

Soybean rust-resistant and tolerant varieties identified through the Pan-African Trial Network

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Abstract

BACKGROUND: The global demand for soybeans is increasing rapidly, with projections indicating an escalation of 70–80 million metric tons over the next decade. Sub-Saharan Africa (SSA) contributes significantly to this growth, with soybean production increasing by 6.8% per year, outpacing the global average increase of 4.7%. Despite the expansion, soybean productivity in Africa remains less than half of the global average. This yield gap is largely due to diseases and pests, such as soybean rust, which can be particularly severe. Effective management of soybean rust depends on several factors, including resistant cultivars. However, there has been limited information on the rust-resistance levels of African cultivars. To address this gap, the Pan-African Trial network conducted soybean varietal trials across diverse locations.

RESULT: Analyzing data from 370 individual trials conducted between 2015–2022, the network identified 81 cultivars with sufficient rust-resistance data. Six cultivars including, Black Hawk, Dundee, Egret, Heron, Ibis, and Peka 06 were found to be resistant, and 12 were classified as tolerant.

CONCLUSION: This research is a significant step forward in improving soybean productivity in Africa, and further assessments are being undertaken to address other crop production challenges in the region.

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Supporting information may be found in the online version of this article.

Keywords: genetic resistance; macro-environments; *Phakopsora pachyrhizi*; soybean productivity; sustainable disease management

1 INTRODUCTION

Soybean (*Glycine max*) is a valuable crop primarily grown for its high protein content (~40%), which supports a broad range of industrial, feed, and nutritional applications. Global demand for soybeans has risen by over 145% in the last 30 years,¹ and projections suggest an additional 70–80 million metric tons will be required by the end of the next decade. In sub-Saharan Africa (SSA), the demand for soybeans is particularly high, with production rising by an average of 6.8% per year compared to a global increase of 4.7%.² Most of the 1.5 million hectares of soybeans in SSA are grown by smallholders, who record average yields of 1.052 t ha⁻¹, which is at least 50% lower than the global average %.² Addressing this yield gap is crucial for ensuring the profitability of farmers and enabling them to benefit from the growing global demand.

Increasing soybean production in Africa can bring significant economic and social benefits at regional and country levels. For instance, recent input–output analyses by the USAID Feed the Future Innovation Lab for Soybean Value Chain Research (Soybean Innovation Lab, 'SIL') demonstrated that a 25% increase in production in Malawi could lead to a \$39 million expansion in

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the Malawian economy. Additionally, data from the Soybean Innovation Laboratory often show yields above 4 t ha^{-1} and as high as 5.8 t ha^{-1} in Mozambique (Pan African Trial Database, 2023), indicating that there is substantial potential for yield improvement in the region.

The sizeable yield gap in SSA soybean production is due to various factors, including low-yielding cultivars, poor agronomic practices, and pressure from diseases and pests. A significant threat to soybean production is soybean rust disease, caused by *Phakopsora pachyrhizi*.^{3–5} This disease can be particularly destructive, causing almost total losses in infected fields.^{4,6} The fungus is disseminated over long distances by wind currents⁷ and manifests quickly at temperatures between 17 to 29 °C and relative humidity of 85%.^{8,9} Upon landing on susceptible soybean leaves, the fungus forms uredinia that produce urediniospores within 7 to 9 days.⁷ Symptoms include leaf lesions, chlorosis, and complete defoliation during severe infections. Leaf yellowing lowers photosynthetic efficiency, reducing flowering, pod and seed formation, and seed size (Kumudini et al., 2012).¹⁰

In SSA, soybean rust was first reported in Uganda in 1996 (Kawuki et al., 2003)¹¹ and has since been detected in at least 15 countries.¹² A field trial in Kanengo, Malawi, in 2020 estimated a 70% yield loss due to soybean rust (SIL internal communication). Currently, synthetic chemical fungicides are relied on to manage soybean rust. However, the high cost of fungicides, their negative environmental impact, and inadequate access among small-holder farmers limit their use in SSA. Host resistance is a cost-effective and environmentally preferable option for managing soybean rust. Germplasm screening for resistance sources has been ongoing, and seven resistance loci, known as *Rpp* (resistance to *P. pachyrhizi*), have been identified and characterized.¹³ However, each *Rpp* gene seems to recognize only a subset of rust pathotypes, and no single *Rpp* gene is effective against all pathotypes. Information on the rust-resistance level of cultivars used in SSA is largely restricted to the private sector, with no known public resistance screening programs. An initiative by the USAID Feed the Future Innovation Lab for Soybean Value Chain Research (Soybean Innovation Lab, 'SIL') to promote soybean productivity in Africa has led to the evaluation of over 300 soybean cultivars under the Pan African Soybean Variety Trials (PATs) network. Conducted in 24 countries at 384 sites since 2015,¹⁴ these trials enable the assessment of a wide range of cultivars for suitability to local conditions and resistance to various soybean diseases and pests. The current study uses data collected from these PAT sites to identify resistance and/or tolerance, promoting sustainable disease management in SSA.

2 MATERIALS AND METHODS

2.1 Soybean entries in the Pan-African soybean variety trials

Three hundred seventy soybean entries were evaluated in this trial. The entries comprised soybean cultivars and experimental lines from private and public sources (Supporting Information, Table S1). Most of the entries were bred for subtropical to tropical conditions. Entries from private companies included nominations of proprietary cultivars and experimental lines; the public soybean entries were selected based on previously being grown in that region or being developed through breeding programs such as IITA.¹⁵ Seeds used in the trials were multiplied in bulk by IITA and harvested in 2018. The seeds were packaged at IITA Lusaka before sending to the various cooperators for planting at the

specified locations. All trials were arranged in a randomized complete block design with four replications. The replications were distinct blocks, with cultivars randomly assigned to each plot inside the blocks. The number of cultivars screened varied between 16–40 per site year, and each plot consisted of $4 \times 5 \text{ m}$ rows spaced 50 cm apart and containing 20 plants per row. Data were only collected from the two inner rows, with the outside rows considered borders. The data collected included various agronomic traits at each location, including information on disease incidence, when present, given the study relied on natural infection of soybean.

Bacterial inoculants were only applied at planting, and no other biological or chemical seed protectants were used. Soya mix fertilizer (7:20:70 N/P/K) was applied at 200 kg ha^{-1} planting. Pre- and post-emergence weed control consisted of imidazolinone (100 g L^{-1}), metolachlor (960 g L^{-1}), quizalofop-pethyl (35 g L^{-1}), and fomesafen (125 g L^{-1}), and hand-weeding. For insect control, lambda-cyhalothrin (50 g L^{-1}) was applied once at growth stage R6 or R7.¹⁶

2.1.1 Evaluation of soybean rust severity

Evaluation depended on natural inoculum in each location with no exogenous inoculation used. When soybean rust was detected, all entries were evaluated once at the R1, R3, and R6, using a visual severity rating for each disease per plot using a pre-transformed rating scale (Little & Hills, 1978) from 1 to 5, where 1 = no visible symptoms, 2 = 1 to 10% of the canopy affected, 3 = 11 to 35% of the canopy affected, 4 = 36 to 65% of the canopy affected and 5 = 66 to 100% of the canopy affected (Fig. 1). The score was recorded based on the most infected leaf, and the average score from six random plants per plot represented the score of each plot. Each cultivar score per trial was based on the average of four plots.

2.2 Selection of site years for the rust classification

A total of 370 separate PAT trials were conducted between 2015 and 2022 in 29 countries, all of which were considered for this study. However, site years were selected for the current study only when the disease was present. The selection was based on three points: rust severity score, the maximum score in one of the plots was higher or equal to 3 and the score recorded was consistent across replications, indicating uniformity.

2.3 Selection of varieties for the rust classification

Once the site years were selected, cultivars within the selected site years were screened for the analysis based on the availability of multi-trial data following criteria: the cultivar should be represented in at least two different site years, with at least three replications in each site year.

2.4 Data analysis

Initially, each cultivar's site year data was analyzed using a linear mixed model approach with PROC MIXED in SAS (version 9.4; SAS Institute, Cary, NC), with site year considered as the dependent factor and replication as a random factor. Replication was removed from the analysis when flagged as an over-estimator for the model. The normality of residuals was assessed using PROC UNIVARIATE. If this assumption was violated, extreme Pearson residual values, visual evaluation of QQ plots and boxplots of the residuals, and Cooks D and leverage values were used to identify outliers, followed by their removal. The assumption of homoscedasticity was tested using the Brown-Forsythe modification of

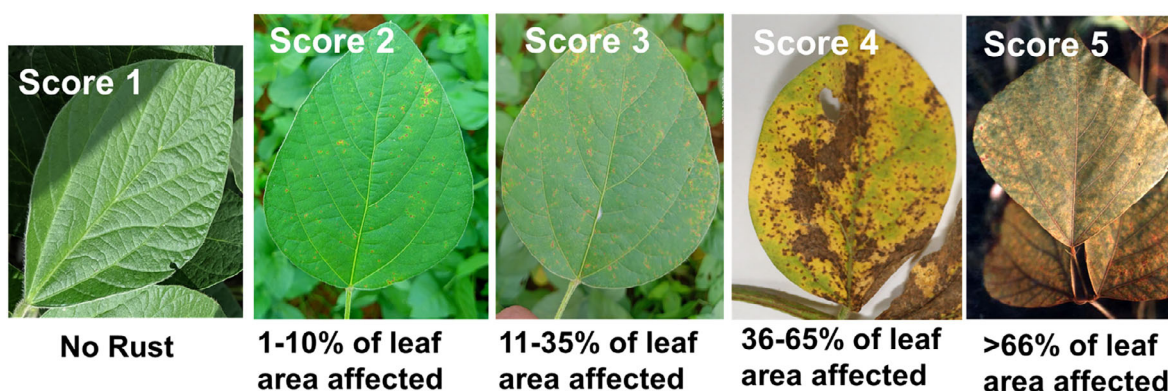


Figure 1. The disease severity scale was used in the PAT experiments to quantify rust infection to the percentage of leaf area infected.

the Levene Test in PROC GLM, considering the site year as the main factor. Additionally, the Coefficient of Variation and the standard deviation of each cultivar and each site year within each cultivar were retrieved with PROC MEANS.

After the initial analysis, the least square means of every site year within each cultivar were averaged, and the 90% confidence interval (CI_{90}) limits were calculated using the formula:

$$CI_{90} = \bar{X} \pm z \frac{SD}{\sqrt{n}}$$

Where:

CI_{90} = 90% Confidence Interval limits.

\bar{X} = cultivar average score across site years.

z = z-score for the desired confidence level (90% = 1.644854).

SD = Standard deviation of the cultivar across site years.

n = Total number of observations for each cultivar.

Once the confidence interval limits were calculated, the cultivar was classified according to its behavior with soybean rust as follows: resistant – if the upper limit of CI_{90} was below 2, tolerant – if 2 fell within the CI_{90} limits and susceptible – if the CI_{90} lower limit was higher than 2.

2.5 Environmental division of locations in macro-environments

Site years were divided into four macro-environments within Africa that pooled countries with similar soybean production characteristics to investigate the effect of the environment on the behavior of tolerant cultivars. Tolerant cultivars present in at least two site years in distinct macro environments were considered for this analysis (Supporting Information, Fig. S1).

3 RESULTS

3.1 Data restrictions

The PAT trials used for this analysis were initially implemented to identify those soybean cultivars best adapted to the specific region and produce the highest grain yields. Therefore, including known rust-susceptible cultivars in each trial was not intentional. While the yield checks would frequently be rust-susceptible, each trial did not guarantee a rust-susceptible check.

Additionally, the PAT trial network included public and private sector partners, with some genotypes included in trials being pre-commercial materials. Given the sensitivity of the data, each genetic owner of the cultivars used in this study was given the

choice of undisclosed varietal information, resulting in the 81 varieties that were the focus of this study.

Lastly, the soybean rust classification achieved for individual cultivars was based on field observations from natural infection. No methodology was used to test for resistance genes, and if the presence of a resistance gene was disclosed, it was information provided by the genetics owner. Rust scoring was made at set growth stages (R1, R3, or R6) when the disease was present in the field, so observations of disease progress and lesion type are absent from this analysis. Additionally, the scale used to score disease severity was chosen due to its simplicity and well-defined thresholds, thus increasing the efficiency of the evaluation while controlling the accuracy. Further studies will be implemented to investigate the cultivars selected for this study.

3.2 Division of trial sites in macro environments

Since the database used for this analysis encompasses 29 countries with diverse environmental characteristics, a division of the research footprint in macro-environments with similar agro-ecological zones was adopted to group locations that shared similar temperature and humidity characteristics for soybean production and rust infection (Table 1). The macro-environments were extrapolated to country limits to better suit the broad scope of the African continent (Fig. 2).

3.3 General variety classification results

Of the 81 cultivars tested, the majority (43) were susceptible to soybean rust, which was expected because the yield performance was the primary target when the varieties were selected for the PAT network, but six were classified as resistant Table 2. Coincidentally, all six resistant cultivars were tested in locations within one macro environment and restricted to less than three site years (Table 3). Thirty cultivars were classified as tolerant, with scores that could also not be differentiated ($P < 0.05$) since the whiskers crossed the two lines and occurred in more than one macro-environment. Of the tolerant cultivars, six were undisclosed, and their detailed rust score per site year is not discussed further. However, the results per site year for all cultivars are available in the supplemental material of this article (Supporting Information, Table S1).

3.4 Tolerant cultivar behavior per macro environment

The cultivar A773 had an average rust score of 1.83 from the three site years in this analysis, all located in macro-environment 1 (Table 1). There was a significant difference among site years

Table 1. Description of the macro-environment division of the African continent for the soybean crop was proposed by the Soybean Innovation Laboratory

Macro-environment	African region	Countries	Agro-ecological zone	Growing season
ME1	Southern	Angola, Malawi, Mozambique, Zambia, Zimbabwe	Tropics; semi-arid	Summer (November–March)
ME2	Central	Burundi, Kenya, Rwanda, South Sudan, Uganda	Tropics; Humid	Summer (October–March)
ME3	Eastern	Ethiopia	Tropics; Humid	Winter (April–September)
ME4	Western	Benin, Cameroon, Ghana, Mali, Nigeria, Senegal, Sudan, Togo	Tropics; sub-Humid	Summer (October–March)
			Tropics; Sub-Humid	Winter (April–September)
			Tropics; humid, sub-humid & semi-arid	Winter (April–September)

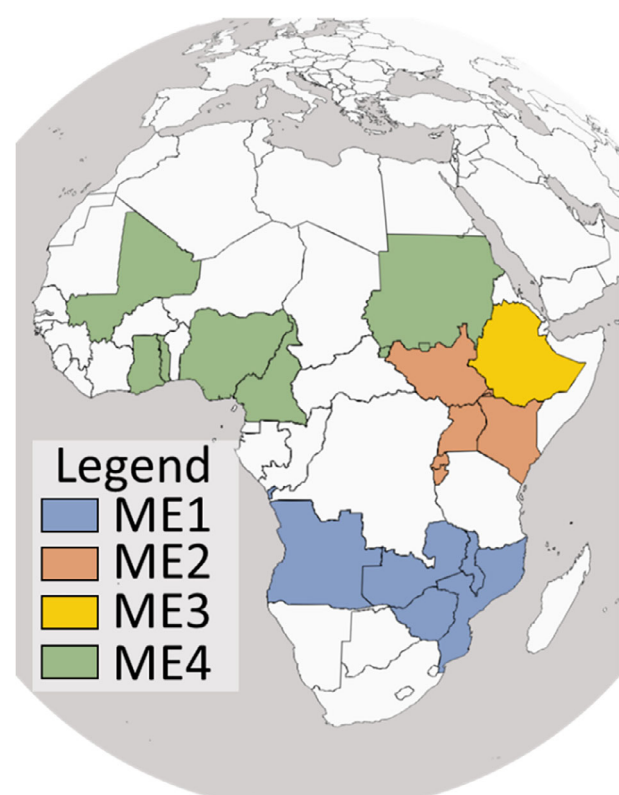


Figure 2. Mapping of the macro-environment (ME) division proposed by the Soybean Innovation Laboratory for soybean production in the African continent.

($P = 0.03$), with a rust score of 1.0, given in Mpale, Malawi, in 2019, being different from the scores from the other two site years (Fig. 3(a)). The rust score was numerically higher than 2.0 in Kabwe, Zambia, in 2021 but not statistically different from the score of 2.0 in Kadoma, Zimbabwe, in 2020. This cultivar, therefore, tends to resist rust infection in macro-environment 1 strongly. The cultivar S882 was tested in macro-environments 1 and 2, with scores differing among site years. However, the difference was not from the macro-environment (Fig. 3(b)). Cultivar Dare (PI 548987) had an average score of 2.17. It was tested in two locations within the macro environment, two in the same year (2018 season), with no difference between the scores ($P = 0.37$) (Fig. 3(c)). Cultivar Gail (PI 548978) had similar results

from the same macro-environment with an average score of 2.17 but no difference between site years ($P = 0.64$) (Fig. 3(d)).

Lukanga was tested 15 times in macro environment 1 and twice in macro environment 2. The average rust score was 2.21, and while site years were statistically different ($P = 0.01$), the most distinct separation was from the Kabwe, Zambia, 2021 and the Chitedze, Malawi, 2020 site years, having a higher score than the others (Fig. 3(e)). The macro-environment was therefore not a good predictor of the behavior for this cultivar.

The cultivars MAKSOY 1 N and MAKSOY 4 N had average rust scores of 2.13 and 1.83, respectively. Both cultivars were tested in macro environments 1 and 2, with MAKSOY 4 N presenting scores around 2.0 across all locations, except in Chitedze, Malawi, 2017, where the lowest score (1.0) was observed (Fig. 3(f)). For MAKSOY 1 N, the three evaluations in macro environment 2 presented scores higher than 2.0, which can be considered susceptible behavior. In comparison, the two evaluations in macro environment 1 resulted in scores lower than 2.0, which indicates tolerant behavior (Fig. 3(g)). Nasoko had an average score of 2.16 and was tested in macro environments 1 and 2. However, the scores observed among site years tended to differ with no clear distinction between macro environments (Fig. 3(h)). Panorama 27 D was tested in two site years in macro environment 4, and no difference was detected between site years (Fig. 3(i)).

From the breeding program of IITA, 12 cultivars were tolerant. TGx 1987-62F was tested in macro environments 1 and 2 with a total of 31 observations (Table 1), with an average score of 1.93 which reflects more resistant behavior than susceptible, with scores above. The remaining IITA tolerant cultivars originated from Zambia and were tested extensively in macro-environments 1 and 2, with differences among site years rarely relating to the macro environments (Fig. 3(j)).

4 DISCUSSION

In this study, we utilized data from the Pan African Soybean Variety Trials (PATs) network, which has been screening globally sourced soybean cultivars across Africa since 2015 to identify the best-adapted and high-yielding genotypes for each macro-environment. The comprehensive datasets from 370 unique combinations of location and year yielded 370 site-years and 98 cultivars for rust resistance evaluation. This unique dataset provides an ideal opportunity to evaluate multiple soybean cultivars against a range of in-field diseases across diverse environments, including soybean rust.

Table 2. Average rust severity score, 90% confidence interval and overall rust classification of each soybean variety

		90% confidence interval limits		
Variety	Average rust severity score	Lower	Upper	Overall rust classification
1 to 5 Score Scale				
TGx 2001-3FM	2.03	1.72	2.34	Tolerant
TGx 2001-6FM	4.11	3.60	4.62	Susceptible
TGx 2001-8DM	2.73	2.42	3.04	Susceptible
TGx 2002-14DM	2.19	1.82	2.56	Tolerant
TGx 2002-23DM	2.67	2.32	3.01	Susceptible
TGx 2002-35FM	2.43	2.03	2.83	Susceptible
TGx 2002-3DM	3.22	2.82	3.62	Susceptible
TGx 2002-3FM	2.27	1.83	2.71	Tolerant
TGx 2002-41FZ*	2.00	2.00	2.00	Tolerant
TGx 2002-46FZ	2.83	2.65	3.02	Susceptible
TGx 2002-9FM	3.00	2.58	3.42	Susceptible
TGx 2014-49FZ	3.33	2.95	3.72	Susceptible
TGx 2014-16FM	2.77	2.56	2.97	Susceptible
TGx 2014-19FM	1.68	1.35	2.01	Tolerant
TGx 2014-22FZ	2.17	1.89	2.44	Tolerant
TGx 2014-23FM	3.78	3.32	4.23	Susceptible
TGx 2014-33FM	3.17	2.60	3.73	Susceptible
TGx 2014-43FM	2.47	2.11	2.82	Susceptible
TGx 2014-5GM	2.81	2.48	3.13	Susceptible
TGx 2020-1GZ	3.11	2.60	3.62	Susceptible
TGx 2029-13F	3.20	2.62	3.78	Susceptible
TGx 2029-25F	2.73	2.04	3.42	Susceptible
TGx 2029-36F	2.87	2.39	3.34	Susceptible
TGx 2029-37F	2.87	2.48	3.26	Susceptible
TGx 2029-38F	2.80	2.31	3.29	Susceptible
TGx 2029-52F	2.47	1.96	2.97	Tolerant
TGx 2029-6F	3.07	2.48	3.66	Susceptible
TGx 2029-9F	2.67	2.32	3.01	Susceptible
TGx 2033-82GZ	2.83	2.33	3.34	Susceptible
TGx 2072-6FZ	4.00	4.00	4.00	Susceptible
TGx 2078-14FZ	3.83	3.56	4.11	Susceptible
TGx 2082-20FZ	3.33	2.99	3.68	Susceptible
TGx 2083-15FZ	3.83	3.56	4.11	Susceptible
TGx 2083-20FZ	3.50	3.13	3.87	Susceptible
TGx 2089-6FZ	3.83	3.56	4.11	Susceptible
TGx 2090-14FZ	3.67	3.32	4.01	Susceptible
TGx 2092-4FZ	3.83	3.56	4.11	Susceptible
TIKOLORE	2.30	2.07	2.53	Susceptible
*No standard deviation estimation given all scores were equal across replications and experiments, so confidence interval limits were null.				

*No standard deviation estimation given all scores were equal across replications and experiments, so confidence interval limits were null.

Soybean rust is a highly diverse pathogen composed of various pathotypes. While genes conferring resistance to *Phakopsora pachyrhizi* have been characterized,⁷ the resistance is often broken due to the diverse nature of the pathogen.¹⁷ To date, none of these resistance genes have been found effective against all known soybean rust pathotypes.¹³ Within Africa, very few studies have actively evaluated or detected sources of resistance. Two notable studies reported consistently high rust disease severity across genotypes, signifying high levels of susceptibility and a lack of resistance (Oloka *et al.*, 2005; Murithi *et al.*, 2021).^{18,19} Similar observations were made in the current study, with the majority (68%) of genotypes proving susceptible to rust. Consequently, with a predominance of susceptible cultivars, diverse pathotypes,

and aggressive pathogens, a strategy for consistent screening of genotypes for stable resistance against rust is required.

In the current study, six cultivars were identified as resistant to rust. These cultivars may be released for direct use or may possess stable resistant genes that can be used as sources of resistance in breeding programs in Africa. However, there is a need for multi-location testing of the resistant lines in other macro-environments to ascertain the durability of rust resistance under varying conditions and their suitability across different agroecologies.

In our study, cultivars such as Maksoy 1 N, Maksoy 2 N, and TGx 2001-3FM were observed as resistant/tolerant in one macro-environment but susceptible in another. This behavior may be

Table 3. Rust resistance characteristic per macro region of overall varieties that had significant presence in different macro-regions

Variety	P-value of the difference among macro regions	Rust-resistance characteristic			
		ME1	ME2	ME3	ME4
Lukanga	0.10	Tolerant	Resistant	-	-
MAKSOY 1N	<0.01	Resistant	Susceptible	-	-
MAKSOY 2N	0.04	Resistant	Susceptible	-	Tolerant
MAKSOY 3N	<0.01	Tolerant	Susceptible	-	-
MAKSOY 4N	0.03	Resistant	Tolerant	-	-
Nasoko	0.28	Tolerant	Tolerant	-	-
Panorama 358	0.34	Tolerant	-	-	Tolerant
S882	0.99	Tolerant	Tolerant	-	-
TGx 1987-62F	0.72	Tolerant	Tolerant	-	-
TGx 2001-13DM	0.71	Tolerant	Tolerant	-	-
TGx 2001-3FM	0.05	Susceptible	Tolerant	-	-
TGx 2002-14DM	0.34	Tolerant	Tolerant	-	-

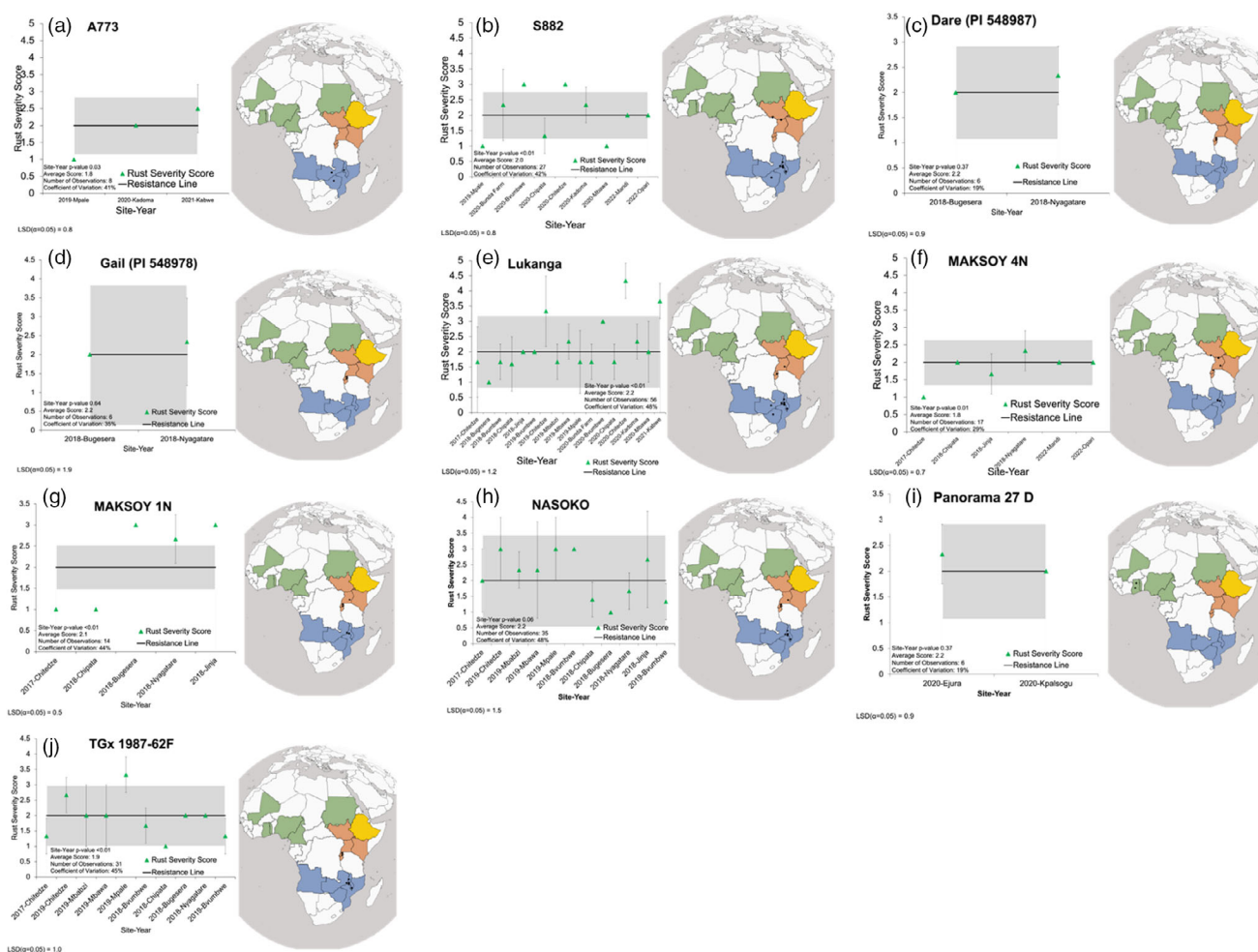


Figure 3. Rust Score severity across macro regions by the varieties identified as tolerant to Rust, letters and varieties names are: (a) A773; (b) S882; (c) Dare (PI 548987); (d) Gail (PI 548978); (e) Lukanga; (f) MAKSOY 4N; (g) MAKSOY 1N; (h) Nasoko; (i) Panorama 27 D; (j) TGx 1987-62F.

due to the presence of different soybean rust populations or pathotypes in the macro-environments. Several *P. pachyrhizi* pathotypes have been reported in Africa, which can differ by country.^{20–22} Consequently, there is a need to determine which

pathotypes are present across geographies and agroecologies and cross-reference this information with genomic studies to pair the resistance genes with pathotypes for the efficiency of future breeding efforts. Consistent screening of multiple genotypes at

different locations is necessary to aid the identification of sources of resistance that could resist multiple pathotypes.

Genetic resistance based on monogenic inheritance, often referred to as qualitative resistance, is generally unstable. Conversely, quantitative genetic resistance controlled by several genes is more stable, as the pathogen is less able to break the resistance.²³ Genetic and molecular analysis of the six resistant genotypes would provide information on the kind of resistance they confer. Understanding which resistance genes are present in these genotypes will assist breeders in identifying and incorporating these genes into elite crop cultivars to enhance durable resistance.

This study presents valuable insights into soybean rust resistance, highlighting the importance of comprehensive screening and genetic analysis for sustainable rust management in SSA. Collaborative efforts such as the PAT network could facilitate the rapid development of rust-resistant soybean cultivars. This is crucial in addressing urgent agricultural challenges such as soybean rust, which can cause significant yield losses.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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