrosses BC_1P_1 and BC_1P_2. Initially, a simple additive-dominance genetic model involving m, [a] and [d] parameters was used.

Components m represents the average value between parents, [a] represents the algebraic sum of the additive effects of all distinct loci between the parents, and [d] the algebraic sum of dominance effects of all distinct loci between the parents. Accuracy of the model was verified by a chi-square (c^2) test and components within each model were evaluated for significance by *t*-test. The adequate model was obtained only when all the components estimated were significant by a *t*-test and non-significant at the chi-square (χ^2) test.

RESULTS

The results of heritability estimates for resistance to LLS are presented in Table 2. Narrow-sense heritability estimates were 12, 27 and 36%, for Redbeauty × ICGV-SM 03590, Valencia C × ICGV-SM 02501 and NuMex-M_3 × ICGV-SM 02501 crosses, respectively.

All values of A, B and C scaling tests were not significantly different from zero (Table 3). Tables 4 and 5 present results of estimates of gene effects along with their standard error; on a 3 and 2-parameter model, respectively. The initial 3-parameter model [m, a and d] (Table 4) was adequate for all crosses as revealed by non-significance of the χ^2 values. However, in the crosses NuMeX-M_3× ICGV-SM 02501 and

TABLE 1. Origin, pedigree, and response to LLS of Valencia groundnut lines used in the study

Genotype	Pedigree	Country of origin	Response to LLS
Redbeauty	Landrace	Uganda	Susceptible
Valencia C	Selection from Colorado Manfredi	USA	Susceptible
NuMex-M_3	Valencia C × ICGV 87157	USA	Susceptible
JL 24(spreader)	-	India	Highly susceptible
ICVG-SM O3590	-	Malawi	Resistant
ICGV-SM 02501	-	Malawi	Resistant

TABLE 2. Genetic variance components and heritability estimates for resistance to late leaf spot in 3 crosses of Valencia groundnuts

Parameters	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
V_A	0.83	0.39	0.10
V_D	0.67	0.15	0.16
h^2_b(%)	64.00	37.00	32.00
h^2_n(%)X	36.00	27.00	12.00

V_E = Environmental variance, V_G = Genotypic variance, V_A = Additive variance, V_D = Dominance variance, h^2_b and h^2_n = Broad and narrow sense heritability respectively, X = Grand mean

TABLE 3. Scaling test estimates along with their standard errors and *t* test for the scaling tests of the 3 crosses Valencia groundnuts in Uganda

Cross	Scaling test	Scaling test values observed	*t* value
NuMex-M_3×ICGV-SM 02501	A	2.58 ± 1.59	1.62 n.s.
	B	0.21 ± 1.37	0.16 n.s.
	C	4.00 ± 3.68	1.09 n.s.
Redbeauty × ICGV-SxM 03590	A	1.00 ± 1.08	0.93 n.s.
	B	-1.50 ± 1.55	-0.97 n.s.
	C	-1.10 ± 1.38	-0.80 n.s.
Valencia C × ICGV-SM 02501	A	-1.78 ± 1.10	-1.61n.s.
	B	1.27 ±1 .33	0.95 n.s.
	C	2.38 ± 1.84	1.29 n.s.

A = Scaling test A, B = Scaling test B and C =Scaling test C, and *t* = calculated *t* values and n.s. = P >0.05

Valencia C × ICGV-SM 02501, the trait had a significantly higher fit to an additive–dominance inheritance model [m, a and d] than in Redbeauty × ICGV-SM 02501 cross (Table 3). It was, therefore, refitted on a 2-parameter model, with m and [a] parameters only so that more precise estimates are obtained in Redbeauty × ICGV-SM 02501 (Table 4). On a 2-parameter model, the trait showed adequate fitness in only Redbeauty × ICGV-SM 02501 cross. The results revealed that

TABLE 4. Genetic parameters for LLS disease score for the three groundnut crosses on a three parameter model for a study in Uganda

3 parameter model	NuMex-M_3 × ICGV-SM 02501	Redbeauty × ICGV-SM 03590	Valencia C × ICGV-SM 02501
M	5.13** ± 0.15	5.23** ± 0.30	5.37** ± 0.19
[a]	-1.66** ± 0.15	-1.57** ± 0.30	-1.93** ± 0.93
[d]	-1.20** ± 0.47	-0.87ns ± 0.57	-1.44** ± 0.42
χ^2	4.45ns	5.99ns	6.374ns
DF	3	3	3

M = mid- parental value,[a] = additive gene effects,[d] = dominance gene effects, DF = degree of freedom and χ^2 = chi-square value; ns = P >0.05 and ** = significant at 1% level of significancy

TABLE 5. Genetic parameters for LLS disease score for the three groundnut crosses on a 2-parameter model

2 parameter model	NuMeX-M_3 × ICGV-SM 02501	Redbeauty × ICGV-SM 03590	Valencia C × ICGV-SM 02501
M	4.98** ± 0.14	4.89** ± 0.19	4.95** ± 0.15
[a]	1.62** ± 0.16	-1.63** ± 0.29	-1.65**± 0.18
χ^2	10.97*	6.02ns	26.11**
DF	4	4	4

M = mid- parental value,[a] = additive gene effects, DF = degree of freedom and χ^2 = chi-square value; ns = P >0.05 and ** = significant at 1% level of significancy

both additive and dominance gene effects contributed significantly to the inheritance of LLS resistance in all the crosses, except in Redbeauty × ICGV-SM 02501 cross where the effects of dominance were not significant. Both additive and dominance gene effects were negative, but the magnitudes of additive effects were positive and higher than that of the dominance effects in all crosses. The mid-parental effects (m) were significant and positive for all the crosses in all the models.

DISCUSSION

Low to moderate values of narrow-sense heritability were observed in all crosses (Table 2). This was due to either larger dominance or environmental effects on the trait than the additive effects. The increase in magnitude of dominance component of the variance (V_D) implies a decrease in h^2_n in the reference F_2 generation (Kearsey and Pooni, 1996). Thus, selection of genotypes from initial generations for resistance to LLS disease may be difficult due to high influence of dominance effects in the expression of the total phenotypic variance. According to Kearsey and Pooni (1996) and Kormsa-art *et al.* (2002), selection for low heritability traits, or those controlled by dominance, is ineffective when carried out in early generations. For this reason, selection based on individual plants for LLS resistance would be more effective when carried out on later generations instead of early ones. In this way, the occurrence of heterozygotes is reduced and the available additive variance for selection is increased, thereby providing higher possibilities of selection gains for the trait.

Jinks and Pooni (1984) reported that if selection is delayed further into the inbreeding programme, there will be an increase in h^2_n and, hence, increase in response to selection. However, if selection is to be based on early generations, then it would be appropriate to use family rather than individual selection. Kearsey and Pooni (1996) recommended that selection in F_2 and other generations of the population should be based on family means in order to get high genetic gain among the progeny, because environmental variation is reduced by working

with means. For characters with low h^2_n estimates, Oeveren and Stam (1993) and Kearsey and Pooni (1996) recommended that bulk and single seed descent (SSD) breeding methods, followed by selection on family mean can ensure high genetic gain among the progenies.

In the present study, the estimate of h^2_n was 36% for the LLS disease score in NuMex-M_3 × ICGV-SM 02501 cross. Ali *et al.* (1999) also reported that heritability estimates higher than 30% allow for genetic gains through selection in initial generations of inbreeding, such as F_3 or F_4 generations. According to Silva *et al.* (2004), it is considered that an F_5 generation individual presents enough homozygosis levels to allow for selection, mainly due to the absence of significant additions to the level of homozygous individuals in future generations, which would necessitate longer periods for selection. Based on our results, it can be concluded that effective selections for LLS resistance can be achieved at F_3 or F_4 for the Cross between NuMex-M_3 and ICGV-SM 02501.

All scaling tests A, B and C were not significant (Table 3), implying that gene action was either additive or dominance or both, which means that additive, dominance model was adequate for explaining resistance to LLS. Based on the joint scaling test, the initial 3-parameter model [m, a &d] (Table 4) was found to be adequate for all crosses as revealed by the non-significance of the χ^2 values, confirming absence of epistatic interactions in these crosses as revealed by results of the scaling tests. Therefore, the interacting terms (additive by additive [aa], additive by dominance [ad], and dominance by dominance [dd]) were not computed.

There was no epistatic effects involved in the expression of LLS resistance in these crosses. This partly agrees with previous findings by Nevill (1982) and Jogoly *et al.* (1999b), who reported that both additive and dominant effects are involved in the expression of LLS resistance. Many authors, however, have reported predominantly additive gene effects for most of the components of resistance to LLS (Kornegay *et al.,* 1980; Anderson *et al.,* 1986 a and b; Jogloy *et al.,* 1987; Jogoly *et al.*, 1999a and b; Vishnuvardhan *et al.*, 2011); which compare well with the results of the current study. The predominance of additive component [a] in the inheritance of LLS disease score over the dominance component in all the 3 crosses, suggests that selection for resistance to LLS would be effective in the populations of these crosses.

In contrast, Shoba *et al.* (2010) reported predominance of non-additive component [d] and epistatic effects (additive by additive and dominance by dominance) in control of LLS resistance in Valencia groundnut. In addition to epistatic effects (additive x additive, additive x dominance and dominance x dominance), Janila *et al.* (2013b) reported that resistance to LLS was controlled by a combination of both, nuclear and maternal gene effects. Such variations in the results are probably due to the genetic background of the parents and variation in environmental conditions in which the populations were evaluated. Therefore, knowledge of gene effects on a given breeding material in a particular environment is important for successful genetic improvement of a quantitative trait.

The presence of significant additive effects in NuMex-M_3 × ICGV-SM 02501 and Valencia C × ICGV-SM 02501 crosses suggests that selection for LLS disease resistance is possible. On the other hand presence of significant dominance effects suggests that selection should be practiced in later generations. The breeding method that exploits both additive and non-additive gene effects may be suitable for the improvement of Valencia groundnuts for LLS resistance. Singh and Oswalt (1991), Nidagundi *et al.* (2012) and Janila *et al.* (2013b) recommended that for traits controlled by additive and dominance gene effects, recurrent selection may be a useful breeding strategy. Janila *et al.* (2013b) suggested use of reciprocal recurrent selection. On the other hand, Dabholkar (1992) recommended biparental mating as the most suitable for improving traits controlled by both additive and non-additive effects.

For Redbeauty × ICGV-SM 02501, additive gene action was the most important for LLS disease score; while dominance effects were less important which indicates that genetic improvement of the populations of this cross could be easier for LLS resistance. However, Ali

and Khan (2007) and Ayele (2011) concluded that effective selection in early generations of segregating materials can be accomplished only when additive genetic effects are substantial and heritability is high. Therefore, in the Redbeauty × ICGV-SM 02501 cross, selection in early generations of segregating materials may not be effective due to high environmental influence on the trait, which could have resulted in low heritability. The high environmental variation could have been as result of variation in relative humidity within the micro-climates, which could have resulted in non-uniform and inadequate disease pressure. In such a case, breeding efforts to increase resistance will require effective control of environmental variance, which can be achieved through proper blocking, use large populations and accurate phenotyping of LLS.

The negative sign of additive effect indicates that ICGV-SM 02501 and ICGV-SM 03590 were the source of LLS resistance which took a low value on the scale; while the negative sign of dominance effects indicates that dominance was in the direction of susceptibility.

CONCLUSION

Based on the result of this study, estimates of narrow-sense heritability and magnitude of gene effects depend on the parental backgrounds. Narrow-sense heritability for LLS disease score ranges from low to moderate. Expression of LLS resistance in Valencia groundnut is controlled by additive and dominance gene effects with predominance of the additive effects. Therefore, genetic improvement of Valencia groundnuts for resistance to LLS is possible in all the crosses. Selection based on individual plants for LLS resistance is more effective when undertaken in later generations in all crosses. Bulk and single seed descent (SSD) breeding methods, followed by selection on family mean can ensure high genetic gain among the progenies.

ACKNOWLEDGEMENT

The United States Agency for International Development (USAID)-Bureau of Food Security, Peanut and Mycotoxin Innovation Laboratory, through the University of Georgia, Project NMS-172, funded this research.

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