

Full Length Research Paper

Evaluation of advanced groundnut lines for resistance to late leaf spot disease and yield

Nabwire Sharon Prisca^{1*}, James Mwololo², Okello David Kalule³, Joseph Juma Mafurah¹ and Pascal P. Okwiri Ojwang¹

¹Department of Crops, Horticulture and Soils (CHS), Faculty of Agriculture, Egerton University, Egerton, Njoro, Nakuru County, Kenya.

²International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Lilongwe, Malawi.

³NARO-National Semi-Arid Resources Research Institute (NaSARRI), Serere, Uganda.

Received 25 December, 2025; Accepted 10 March, 2026

Late Leaf Spot (LLS), caused by *Nothopassalora personata*, is a major threat to groundnut (*Arachis hypogaea* L.) production, with yield losses of up to 70% under severe infestations. The limited availability of resistant germplasm hampers the development of elite breeding lines with LLS resistance. Incorporating novel resistance genes into adapted groundnut backgrounds offers a promising solution. This study evaluated 25 groundnut genotypes for LLS resistance and yield stability at two sites in Uganda: The National Semi-Arid Resources Research Institute (NaSARRI) in Serere and the Nakabango Technology Verification Center in Jinja. The experiment followed an alpha-lattice design with two replications at each site. Linear mixed model analysis revealed significant genotype and environment effects, as well as genotype-by-environment interactions ($p < 0.05$). Genotypic variation in disease severity was observed, with Area under Disease Progress Curve (AUDPC) values ranging from 175 (ICGV-SM 16605) to 448 (ICGV-SM 16587). The genotypes ICGV-SM 16605, ICGV-SM 16615, and ICGV-SM 16597 demonstrated both low disease severity and high yield potential. Pod production was higher at Nakabango (0.405 t/ha) compared to NaSARRI (0.158 t/ha). A strong negative correlation between AUDPC and yield indicated that increased disease severity reduces productivity. The Superiority Index (Pi) identified ICGV-SM 16605 as the most stable genotype, suitable for smallholder farmers.

Key words: Late leaf spot (LLS), groundnut (*Arachis hypogaea* L.), resistance, genotype-by-environment interaction, yield stability.

INTRODUCTION

Groundnut (*Arachis hypogaea* L.), also known as peanut, is a valuable food and cash crop grown in sub-Saharan Africa. The crop contributes to household food security and nutrition, income, and soil fertility improvement through the nitrogen-fixing effect (Essandoh et al., 2022a). Groundnut is among the five major legume crops

in Uganda, which are predominantly grown by small-scale farmers across different agro-ecological zones. It is an important crop in farm diets because it provides protein, oil for eating, and micronutrients, and contributes significantly to family earnings through regional and local market trade (Okello et al., 2010). The ability of

*Corresponding author. E-mail: sharonpriscah1997@gmail.com/nabwire.1001423@student.egerton.ac.ke.

groundnut to thrive in a wide range of environments and has a short maturity period, making it a crop of choice for smallholder farmers, particularly where rainfall is not reliable (Kumakech et al., 2025). Despite its agronomic and socioeconomic importance, groundnut production in Uganda is severely constrained by foliar fungal diseases, with late leaf spot disease, caused by the fungus *Nothopassalora personata* (Berk. and M.A. Curtis) (S.A. Khan & M. Kamal), being the most predominant. *N. personata* is a cosmopolitan plant pathogenic fungus responsible for late leaf spot in *A. hypogaea* (groundnut) and occurs in all major peanut-growing regions of the world, including Africa, Asia, the Americas, and Oceania, where warm, humid conditions favor disease development and spread. The disease has been reported widely in major groundnut cultivation zones such as Sub-Saharan Africa, the southeastern United States, and Argentina, and can cause severe defoliation and significant yield reductions if not managed effectively (Sharma et al., 2020; Lucidcentral, 2025). The symptoms of this disease on groundnut include premature defoliation of leaves, reduction of photosynthetic surface area, impairment of pod filling, and substantial yield losses. Epidemics of Late Leaf Spot (LLS) spread rapidly under conducive environmental conditions, viz., warm weather and humid conditions, and can lower yield from between 20% and over 80% (Nutsugah et al., 2008; N'Gbesso et al., 2024). These losses threaten the livelihoods of farmers and food security in Uganda, where over-reliance on the susceptible local cultivar continues to prevail. Though the application of fungicides is likely to provide some level of control, their use by smallholder farmers is minimal due to high costs, limited availability, and concerns about environmental sustainability (Janila et al., 2016). Cultural practices such as rotation of crops and sowing during the appropriate time can also help, but their effectiveness is seriously impacted when inoculum loads are high. Hence, resistant cultivar deployment and production remain the most effective and friendly environmental method of LLS control (Shaibu et al., 2020).

Seed yield is highly influenced by genotype-by-environment (GE) interactions. Differential performance of genotypes across environments complicates the identification and selection of new breeding lines. This necessitates multi-location testing to help identify varieties with high levels of resistance and consistent yielding ability in different agroecologies (Chaudhari et al., 2019). International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) has developed a set of improved groundnut genotypes with putative resistance to LLS and other foliar diseases. Some of these lines were well-performing under controlled and field conditions in Malawi, Nigeria, and Ghana (Shaibu et al., 2020; Essandoh et al., 2022b). However, for their beneficial application in Uganda, their performance needs

to be evaluated under conditions that differ by soil fertility, rainfall type, and disease pressure. The large production fields of Uganda, such as NaSARRI at Serere and Nakabango at Jinja, present varied testing conditions: NaSARRI has sandy soil and reduced rainfall, and Nakabango has a higher soil fertility level and humidity, both of which are conducive to foliar epidemic disease (Kumakech et al., 2025).

Assessment of the genotype-by-environment interactions (GEI) is critical for the identification of superior and stable breeding lines GEI adapted to target environments (Chaudhari et al., 2019; Essandoh et al., 2022b; Kang, 2020). Groundnut is largely grown under variable conditions presented by the small-scale farmer conditions. To obtain a suitable variety adapted to such conditions, it requires evaluation in representative environments that allow phenotypic expression (Yan and Hunt, 2001). Previous studies have highlighted the significant impact of GEI on the performance of groundnut genotypes. For instance, research in semi-arid West Africa demonstrated that genotype $\times$ environment interactions significantly influenced both yield and resistance to LLS, underscoring the necessity for multi-location testing to identify stable genotypes (Chaudhari et al., 2019). Similarly, studies in Ethiopia and India have utilized Additive Main Effects and Multiplicative Interaction (AMMI) and Genotype plus Genotype-by-Environment (GGE) biplot analyses to evaluate the stability of groundnut genotypes across various environments, identifying genotypes with consistent performance and resistance to diseases (Kumakech et al., 2025). Conversely, some studies have reported limited stability in disease resistance across different environments. For example, research in Nigeria found that certain groundnut genotypes exhibited inconsistent resistance to early leaf spot and LLS across diverse environments, suggesting that resistance mechanisms may be environment-specific (Chaudhari et al., 2019). These contrasting findings highlight the complexity of GEI and the need for comprehensive evaluations under varied conditions. The aim of this study is to evaluate 25 advanced groundnut lines for resistance to LLS with high and stable yield in two diverse locations in Uganda, NaSARRI in Serere and Nakabango in Jinja. By evaluating these genotypes under different environmental conditions, this research seeks to identify lines with consistent resistance to LLS and stable high yields, thereby contributing to the development of resilient groundnut varieties suitable for smallholder farmers in Uganda.

MATERIALS AND METHODS

Experimental site description and soil analysis

The study was conducted during the off-season from October 2024 to January 2025, hereafter referred to as the 2024B season, at

Table 1. A list of genotypes used in the study.

No	Sample code	Source of the material
1	ICGV-SM16609	ICRISAT
2	ICGV-SM16603	ICRISAT
3	ICGV-SM16605	ICRISAT
4	ICGV-SM16587	ICRISAT
5	ICGV-SM16597	ICRISAT
6	ICGV-SM16617	ICRISAT
7	ICGV-SM16615	ICRISAT
8	ICGV-SM16589	ICRISAT
9	ICGV-SM16616	ICRISAT
10	JL24	ICRISAT
11	ICGV-SM16613	ICRISAT
12	ICGV-SM16598	ICRISAT
13	ICGV-SM16614	ICRISAT
14	ICGV-SM01514	ICRISAT
15	ICGV-SM16596	ICRISAT
16	ICGV-SM16612	ICRISAT
17	ICGV-SM16602	ICRISAT
18	ICGV-SM16691	ICRISAT
19	ICGV-SM16637	ICRISAT
20	ICGV-SM16692	ICRISAT
21	ICGV-SM16604	ICRISAT
22	ICGV-SM16618	ICRISAT
23	ICGV-SM16608	ICRISAT
24	ICGV-SM16601	ICRISAT
25	ICGV-SM16619	ICRISAT

two locations in Eastern Uganda: the National Semi-Arid Resources Research Institute (NaSARRI) in Serere District (1.0000° N, 33.33000° E) and the Nakabango Technology Verification Center in Jinja District (0.31017° N, 33.12049° E). The sites were selected because they are hotspots for screening late leaf spot disease (LLS) (Okello et al., 2010). Both locations experience bimodal rainfall, with the first season occurring from March to May and the second from August to October, making them suitable for groundnut cultivation and disease evaluation. Soil test analyses were conducted at both locations before planting to provide crucial information on soil fertility and pH, which are important factors influencing the growth of groundnut genotypes and their resistance to diseases

Experimental design

Twenty advanced groundnut lines, including checks, were selected for the study. The advanced lines were obtained from ICRISAT and possessed different levels of resistance to LLS, as shown in Table 1. The experiment was laid out in a 5 x 5 alpha-lattice design with two replications as indicated in Figure 1. Each entry was planted in a two-row plot, 1 m long. The experimental design was generated from the Breeding Management Systems (BMS) platform [The IBP Breeding Management System (BMS Pro) Version 16 (2024)]. The spacing between the plots within the blocks was 60 cm, 45 cm between rows within the plot, and 15 cm between plants within the

row. A distance of 0.9 m was kept between the blocks and 1.5 m between the replicates.

Field management

Standard agronomic practices were followed for the cultivation of the groundnut crop. Land preparation involved ploughing and harrowing to create a fine seedbed. Seeds were planted using a hand hoe. Weeding was carried out manually to control competing vegetation. The plants were monitored regularly for any signs of pest or disease damage, and disease symptoms were recorded at different stages of growth. Irrigation was not required, as both locations received adequate rainfall during the growing season. Late leaf spot disease assessment Disease data were collected four times across the growing season, each data point corresponding with a particular phenological stage of the groundnut. Precisely, disease severity was assessed at different stages of plant growth, specifically at 4, 8, and 12 weeks after planting, as well as at final harvest corresponding to R2 (beginning of peg formation), R4 (beginning of pod formation), R7 (beginning of maturity), and R8 (harvest maturity) as described by Boote (1982). Disease severity was measured based on visual symptoms, including the number of lesions and the extent of leaf area affected. LLS severity was scored based on a 1 to 9 visual scale as described in Table 2 (Yan and Tinker, 2005). Observations were made on five plants within each plot, and the average disease

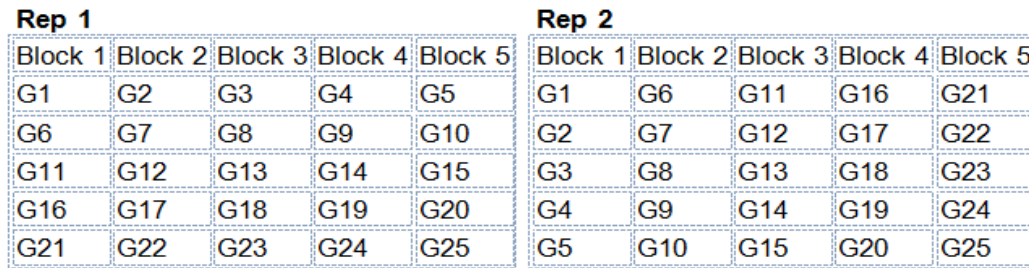


Figure 1. Field experimental layout used.

Table 2. The 9-point scale is used for screening groundnut for resistance to late leaf spot.

Leaf spot score	Description	Disease severity (%)
1	No disease	0
2	Lesions are largely on lower leaves; no defoliation	1-5
3	Lesions are largely on lower leaves; very few lesions are on middle leaves; defoliation of some leaflets is evident on lower leaves	6-10
4	Lesions on lower and middle leaves, but severe on lower leaves; defoliation of some leaflets is evident on lower leaves	11-20
5	Lesions on all lower and middle leaves; over 50% defoliation of lower leaves	21-30
6	Severe lesions on lower and middle leaves; lesions on top leaves but less severe; extensive defoliation of lower leaves; defoliation of some leaflets evident on middle leaves.	31-40
7	Lesions on all leaves, but less severe on top leaves; defoliation of all lower and some middle leaves	41-60
8	Defoliation of all lower and middle leaves; lesions are severe on the top leaves, and some defoliation of the top leaves is evident	61-80
9	Defoliation of almost all leaves, leaving bare stems; some leaflets may be present, but with severe leaf spots.	81-100

≤3: resistance, 3-4: tolerance, 5-9: susceptible.
Source: Yan and Tinker (2005).

severity score per plot was recorded. The disease assessments were done by trained personnel, and disease pressure was monitored at each location.

Yield and agronomic traits

At maturity, the following yield components were measured. The pod yield was measured as the total weight of pods harvested from a 5-plant sample from each plot. This measurement was used to estimate fresh pod yield per hectare. The number of pods per plant was counted from a representative sample of 5 plants in each plot.

The total biomass (haulm) of the plants was measured by weighing the plant material (stems, leaves) from a 5-plant sample after harvest. The weight of the dried pods from each plot was taken. The weight of seed from each plot was measured. These yield components were measured to assess the overall productivity of each genotype and determine whether disease resistance had an effect on yield.

Statistical analyses

A linear mixed model (LMM) was fitted using the lme4 package in R, with replication, block, and location considered as fixed effects,

while genotype and the genotype-by-location interaction were treated as random effects. The general form of the model can be expressed in Equation 1 as;

$$Y_{ijkl} = \mu + R_k + B_{i(k)} + G_i + L_j + GL_{ij} + \varepsilon_{ijkl} \quad (1)$$

where Y_{ijkl} is the observed trait value, μ is the overall mean, R_k is the effect of the k^{th} replication, $B_{i(k)}$ is the effect of the block nested within replication, L_j is the fixed effect of the j^{th} location, G_i is the random effect of the i^{th} genotype, GL_{ij} is the random interaction effect between genotype and location, and ε_{ijkl} is the residual error, assumed to be normally distributed with mean zero and variance, σ_e^2 . The model partitioned variance into components due to genotypes, locations, genotype-by-location interaction and residual error, allowing estimation of variance components and adjusted means (BLUPs). This approach has been intensively promoted for the analysis of multi-environment trials because it accommodates unbalanced data and provides shrinkage estimates of genotypic means (Subrahmanyam et al., 1995; Cullis et al., 2014). Likelihood ratio tests via analysis of variance were used to assess the significance of random terms for all parameters. The coefficient of variation (CV%) was computed to assess experimental precision. The least significant difference (LSD) post-hoc test was used to compare genotypic means at a $p < 0.05$ level of significance (Piepho et al., 2008). The LMM-estimated variance components were utilized to estimate broad-sense heritability (H^2) on a plot-mean basis following the formula in Equation 2:

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{ge}^2}{e} + \frac{\sigma_e^2}{re}} \quad (2)$$

where σ_g^2 is the genotypic variance, σ_{ge}^2 is the genotype-by-environment interaction variance, σ_e^2 is the residual variance, e is the number of environments, and r is the number of replications.

Pearson's correlation coefficients were determined with a view to studying the correlations between disease severity (AUDPC) and yield-related traits such as pods per plant, fresh pod yield, haulm yield, dry pod yield, and seed weight. Genotypic superiority was estimated by Campbell et al. (2015) using the superiority measure (Pi), which approximates a genotype's deviation from the highest observed performance across environments, where lower values of Pi indicate superior and more stable performance. Superiority indices (Pi) were calculated from genotype BLUPs to rank genotypes based on adjusted means of AUDPC for late leaf spot, identifying resistant and susceptible genotypes. All analyses were performed using R statistical software version 4.4.1 (Lin and Binns, 1988) with the lme4 package for mixed model analysis and emmeans for post-hoc analysis. The area under the disease progress curve (AUDPC) was calculated from the severity for LLS as described by Hyndman et al. (2025) as follows in Equation 3:

$$AUDPC = \sum_{i=1}^{n-1} \frac{y_i + y_{i+1}}{2} \times (t_{i+1} - t_i) \quad (3)$$

RESULTS

Variance components

The Linear mixed model and restricted maximum

likelihood (REML) analysis showed that genotypic effects were highly significant ($p < 0.001$) for all traits evaluated (Appendix 1). For AUDPC, a highly significant genotypic effect ($p < 0.001$) was observed, whereas both environmental and genotype-by-environment (G×E) interaction effects were non-significant ($p = 0.468$ and $p = 0.324$, respectively). In contrast, haulm yield and dry pod yield exhibited significant effects for both genotype ($p = 0.005$ and $p = 0.0006$, respectively) and G×E interaction ($p = 0.001$ and $p < 0.001$, respectively), while environmental effects were non-significant, suggesting differential genotype performance across environments. For seed weight, all sources of variation were genotype ($p < 0.001$), G×E interaction ($p < 0.001$), and environment ($p = 0.012$) were statistically significant. Similarly, fresh pod yield showed significant genotypic ($p = 0.001$) and G×E interaction ($p = 0.002$) effects, with a non-significant environmental effect ($p = 1.000$), suggesting specific genotypic responses to environmental conditions. For days to flowering, significant effects were detected for genotype ($p < 0.001$) and G×E interaction ($p = 0.008$), whereas the environmental effect remained non-significant ($p = 0.421$). Finally, days to emergence were significantly influenced by genotype ($p < 0.001$) and G×E interaction ($p = 0.045$), with no significant environmental effect ($p = 1.000$).

Genotypic performance

Tables 3 and 4 present comprehensive multi-environment evaluation data for 25 groundnut genotypes assessed at NaSARRI and Nakabango for key phenological traits (days to emergence and flowering), yield-related traits (dry pod yield, seed weight, haulm yield, and fresh pod yield), and LLS resistance, measured by AUDPC. Significant genotypic variation was observed across all traits. Days to emergence ranged from 5.5 to 8.5 days (mean = 6.88), and days to flowering ranged from 27.5 to 36 days (mean = 33.00), with early-maturing genotypes such as ICGV-SM 16615, ICGV-SM 16612, and ICGV-SM 16637. Substantial variation in LLS resistance was also observed, with AUDPC values ranging from 154 to 462 and a mean of 348.08. Genotype ICGV-SM 16605 displayed the lowest mean AUDPC (154), while ICGV-SM 16615 (189), ICGV-SM 16597 (203), ICGV-SM 16613 (220), and ICGV-SM 16602 (210) showed moderate resistance with minimal genotype × environment interaction. Genotypes such as ICGV-SM 16591, ICGV-SM 16598, ICGV-SM 16587, and the check variety JL 24 exhibited AUDPC values exceeding 440, confirming their high susceptibility. In terms of yield, ICGV-SM 16605 was superior across all parameters, producing the highest dry pod yield (0.73 t/ha), seed weight (83.8 g), haulm yield (0.84 t/ha), and fresh pod yield (0.90 t/ha). ICGV-SM 16615 combined strong

Table 3. Means of 25 genotypes evaluated for yield variables over two locations, NaSARRI and Nakabango TVC.

Genotype	Days to emergence			Days to flowering			AUDPC_LLS		
	NaSARRI	Nak	Mean	NaSARRI	Nak	Mean	NaSARRI	Nak	Mean
ICGV-SM 16591	6.00	6.50	6.25	29.50	34.00	31.80	441	462	452
ICGV-SM 16612	5.50	7.00	6.25	28.00	34.00	31.00	392	385	388
ICGV-SM 16596	7.50	6.00	6.75	29.50	35.50	32.50	343	413	378
ICGV-SM 16617	6.00	6.50	6.25	30.00	35.00	32.50	420	420	420
ICGV-SM 16619	6.00	7.00	6.50	27.50	33.00	30.20	385	371	378
ICGV-SM 16601	8.00	8.00	8.00	32.00	36.00	34.00	399	399	399
JL 24	6.00	8.00	7.00	30.50	34.00	32.20	448	441	444
ICGV-SM 16618	6.50	8.00	7.25	29.50	34.50	32.00	441	462	452
ICGV-SM 16605	7.00	7.50	7.25	30.00	34.00	32.00	154	154	154
ICGV-SM 16616	7.50	7.50	7.50	35.00	35.00	35.00	399	420	410
ICGV-SM 16603	8.00	8.50	8.25	35.00	35.00	35.00	392	406	399
ICGV-SM 16609	7.00	7.00	7.00	35.00	35.50	35.20	406	406	406
ICGV-SM 16602	8.00	8.00	8.00	35.50	34.50	35.00	182	238	210
ICGV-SM 16604	8.00	8.50	8.25	36.00	35.00	35.50	329	343	336
ICGV-SM 16598	7.00	7.00	7.00	34.00	34.50	34.20	448	448	448
ICGV-SM 16614	6.00	7.00	6.50	29.50	33.50	31.50	280	266	273
ICGV-SM 16615	5.50	6.00	5.75	29.00	34.50	31.80	217	161	189
ICGV-SM 16587	5.50	7.50	6.50	29.00	34.50	31.80	448	448	448
ICGV-SM 16589	6.50	7.50	7.00	30.50	35.00	32.80	350	329	340
ICGV-SM 16592	5.50	6.50	6.00	30.00	35.00	32.50	294	294	294
ICGV-SM 16597	6.00	6.00	6.00	34.00	34.50	34.20	210	196	203
ICGV-SM 01514	6.00	8.00	7.00	33.50	35.00	34.20	371	427	399
ICGV-SM 16608	5.50	7.50	6.50	31.50	35.00	33.20	420	427	424
ICGV-SM 16613	5.50	8.50	7.00	30.50	36.00	33.20	196	245	220
ICGV-SM 16637	5.50	7.00	6.25	29.00	34.50	31.80	238	238	238
Mean	6.46	7.30	6.88	31.34	34.68	33.00	344.12	351.96	348.08
LSD	1.65	2.20	1.41	3.33	1.63	3.04	49.72	53.61	39.80
CV	17.59	14.6	17.29	8.31	2.57	8.12	26.82	27.46	27.03

Nak: Nakabango Technology Verification Center, NaSARRI: National Semi-Arid Resources Research Institute, LSD: Least significance difference ($p>0.05$), CV%: Percent phenotypic coefficient of variation.

resistance with high yield (0.77 t/ha dry pod yield, 76.2 g AUDPC_LLS was negatively and highly significantly correlated with all yield

Table 3. Contd.

Genotype	Dry pod yield(t/ha)			Seed weight(g)			Haulm yield (t/ha)			Fresh pod yield (t/ha)		
	NaSARRI	Nak	Mean	NaSARRI	Nak	Mean	NaSARRI	Nak	Mean	NaSARRI	Nak	Mean
ICGV-SM 16591	0.06	0.13	0.10	14.50	26.00	20.20	0.25	0.32	0.29	0.19	0.17	0.18
ICGV-SM 16612	0.06	0.11	0.09	15.50	27.00	21.20	0.26	0.13	0.19	0.09	0.60	0.35
ICGV-SM 16596	0.07	0.14	0.11	16.50	19.00	17.80	0.15	0.19	0.17	0.09	0.19	0.14
ICGV-SM 16617	0.12	0.25	0.19	8.50	11.00	9.75	0.45	0.50	0.47	0.21	0.35	0.28
ICGV-SM 16619	0.42	0.17	0.29	55.50	43.00	49.20	0.72	0.37	0.54	0.54	0.28	0.41
ICGV-SM 16601	0.07	0.19	0.13	14.50	23.00	18.80	0.27	0.24	0.25	0.12	0.19	0.15
JL 24	0.14	0.30	0.22	6.50	5.50	6.00	0.40	0.70	0.55	0.23	0.32	0.28
ICGV-SM 16618	0.16	0.14	0.15	9.50	16.00	12.80	0.34	0.23	0.28	0.23	0.20	0.22
ICGV-SM 16605	0.90	0.55	0.73	65.00	102.00	83.80	1.16	0.53	0.84	1.00	0.79	0.90
ICGV-SM 16616	0.09	0.19	0.14	14.50	21.00	17.80	0.37	0.52	0.44	0.12	0.18	0.15
ICGV-SM 16603	0.12	0.04	0.08	11.50	10.00	10.80	0.47	0.19	0.33	0.28	0.05	0.16
ICGV-SM 16609	0.18	0.13	0.15	18.00	32.00	25.00	0.44	0.23	0.34	0.23	0.12	0.18
ICGV-SM 16602	0.55	0.13	0.34	55.50	70.00	62.80	0.79	0.24	0.51	0.66	0.21	0.43
ICGV-SM 16604	0.08	0.09	0.09	25.50	42.00	33.80	0.27	0.31	0.29	0.12	0.12	0.12
ICGV-SM 16598	0.13	0.14	0.14	5.00	9.50	7.25	0.40	0.18	0.29	0.16	0.19	0.17
ICGV-SM 16614	0.08	0.28	0.18	30.00	92.00	61.00	0.37	0.40	0.38	0.11	0.49	0.30
ICGV-SM 16615	0.85	0.70	0.77	66.50	86.00	76.20	1.14	1.10	1.12	0.95	0.90	0.92
ICGV-SM 16587	0.21	0.22	0.21	24.00	41.00	32.50	0.36	0.51	0.44	0.32	0.48	0.40
ICGV-SM 16589	0.09	0.26	0.18	20.00	30.00	25.00	0.18	0.36	0.27	0.15	0.31	0.23
ICGV-SM 16592	0.13	0.31	0.22	38.50	52.50	45.50	0.32	0.46	0.39	0.24	0.37	0.31
ICGV-SM 16597	0.21	0.23	0.22	26.00	32.00	29.00	0.26	0.49	0.37	0.24	0.32	0.28
ICGV-SM 01514	0.23	0.35	0.29	22.00	16.00	19.00	0.40	0.43	0.41	0.29	0.38	0.33
ICGV-SM 16608	0.10	0.15	0.13	24.00	16.00	20.00	0.27	0.13	0.20	0.16	0.27	0.22
ICGV-SM 16613	0.46	0.20	0.33	56.00	63.50	59.80	0.71	0.74	0.72	0.62	0.22	0.42
ICGV-SM 16637	0.20	0.36	0.28	52.00	75.50	63.80	0.59	0.81	0.70	0.36	0.43	0.40
Mean	0.23	0.23	0.23	27.80	38.46	33.15	0.45	0.41	0.43	0.31	0.33	0.32
LSD	0.075	1.65	0.23	4.46	18.02	21.09	0.138	0.417	0.33	0.056	0.219	0.30
CV	101.91	65.04	85.07	69.89	72.42	74.69	58.96	63.89	60.86	81.77	64.41	73.50

Nak: Nakabango Technology Verification Center, NaSARRI: National Semi-Arid Resources Research Institute, LSD: Least significance difference ($p > 0.05$), CV%: Percent phenotypic coefficient of variation.

components. Specifically, AUDPC had strong negative correlations with seed weight ($r = -0.821$, $p < 0.001$), dry pod yield ($r = -0.660$, $p <$

Table 4. Correlation coefficient for AUDPC and all yield traits for LLS resistance over two locations, NaSARRI and Nakabango.

Trait	AUDPC_LLS	Dry pod yield(t/ha)	Seed weight (g)	Haulm yield (t/ha)	Fresh pod yield (t/ha)
AUDPC_LLS	1.000	-0.660***	-0.821***	-0.594***	-0.648***
Dry pod yield(t/ha)	-0.660***	1.000	0.664***	0.871***	0.953***
Seed weight (g)	-0.821***	0.664***	1.000	0.545***	0.710***
Haulm yield (t/ha)	-0.594***	0.871***	0.545***	1.000	0.810***
Fresh pod yield (t/ha)	-0.648***	0.953***	0.710***	0.810***	1.000

*, ** and ***: significance at $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$, respectively.

Table 5. Estimates of variation and heritability for genotypes evaluated over two locations, NaSARRI and Nakabango.

Trait	Genetic variance (σ^2G)	Genotype $\times$ location variance ($\sigma^2G \times L$)	Residual variance (σ^2e)	Broad-sense heritability (H^2)
AUDPC_LLS	8587.262	86.137	623.959	0.977
Dry pod yield(t/ha))	0.023	0.012	0.004	0.774
Seed weight (g)	445.872	93.657	35.891	0.889
Haulm yield (t/ha)	0.033	0.018	0.020	0.704
Fresh pod yield (t/ha)	0.030	0.020	0.005	0.734
Days to emergence	0.136	0.000	0.998	0.353
Days to flowering	0.660	1.575	1.492	0.362

0.001), and fresh pod yield ($r = -0.648$, $p < 0.001$). For example, genotypes with lower AUDPC values, such as those with higher seed weight (1.12 t/ha), haulm yield (0.92 t/ha), and fresh pod yield, tended to be more productive. Similarly ICGV-SM 16602, ICGV-SM 16613, and ICGV-SM 16637 show moderate resistance with favorable yield performance. In contrast, susceptible genotypes such as JL 24 and ICGV-SM 16591 had both high AUDPC values and low yield performance.

Correlation analysis

The Pearson correlation analysis revealed significant associations between AUDPC for LLS and key yield-related traits across NaSARRI and Nakabango (Table 4). and haulm yield ($r = -0.594$, $p < 0.001$). In contrast, all yield traits were positively and significantly correlated with each other. The strongest positive correlation was observed between dry pod yield and fresh pod yield ($r = 0.953$, $p < 0.001$), followed by dry pod yield and haulm yield ($r = 0.871$, $p < 0.001$), and seed weight and fresh pod yield ($r = 0.710$, $p < 0.001$).

Heritability

The results presented in Table 5 reveal significant

variation in genetic control and environmental influence across the evaluated traits. AUDPC_LLS exhibited very high genetic variance and exceptionally high broad-sense heritability ($H^2 = 0.977$). Seed weight and dry pod yield also showed high heritability ($H^2 = 0.889$ and 0.774 , respectively). Haulm yield and fresh pod yield had moderate genetic variance and heritability ($H^2 = 0.704$ and 0.734). In contrast, days to emergence and days to flowering displayed low heritability ($H^2 = 0.353$ and 0.362 , respectively) and high residual and interaction variances. Table 6 presents the adjusted means, Best Linear Unbiased Predictors (BLUPs), and Superiority Index (Pi) values for 25 groundnut genotypes evaluated for resistance to LLS at NaSARRI and Nakabango. The analysis revealed significant genotypic differences, with a subset of genotypes showing consistently low AUDPC values and high Pi scores. Notably, ICGV-SM 16605 ranked first, with an adjusted mean AUDPC of 158.13 and the highest Pi value (192.68), signifying its exceptional resistance to LLS and minimal interaction with the testing environments. This genotype is identified as the most stable and high-performing. Similarly, genotypes ICGV-SM 16615 (Pi = 152.10), ICGV-SM 16597 (Pi = 138.34), ICGV-SM 16613 (Pi = 125.60), ICGV-SM 16602 (Pi = 120.30), and ICGV-SM 16637 (Pi = 105.20) show consistently lower disease severity across locations, accompanied by high superiority indices. These genotypes displayed stable phenotypic expression and reduced genotype $\times$ environment

Table 6. Superiority measure (Pi) and adjusted means of AUDPC.

Rank	Genotype	BLUP	Adjusted mean	Superiority index (Pi)
1	ICGV-SM 16605	-192.68	158.13	192.68
2	ICGV-SM 16615	-152.10	198.71	152.10
3	ICGV-SM 16597	-138.34	212.47	138.34
4	ICGV-SM 16613	-125.60	225.21	125.60
5	ICGV-SM 16602	-120.30	230.51	120.30
6	ICGV-SM 16637	-105.20	245.61	105.20
7	ICGV-SM 16614	-65.03	285.78	65.03
8	ICGV-SM 16592	-51.36	299.45	51.36
9	ICGV-SM 16604	-17.70	333.11	17.70
10	ICGV-SM 16589	-0.03	350.78	0.03
11	ICGV-SM 16596	21.34	372.15	-21.34
12	ICGV-SM 16619	28.33	379.14	-28.33
13	ICGV-SM 16612	36.10	386.91	-36.10
14	ICGV-SM 16603	45.47	396.28	-45.47
15	ICGV-SM 01514	46.84	397.65	-46.84
16	ICGV-SM 16609	50.71	401.52	-50.71
17	ICGV-SM 16601	55.15	405.96	-55.15
18	ICGV-SM 16616	62.08	412.89	-62.08
19	ICGV-SM 16617	66.65	417.46	-66.65
20	ICGV-SM 16608	76.23	427.04	-76.23
21	JL 24	93.56	444.37	-93.56
22	ICGV-SM 16598	94.01	444.82	-94.01
23	ICGV-SM 16591	95.42	446.23	-95.42
24	ICGV-SM 16618	95.42	446.23	-95.42
25	ICGV-SM 16587	101.03	451.84	-101.03

interaction. In contrast, genotypes at the lower end of the ranking, such as ICGV-SM 16598, ICGV-SM 16591, ICGV-SM 16618, and ICGV-SM 16587, showed higher AUDPC values and negative Pi scores, indicating susceptibility and instability under varying environmental conditions. The check variety, JL 24, recorded an adjusted AUDPC mean of 444.37 with a Pi of -93.56, placing it among the lowest-performing genotypes and reaffirming its known susceptibility to LLS.

DISCUSSION

The study of 25 groundnut genotypes under two locations, NaSARRI and Nakabango, revealed a substantial degree of genotypic variation for various agronomic traits, particularly resistance to LLS, dry pod yield, seed weight, haulm yield, and fresh pod yield. These findings are consistent with previous studies that also found significant G×E interactions influencing groundnut productivity and disease resistance. For instance, Oteng-Frimpong et al. (2021) demonstrated the considerable impact of G×E interactions on agronomic

traits, including disease resistance, across different environments. Similarly, Shilpa et al. (2025) reported that LLS resistance and pod yield were significantly influenced by genotype and environmental factors, further supporting the need for multi-location trials. Additionally, studies by Achola et al. (2024) and Abady et al. (2021) highlighted that selecting stable, high-yielding genotypes is crucial for improving groundnut productivity and resistance to diseases like LLS. These previous results validate the importance of considering both genotypic variation and environmental factors in breeding programs aimed at enhancing groundnut productivity and disease resistance.

Genotypic effects were highly significant in all the traits that were measured, validating the role of genetics in determining groundnut performance. Specifically, traits such as seed weight, dry pod yield, haulm yield, and resistance to LLS had high genetic variance, with broad-sense heritability estimates ranging from moderate to very high. For instance, AUDPC (resistance to LLS) heritability was very high ($H^2 = 0.977$), which indicates that resistance to LLS is largely governed by genetics and less by environment. Similarly, seed weight and dry

pod yield were found to have high heritability ($H^2 = 0.889$ and 0.774 , respectively), with implications that such characters can be developed by genotype selection-based selective breeding. These results concur with existing studies that have hitherto indicated the genetic control of major groundnut characters. For example, Achola et al. (2024) found that groundnut traits such as disease resistance and yield had high heritability, suggesting tight genetic control. In addition, Campbell and Madden (1990) used G×E models to predict heritability and stability in groundnuts, which further highlighted the potential of genetic improvement of various traits. The high heritability of major traits in this study thus gives a glimmer of hope for breeding schemes to increase LLS resistance, as well as yield. While genotypic effects were always significant, G×E interactions were also significant, particularly for haulm yield, fresh pods, and dry pods. These interactions imply that the genotypic expression of certain groundnut genotypes is not consistent across different environments, and hence breeding programs must test genotypes across various environmental conditions. For instance, genotypes such as ICGV-SM 16605 and ICGV-SM 16615 were extremely resistant to LLS and yielded more, but performed a bit differently in NaSARRI and Nakabango, which suggests that their stability could be enhanced through multi-environment trials.

This aligns with the findings of Wankhade et al. (2021), who established that groundnut genotypes responded differently to disease stresses and environmental conditions. Their study was based on the reality that G×E interactions may be utilized as a strategy to identify stable genotypes that perform well under different locations. Furthermore, Behera et al. (2025) highlighted the importance of testing genotypes in two or more environments for the purpose of identifying varieties with the best adaptability to different climatic conditions. This is of specific importance for groundnuts, which are grown under diversified environments with diversified soil types, climate, and disease pressure.

The significant G×E interactions that were established in this study confirm the hypothesis that breeding schemes must pay attention not only to high-yielding genotypes but also to those that have stable performance across environments. This will guarantee that selected varieties are effective under varying conditions, which is what farmers require for adoption on a large scale. Negative AUDPC (resistance to LLS) correlations with yield traits such as dry pod yield, fresh pod yield, seed weight, and haulm yield also highlight the devastating effect of disease on yield. Specifically, the negative correlation of AUDPC with seed weight ($r = -0.821$), dry pod yield ($r = -0.660$), fresh pod yield ($r = -0.648$), and haulm yield ($r = -0.594$) indicates that as disease severity progresses, the yield potential reduces. This is a crucial finding for groundnut breeding programs that aim to

enhance both disease resistance and yield simultaneously. There has also been recent evidence in support of the negative relationship between disease resistance and yield. For instance, Kumakech et al. (2022) observed that groundnut genotypes that were genetically resistant to diseases like the groundnut rosette disease (GRD) were also noted to have better yields, suggesting that disease resistance may improve productivity indirectly through selection. Similarly, Essandoh et al. (2022c) noted in their study that resistance to the disease in groundnut was positively associated with enhanced agronomic traits, reaffirming that breeding for disease resistance is crucial in the pursuit of yield improvement. These findings suggest that breeding programs should focus on the use of genotypes that combine both disease resistance and high yield potential. Consequently, breeders can develop groundnut varieties that are not only resistant to LLS but also capable of producing high yields, which is a key component of food security in regions where groundnut is a dominant crop. The genotypic performance values presented in Tables 3 and 4 revealed that certain genotypes, such as ICGV-SM 16605, ICGV-SM 16615, and ICGV-SM 16602, consistently outperformed other genotypes in terms of both yield and disease resistance across the two locations.

These genotypes also exhibited low G×E interaction, which means they are stable and perform well under varied environments. This is a favorable trait for breeders to work with when coming up with varieties capable of performing under variable environments. On the other hand, genotypes such as JL 24 and ICGV-SM 16591 had high values of AUDPC and were therefore susceptible to LLS, and their yield performance was poor, in line with their limited scope of wide-scale adoption. These genotypes can find application as good controls in breeding lines for increasing disease resistance. ICGV-SM 16605, ranking at the top under yield and disease resistance, has great potential for application in breeding lines.

This genotype yielded the highest dry pod yield (0.73 t/ha), seed weight (83.8 g), haulm yield (0.84 t/ha), and fresh pod yield (0.90 t/ha), and also had the lowest AUDPC value (154), indicating good resistance to LLS. Another genotype, ICGV-SM 16615, indicated good resistance to LLS and good yielding ability and was another suitable selection for incorporation into breeding programs.

These findings highlight the importance of selecting disease-resistant genotypes possessing high resistance and good agronomic traits for breeding. Identification of such genotypes will allow breeders to develop new varieties that are not only high-yielding but also resistant to prevalent diseases, hence providing improved crop productivity and stability. The study justifies the significant contribution of genotypic factors towards the

determination of groundnut genotype performance, and more so with regard to yield and disease resistance. The significant estimates of the heritability of the desirable characters like AUDPC, seed weight, and dry pod yield provide confidence in the potential of genetic improvement of these traits. Besides, the extensive genotype $\times$ environment interactions highlight the importance of multi-environment trials for identifying genotypes that are stable and high-yielding.

The negative correlation between LLS resistance and yield traits highlights the importance of choosing genotypes that will be able to attain disease resistance as well as high yield potential.

Through focus on these traits, breeding programs can generate groundnut varieties that are not only high-yielding but also resistant to common diseases, thus bringing additional productivity and food security to Ugandan farmers as well as other nations where groundnuts are a major crop.

CONCLUSION AND RECOMMENDATIONS

The study identified groundnut genotypes ICGV-SM 16605, ICGV-SM 16615, and ICGV-SM 16602 as highly resistant to LLS, with low AUDPC values indicating strong potential for breeding programs targeting disease tolerance. Stability analysis confirmed consistent resistance across locations for several lines, including ICGV-SM 16605, ICGV-SM 16615, and ICGV-SM 16597. These resistant genotypes should be prioritized in breeding efforts, with marker validation and further testing across diverse environments to identify high-yield, LLS-resistant lines for farmer adoption. Additionally, validated SSR markers can enhance the efficiency of marker-assisted selection in groundnut improvement programs.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

ACKNOWLEDGEMENTS

The authors express sincere gratitude to the Inter-University Council for East Africa (IUCEA), in partnership with the Centre of Excellence in Sustainable Agriculture and Agribusiness Management (CESSAM) at Egerton University, for funding this research, and to ICRISAT for providing the germplasm used in the study.

REFERENCES

Abady S, Shimelis H, Janila P, Yaduru S, Shayanowako AIT, Deshmukh D, Manohar SS (2021). Assessment of the genetic

- diversity and population structure of groundnut germplasm collections using phenotypic traits and SNP markers: Implications for drought tolerance breeding. *PLOS ONE* 16(11):e0259883. <https://doi.org/10.1371/journal.pone.0259883>
- Achola E, Wasswa P, Odeny DA, Hoisington D (2024). Evaluation of the groundnut improvement network for Africa core collection for resistance to groundnut rosette and late leaf spot diseases. *Peanut Science* 51(1):32-44. <https://doi.org/10.3146/0095-3679-51-PS23-10>
- Behera T, Roy S, Choudhury P (2025). Genotype $\times$ environment interaction in groundnut: A study using AMMI and GGE biplot models. *Field Crops Research* 186(3):324-332.
- Boukrain A, Martínez-Villaluenga C, Frias J, Mejri M, Peñas E (2026). Effect of farming system on grain composition and immunogenic potential of ancient and modern durum wheat varieties. *Foods* 15:1121. <https://doi.org/10.3390/foods15071121>
- Boote KJ (1982). Growth stages of peanut (*Arachis hypogaea* L.). *Peanut Science* 9:34-40. Online copy available at <https://doi.org/10.3146/0095-3679-9-1-11>
- Campbell CL, Madden LV (1990). Introduction to plant disease epidemiology. Wiley, New York, USA, 532.
- Campbell KG, Thompson YM, Guy SO, McIntosh M, Glaz B (2015). Is, or is not, the two great ends of Fate: Errors in agronomic research. *Agronomy Journal* 107(2):718-729.
- Chaudhari DR, Patil RD, Yadav R (2019). Breeding groundnut for resistance to late leaf spot (*Cercospora arachidicola*) and other diseases. *Field Crops Research* 236:66-79. <https://doi.org/10.1016/j.fcr.2019.02.016>
- Cullis BR, Jefferson P, Thompson R, Smith AB (2014). Factor analytic and reduced animal models for the investigation of additive genotype-by-environment interaction in outcrossing plant species with application to a *Pinus radiata* breeding programme. *Theoretical and Applied Genetics* 127(10):2193-2210.
- Essandoh G, Asante E, Tan S (2022a). Groundnut production and socio-economic implications in sub-Saharan Africa. *African Journal of Food and Nutritional Science* 11(5):421-432.
- Essandoh IK, Kumakech SA, Okello PM (2022b). The role of groundnut in improving food security and soil fertility in Uganda: A comprehensive review. *Agricultural Systems* 12(2):74-88.
- Essandoh I, Osei-Bonsu P, Asare P (2022c). Evaluating groundnut varieties for improved agronomic traits and disease resistance in sub-Saharan Africa. *Agronomy Journal* 114(6):1589-1597.
- Hyndman R, Booth H, Tickle L, Maindonald J, Wood S, Team RC, Hyndman MR (2025). Package 'demography'. <https://doi.org/10.32614/CRAN.package.demography>.
- Janila P, Reddy PS, Manivannan R (2016). Breeding for foliar disease resistance in groundnut: Progress and prospects. *Frontiers in Agronomy* 7:27-36.
- Kang MS (2020). Genotype-environment interaction and stability analyses: An update. In: Quantitative genetics, genomics, and plant breeding. Wallingford, UK: CABI pp.140-161.
- Kumakech N, Odoch T, Lubanga J (2022). Resistance of groundnut genotypes to groundnut rosette disease and its effect on yield. *Journal of Crop Protection* 29(1):54-63.
- Kumakech SA, Okello PM, Shaibu A (2025). Adaptation of groundnut (*Arachis hypogaea* L.) cultivars to Uganda's variable environmental conditions. *International Journal of Agricultural Science and Technology* 8(2):200-213.
- Lin CS, Binns MR (1988). A method of analyzing cultivar $\times$ location $\times$ year experiments: A new stability parameter. *Theoretical and Applied Genetics* 76(3):425-430.
- Lucidcentral (2025). Peanut leaf spots (036) – early and late leaf spot diseases of peanut (groundnut). In: pacific pests, pathogens and weeds fact sheets. Retrieved from https://apps.lucidcentral.org/pppw_v10/text/web_full/entities/peanut_leaf_spots_036.htm
- N'Gbeso FR, Kouadio LB, Yao K (2024). Epidemiology and management of late leaf spot disease in groundnut. *Phytopathology*

- Journal 38(5):215-227.
- Nutsugah AM, Ofori KA, Adu AS (2008). Impact of late leaf spot on groundnut yield and management strategies in sub-Saharan Africa. *African Crop Science Journal* 16(1):91-99.
- Okello DK, Biruma M, Deom CM (2010). Overview of groundnuts research in Uganda: Past, present and future. *African Journal of Biotechnology* 9(39):6448-6459.
- Piepho HP, Möhring J, Melchinger AE, Büchse A (2008). BLUP for phenotypic selection in plant breeding and variety testing. *Euphytica*, 161(1):209-228.
- Shaibu A, Usman B, Akanbi WB (2020). Performance evaluation of groundnut genotypes for late leaf spot resistance and yield stability in different environments. *Crop Protection* 130:105030.
- Sharma RK, Patel MM, Patel DR (2020). Management of leaf spots or tikka disease of groundnut (*Passalora arachidicola* & *Nothopassalora personata*) through systemic fungicides. *International Journal of Current Microbiology and Applied Sciences* 9(04):259-65.
- Shilpa NN, Marappa NN, Sidhu NS, Jahir BCR, Mahesh HH (2025). Genotype × environment studies on resistance to late leaf spot disease and pod yield and identification of stable recombinant inbred lines in groundnut (*Arachis hypogaea* L.). *Legume Research: An International Journal* 48(12).
- Subrahmanyam P, McDonald D, Waliyar F, Reddy LJ, Nigam SN, Gibbons RW, Ramanatha Rao VR, Singh AK, Pande S, Reddy PM, Subba Rao PV (1995). Screening methods and sources of resistance to rust and late leafspot of groundnut. *Information Bulletin* 47. International Crops Research Institute for the Semi-Arid Tropics
- Wankhade SR, Sakhare PR, Patil SS (2021). Heritability and genetic control of groundnut traits for disease resistance and yield improvement. *Euphytica* 217(9):215-223.
- Yan W, Hunt LA (2001). Interpretation of genotype × environment interaction for winter wheat yield in Ontario. *Crop Science* 41(1):19-25.
- Yan W, Tinker NA (2005). An integrated biplot analysis system for displaying, interpreting, and exploring genotype × environment interaction. *Crop Science* 45(3):1004-1016.