

Potential for soybean rust tolerance among elite soybean lines in Uganda

Herbert K. Oloka^{a,b,*}, P. Tukamuhabwa^a, T. Sengooba^b, E. Adipala^c, P. Kabayi^d

^a Department of Crop Science, Makerere University, PO Box 7062, Kampala, Uganda

^b Program for Biosafety Systems, IFPRI – Kampala, PO Box 28565, Kampala, Uganda

^c Regional Universities Forum for Capacity Building in Agriculture, PO Box 7062, Kampala, Uganda

^d National Crops Resources Research Institute, PO Box 7084, Kampala, Uganda

ARTICLE INFO

Article history:

Received 12 February 2009

Received in revised form

18 August 2009

Accepted 19 August 2009

Keywords:

Lines

Rust tolerance index

Resistance

Phakopsora pachyrhizi

Yield

ABSTRACT

Soybean rust, (*Phakopsora pachyrhizi*), currently the most devastating disease of soybeans worldwide, is known to challenge single resistance genes deployed against it and therefore, disease tolerance is indisputably the most viable measure in controlling the pathogen. Studies were conducted at Namulonge in Central Uganda to assess the level of tolerance to soybean rust among selected elite soybean lines. Seven elite lines together with three local checks were tested in a split-plot design where some plots were protected with fungicide to estimate the level of tolerance to soybean rust. The experiment was conducted for three cropping seasons beginning second rains of 2005. A rust tolerance index (RTI) was computed for each test line as the ratio of yield from unprotected plots to yield from protected plots. The study showed that high levels of tolerance to soybean rust were present in the test lines. The soybean lines that showed high levels of tolerance included MNG 10.3 and MNG 3.26 all showing RTIs higher than 0.93. These lines also out-yielded the local checks by about 400 kg ha⁻¹ and are recommended for multi-location testing.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

Soybean, *Glycine max*, has been dubbed a crop of the future for sub-Saharan Africa for enhancing food security and incomes of rural households (Keyser and Li, 1992; Ogoke et al., 2003). The crop is important particularly for its high protein content (40%), high quality vegetable oil (20%) and its short growth period (McKeivith, 2005). Worldwide production of soybean is threatened by the Asian soybean rust, caused by *Phakopsora pachyrhizi* Sydow, a disease previously only known to the Orient. Soybean rust was first reported in Uganda in 1996 but has now spread to all soybean growing countries in Africa, South America and North America (Anon, 2001; Rossi, 2003; Levy, 2005; Schneider et al., 2005). The use of fungicides is effective against soybean rust but their use among resource poor farmers is limited due to associated high costs and technical knowledge limitations (Kawuki et al., 2004; Dorrance et al., 2007). Host plant resistance is the best long-term strategy for managing the disease in endemic areas as it provides the cheapest and most sustainable alternative.

Breeding for resistance to soybean rust is complicated by the aggressiveness of the rust pathogen. *P. pachyrhizi*, the causal agent

of soybean rust is known to have multiple virulence genes that are reported to challenge single resistance genes deployed to control the disease (Hartwig and Bromfield, 1983; Bromfield, 1984; AVRDC, 1992; Hartman, 1995; Oloka et al., 2008). As a consequence, soybean rust resistance breeding efforts now focus on other resistance mechanisms such as partial resistance (rate reducing resistance) and tolerance in the management of the disease. Partial resistance occurs in situations when the rate of rust development is slowed down in a particular genotype. Lines with partial resistance in field evaluations are rated as moderately resistant because few rust lesions (usually non-sporulating) develop on soybean plants in the course of crop growth and development (Hartman et al., 2005).

Rust tolerance, which is yielding ability under rust stress, is a strategy of selecting lines with high yield potential and less yield loss from soybean rust and the strategy is considered more durable than specific resistance since it eliminates chances of resistance break down (Kawuki et al., 2004; Hartman et al., 2005). Rust tolerance has been used in Asia to minimize losses attributed to soybean rust (AVRDC, 1992). The Department of Crop Science at Makerere University, Kampala and the National Agricultural Research Organisation, Uganda identified seven soybean lines in 2004 which showed high yields under severe rust pressure, suggesting good levels of tolerance to soybean rust in these materials under Namulonge conditions. The objectives of this study were to: (1) evaluate the level of tolerance to soybean rust among

* Corresponding author. Department of Crop Science, Makerere University, PO Box 7062, Kampala, Uganda. Tel.: +256 782 833786.

E-mail address: olokahk@agric.mak.ac.ug (Herbert K. Oloka).

selected elite soybean lines in Uganda, and (2) assess the potential of the elite lines in management of soybean rust in the tropics.

2. Materials and methods

An experiment was set up at the National Crops Resources Research Institute in Namulonge for three cropping seasons beginning second rains of 2005. Namulonge is located in central Uganda at 0° 32'N and 32° 37'E at an elevation of 1150 m above sea level. The area experiences a bimodal rainfall distribution (average total annual rainfall of 1100 mm) with a general wet and mild dry climate and slightly humid conditions (average 65% relative humidity). There was less rainfall (peak at 116 mm for the month of September 2005) in the second rains of 2005 than the first rains of 2006 (peak at 149 mm in April) while the second rains of 2006 had the highest rainfall amounts (peak at 232 mm in November 2006). Maximum temperatures for the two seasons of 2006 were comparable, averaging 28.5 °C while slightly higher maximum temperatures (average 30 °C) were observed during the second season of 2005.

A total of seven elite soybean lines, derived from crosses between a rust susceptible line (Duiker) and a rust resistant line (TGX 1835-10E), and three local checks were included in the study. The local checks were the moderately resistant cultivars Maksoy 1N and Namsoy 4M and a rust susceptible cultivar, Nam 1. The elite lines were selected for high yields under natural soybean rust pressure. Planting was done on 15 September 2005 for the second rains of 2005 (2005B), on 28 February 2006 for the first rains of 2006 (2006A) and on 15 September 2006 for the second rains of 2006 (2006B).

For each season, the test materials were established in a split-plot design with three replicates. Each entry was represented by three 5 m rows spaced 60 cm apart with an intra-row spacing of 5 cm. The main plots were the rust protected and unprotected treatments while the genotypes constituted the sub-plots. The highly rust susceptible check Nam 1 was planted around the test plots as a spreader line.

The rust protected plots were sprayed with the systemic fungicide *Score* (active ingredient *difenoconazole*) at 1 ml l⁻¹ at R3 growth stage (beginning of pod formation) and at R6 (full seed formation) (Tukamuhabwa et al., 2001). Fungicides were applied to enable computation of rust tolerance indices from yields of protected and unprotected plots. Rust assessment was conducted on the unprotected plots at growth stages R2 (full bloom), R4 (full pod) and at R6 (full seed) using a 0–9 severity scale modified from Kawuki et al. (2003) where 0 = no visible rust symptoms, and 1.0, 2.0, 3.0, 4.0, 5.0, 6.0, 7.0, 8.0 indicate 10% to 80% disease severity and 9 = 90% disease severity plus defoliation based on number and distribution of rust spots on leaves. At maturity, all plots were harvested, sun dried, threshed and seed yield per plot and moisture content established. Yield values from each plot were standardised to 12% moisture content and converted to yield per hectare.

Rust tolerance was quantified using the rust tolerance index (RTI) computed from:

$$RTI = \frac{\text{Yield from rust unprotected plots}}{\text{Yield from rust protected plots}}$$

(Adapted from Kawuki et al., 2003).

Results for each season were analysed separately and also combined over seasons. Rust tolerance indices, rust severities and seed yield were subjected to analysis of variance (ANOVA) in Genstat 9th Edition (Lawes Agricultural Trust, Rothamstead, UK) to test for differences in rust reaction and yield among the test materials. Rust severities were angular transformed in order to

normalise the data prior to ANOVA (Sokal and Rohlf, 1995). Lines with RTIs higher than susceptible checks were categorised as rust tolerant materials. Mean RTIs and seed yield were separated using Least Significant Difference (LSD) of means at the 5% level of significance.

3. Results

3.1. Rust severities on test lines

During the three seasons, no rust symptoms were observed on any plot at growth stage R2. Variations were observed in rust severity ($P < 0.001$) among the test lines except at growth stage R4 during 2005B and 2006A (Table 1). During 2005B, at R4, rust was observed on many lines except MNG 8.24, Maksoy 1N and MNG 9.17. Highest rust severity was observed on line MNG 3.26. At R6, rust severity increased considerably in all test lines. The lowest rust severities were observed in lines MNG 10.3, Maksoy 1N, Namsoy 4M and MNG 4.19 while Nam 1 had the highest rust severity.

During 2006A, at R4, rust lesions were observed from only five test lines. The susceptible local check, Nam 1 also showed no rust lesions at this stage. The highest rust severities were observed in lines MNG 3.26 and MNG 8.24. At R6, differences ($P < 0.001$) were observed in reaction to rust among the test lines. The lowest rust severities were observed in line MNG 10.3 and in the cultivars Maksoy 1N and Namsoy 4M while the highest rust scores were observed in the susceptible check, Nam 1 and in lines MNG 9.17 and MNG 8.6(B).

During 2006B, at R4, no rust symptoms were observed on lines MNG 8.24, MNG 10.3, MNG 4.19, and on the cultivars Maksoy 1N and Namsoy 4M. There were differences in rust reaction ($P < 0.001$) among the test lines at both R4 and R6 growth stages. Lines that showed very high rust scores at R6 included MNG 9.17, Nam 1, MNG 8.6(B) and MNG 8.22 with mean rust score of over 7.0.

Across seasons, the lowest rust severities at R6 were observed on lines MNG 10.3, MNG 8.24, MNG 4.19 and in the cultivars Maksoy 1N and Namsoy 4M. The susceptible check, Nam 1 and line MNG 8.6(B) showed the highest rust severity. Rust was more severe, though not significant, during the two cropping seasons of 2006 than during the second rains of 2005.

3.2. Effect of rust control on yield

The application of the systemic fungicide, *Score* on soybean lines improved the yield ($P < 0.05$) of soybean during the three cropping

Table 1

Rust severities on test soybean lines under natural *Phakopsora pachyrhizi* infection at Namulonge, Uganda during growing seasons beginning with second rains of 2005 (2005B), first rains of 2006 (2006A), and second rains of 2006 (2006B).

Line	Rust severity (0–9 scale)							
	2005B		2006A		2006B		Mean	
	R4	R6	R4	R6	R4	R6	R4	R6
MNG 8.24	0.0	2.5	1.0	3.2	0.0	2.3	0.33	2.7
MNG 8.22	0.3	3.2	0.0	5.2	5.0	8.7	1.8	5.7
MNG 10.3	0.3	2.0	0.3	2.8	0.0	0.0	0.22	1.6
MNG 8.6(B)	0.3	5.3	0.0	6.2	4.5	8.7	1.6	6.7
Maksoy 1N	0.0	2.0	0.3	1.7	0.0	0.0	0.11	1.2
Nam 1	0.3	6.2	0.0	6.8	4.3	7.7	1.6	6.9
Namsoy 4M	0.3	2.0	0.0	1.7	0.0	1.3	0.11	1.7
MNG 3.26	1.2	4.7	1.3	4.8	3.7	6.2	2.1	5.2
MNG 4.19	0.5	2.0	0.0	4.0	0.0	2.3	0.17	2.8
MNG 9.17	0.0	3.5	0.3	6.5	2.8	7.2	1.1	5.7
Mean	0.33	3.33	0.33	4.28	2.03	4.43	0.90	4.02
F-prob ^a	0.306	<0.001	0.236	<0.001	<0.001	<0.001	<0.001	<0.001

^a ANOVA was carried out on angular transformed values.

seasons (Table 2). The overall increase in yield with fungicide application was 125 kg ha^{-1} . A combined ANOVA (all seasons) showed differences in mean yields ($P < 0.001$) among test lines and among seasons. In 2005B, the highest yielding line without rust protection was MNG 10.3 while lowest yields were observed from Nam 1 and Namsoy 4M (Table 3). With rust protection, the highest yields were observed from lines MNG 8.22 and MNG 10.3.

In 2006A, the highest yielding lines without rust protection included MNG 10.3 and MNG 3.26. The lowest yields were observed from lines MNG 9.17 and Nam 1 ($P < 0.001$). With rust protection in 2006A, the highest yields were observed in lines MNG 8.24, MNG 3.26 and MNG 4.19. The highest yield improvements ($P = 0.06$) with fungicide application were observed from lines MNG 4.19 and Nam 1 where seed yield increased by 15% and 18% respectively. During this season, fungicide application increased the overall mean yield by only 38 kg ha^{-1} .

During 2006B, highest yields ($P = 0.021$) without rust protection were observed from lines MNG 4.19, Maksoy 1N and Namsoy 4M (Table 3). Lowest yields were observed from Nam 1 and MNG 8.22. With rust protection, the highest yielding lines included MNG 4.19 and MNG 9.17, while the lowest yields were observed from lines Nam 1 and Maksoy 1N. Line MNG 8.22 showed the greatest yield increase of over 47% when the systemic fungicide score was applied. Fungicide application improved ($P < 0.001$) the overall mean yield of the test lines by 253 kg ha^{-1} , representing a 15% yield improvement.

Over the three seasons, 2006B yielded more ($P < 0.001$) than 2006A and 2005B (Table 3). Without rust protection, the highest yields were obtained from lines MNG 10.3, MNG 3.26 and Maksoy 1N while Nam 1 and MNG 9.17 had the lowest mean yields of less than 1100 kg ha^{-1} . The highest yielding lines when rust was controlled were MNG 10.3, MNG 4.19 and MNG 8.22. The application of fungicide improved yield of the soybean lines by 9.4% over the three seasons.

3.3. Rust tolerance indices for elite soybean lines

During the three seasons of testing, the elite soybean lines showed differing levels of rust tolerance but the differences in mean rust tolerance indices were not significant at the 5% level during 2005B and 2006A. Differences ($P < 0.05$) were, however, observed during 2006B (Table 3). During 2005B, one test line, MNG 4.19 responded negatively to rust protection using the systemic fungicide Score. Similarly two moderately rust resistant local

checks, Maksoy 1N and Namsoy 4M, responded negatively to rust control, with reduced yields when fungicide was applied, in 2006A and 2006B. Soybean lines which yielded nearly as high without rust protection included MNG 10.3 and MNG 8.6(B) (Table 3).

In 2006A, only two test lines, MNG 8.24 and MNG 4.19, and the susceptible check Nam 1 responded positively to rust protection. Lines that showed high tolerance to soybean rust included MNG 3.26 and MNG 8.24 that showed RTIs of over 0.97. The lowest RTIs were observed from lines MNG 8.22, MNG 9.17 and MNG 8.6(B) that showed RTI values of < 0.73 . Across seasons, the checks Maksoy 1N and Namsoy 4M responded negatively to rust protection using fungicides (Table 3). Highly rust tolerant lines included MNG 10.3, and MNG 3.26 which showed RTI values greater than 0.92, implying a less than 8% yield loss under rust infestation.

3.4. Relationship between rust severity and seed yield

The yield of soybean lines was reduced with increases in rust severity (Fig. 1). Relative yield (measured as seed yield from unprotected plots expressed as a percentage of seed yield from rust protected plots) decreased with increasing rust severity at R6. Combined results for the three seasons were best described by a simple linear regression model that explained 23% of the variation ($P < 0.05$) observed.

4. Discussion

Disease tolerance has been used in the Orient to manage soybean rust (AVRDC, 1992; Shanmugasundram et al., 2004). Results of our experiments confirmed that soybean rust incidence was very high at Namulonge, making the location a hotspot for soybean rust evaluations in Uganda. The incidence and severity of soybean rust on test lines was comparable between the two cropping seasons of 2006 but were lower during 2005B. The differences resulted from very limited rainfall and high temperatures during 2005B that hindered soybean rust development. Studies by Kawuki et al. (2003) demonstrated that rust severity was influenced by seasons. Soybean rust development and spread is known to be influenced by moisture, relative humidity and temperature, with high relative humidity and moderate temperatures favouring rapid pathogen multiplication and spread (Hartman et al., 2003). Temperatures above 28°C , as observed during 2005B, are known to reduce soybean rust lesion development in the field (Wang and Hartman, 1992).

The soybean lines that showed consistently low rust scores (< 3.0) at full seed stage (R6) over the three seasons included MNG 10.3, Maksoy 1N, and Namsoy 4M. The two moderately resistant local checks showed greater resistance to soybean rust than all the other test lines. This is due to the genetic background in these two lines which has been confirmed to possess partial resistance to soybean rust (Kiryowa et al., 2005). The materials being tested were selected particularly for their yield potential under severe rust pressure and not for resistance to soybean rust during field observations at Namulonge.

P. pachyrhizi is known to infect soybean at any growth stage (Hartman et al., 2003), but during the three seasons of testing, rust was not observed at flowering (R2) in Namulonge because the inoculum pressure at R2 was insufficient to cause disease on any line during the three seasons. According to Hartman et al. (2003), the rate of rust development under field conditions is related to the physiological age of the plant, with rapid increases in lesion numbers occurring during the onset of flowering and progressively increasing up to maturity depending on micro-climatic conditions. This explains the increase in lesion density (recorded as rust scores) among test lines from R2 through to R4 and R6 growth stages.

Table 2
ANOVA for effect of fungicide application on yield of elite soybean lines during three seasons of testing at Namulonge.

Source of variation	Degrees of freedom	Sums of squares	Mean square	Variance ratio	F-prob.
Block	2	423 796	211 898	35.07	
Block $\times$ fungicide stratum					
Fungicide	1	699 301	699 301	115.73	0.009
Residual	2	12 085	6042	0.14	
Block $\times$ fungicide $\times$ genotype stratum					
Genotype	9	4 187 847	465 316	10.93	< 0.001
Fungicide $\times$ genotype	9	1 005 733	111 748	2.62	0.019
Residual	36	1 533 041	42 584	0.76	
Block $\times$ fungicide $\times$ genotype stratum					
Season	2	31 483 171	15 741 586	279.34	< 0.001
Fungicide $\times$ season	2	384 824	192 412	3.41	0.037
Genotype $\times$ season	18	4 296 984	238 721	4.24	< 0.001
Residual	98	5 522 637	56 353		
Total	179	49 549 418			

Table 3

Yield of elite soybean lines and rust tolerance indices during three seasons of testing at Namulonge, Uganda.

Line	Mean yield (kg ha ⁻¹)								Rust tolerance index			
	Unprotected				Rust protected							
	2005B	2006A	2006B	Mean	2005B	2006A	2006B	Mean	2005B	2006A	2006B	Mean
MNG 8.24	870	1657	1796	1441	1019	1851	1880	1583	0.86	0.92	0.97	0.92
MNG 8.22	852	1702	1407	1320	1176	1679	2074	1643	0.72	1.05	0.68	0.82
MNG 10.3	1019	1831	1556	1468	1065	1749	2130	1648	0.99	1.06	0.75	0.93
MNG 8.6(B)	852	1560	1537	1316	926	1550	2130	1535	0.99	1.01	0.72	0.91
Maksoy 1N	852	1628	1889	1456	843	1442	1426	1237	1.08	1.17	1.35	1.20
Nam 1	519	1231	1278	1009	713	1457	1352	1174	0.73	0.86	0.97	0.85
Namsoy 4M	519	1331	1981	1277	491	1353	1889	1244	1.18	1.00	1.07	1.08
MNG 3.26	796	1847	1722	1455	824	1848	1796	1489	0.97	1.00	0.97	0.98
MNG 4.19	778	1580	2000	1453	759	1822	2352	1644	1.03	0.88	0.85	0.92
MNG 9.17	685	923	1593	1067	759	918	2259	1312	0.92	1.08	0.70	0.90
Mean	774	1529	1676	1326	857	1567	1929	1451	0.95	1.00	0.90	0.95
LSD _{5%}	238.5	348.1	413.9	192.8	268.8	431.6	411.2	224.0	NS ^a	NS	0.31	0.22
CV%	18.0	13.3	14.4	15.4	18.3	16.1	12.4	16.4	28.8	24.0	20.2	25.0
F-prob	0.007	<0.001	0.021	<0.001	0.002	0.006	<0.001	<0.001	0.589	0.877	0.006	0.050

^a NS – not significant at the 5% probability level.

Differences in rust reaction at R4 were insignificant at the 5% level during 2005B and 2006A but were significant during 2006B. This suggests that the inoculum levels at R4 during 2005B and 2006A were too low to cause severe rust infestation on the susceptible soybean lines. At R6, the lines clearly showed differences in reaction to soybean rust, with highly significant differences in response to rust infection during the three cropping seasons confirming that R6 is the best growth stage for assessing soybean rust severities in Uganda.

Many of the test lines showed high rust tolerance indices compared to the susceptible local check Nam 1. This finding is important as it is evidence of the presence of high levels of rust tolerance among some of the test lines. Specifically, lines MNG 10.3 and MNG 3.26 are suitable candidates for on-farm and multi-location evaluation as rust tolerant cultivars. These lines out-yielded the moderately resistant local checks, Maksoy 1N and Namsoy 4M by over 400 kg ha⁻¹, in some cases, with or without rust protection. Adoption of these lines would significantly boost soybean yields in Uganda that have been affected by soybean rust epidemics. Rust tolerance indices greater than 0.9 imply yield losses of less than 10%, that may be acceptable if the actual yield under rust pressure is optimal (>2000 kg ha⁻¹) (Kawuki et al., 2003, 2004). Soybean lines that yield high under severe rust pressure can also be used as parental lines in future rust tolerance breeding programmes. The study also showed that at times application of

fungicides lowers yields of resistant lines such as Maksoy 1N and Namsoy 4M. These findings are consistent with the report by Tukamuhabwa et al. (2001) who also observed the same while working with other soybean lines. The mechanism for this observation is not yet well understood.

Regression analysis of yield against disease severity showed that yield decreases as rust severity increases. The relationship observed was weak but this is not surprising as yield is influenced by several factors during any given planting season. The trend is however consistent with findings from Pataky et al. (1998) who observed that yield of maize was negatively correlated to northern corn blight severity. Models from such analyses, if significant, can be used to estimate disease severities at which chemical control measures should be applied to avert economically significant yield losses (Gaunt, 1995).

Therefore, countries in which soybean rust have become endemic should pursue disease tolerance as a more appropriate management method against soybean rust as tolerance is durable and farmers are guaranteed stable yields despite high instances of rust in their locations. The elite lines evaluated in Uganda clearly showed that soybean yields in the country can be improved using rust tolerant cultivars rather than cultivars constituted of single resistance genes, where resistance break down is very likely.

Acknowledgments

The authors are grateful to the Regional Universities Forum for Capacity Building in Agriculture that funded the research. We also thank Makerere University and the National Agricultural Research Organisation for providing fields and facilities used in this study.

References

- Anonymous, 2001. Soybean Rust Disease: a Report to the National Agricultural Research Organisation. Uganda Seed Project, Kampala, Uganda.
- AVRDC, 1992. Annotated Bibliography of Soybean Rust (*Phakopsora pachyrhizi* Sydow). Library Bibliography series 4–1. Tropical Vegetable Information Service, Asian Vegetable Research and Development Center.
- Bromfield, K.R., 1984. Soybean Rust. Monograph No. 11. The American Phytopathological Society, St. Paul, MN.
- Dorrance, A.E., Draper, M.A., Hershman, D.E. (Eds.), 2007. Using Foliar Fungicides to Manage Soybean Rust. Land-Grant Universities Cooperating NCERA-208 and OMAF.
- Gaunt, R.E., 1995. The relationship between plant disease severity and yield. Annu. Rev. Phytopathol. 33, 119–144.
- Hartman, G.L., 1995. Highlights of soybean rust research at the Asian Vegetable Research and Development Center. In: Sinclair, J.B., Hartman, G.L. (Eds.),

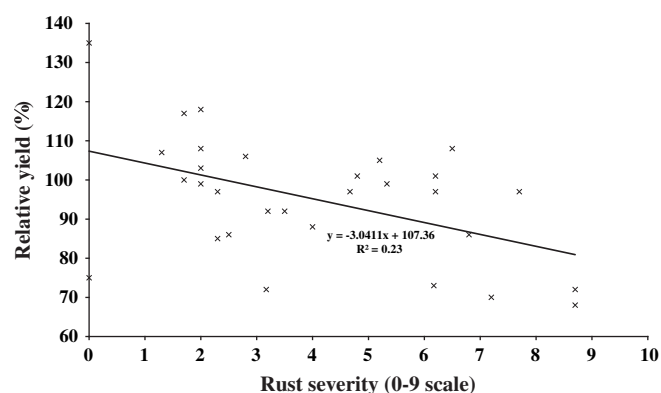


Fig. 1. Variation of relative yield (yield of non-protected plots expressed as a percentage of yield from protected plots) with rust severity at growth stage R6 during three seasons of testing at Namulonge, Uganda.

- Proceedings of the Soybean Rust Workshop, 9–11 Aug. 1995. College of Agricultural, Consumer, and Environmental Sciences, National Soybean Research Laboratory, Urbana, IL, pp. 19–28.
- Hartman, G.L., Miles, M.R., Frederick, R.D., 2003. Epidemiology and spread of soybean rust. In: 2003 Corn & Sorghum and Soybean Conference. American Seed Trade Association Pub. No. 33.
- Hartman, G.L., Miles, M.R., Frederick, R.D., 2005. Breeding for resistance to soybean rust. *Plant Dis.* 89, 664–666.
- Hartwig, E.E., Bromfield, K.R., 1983. Relationships among three genes conferring specific resistance to rust in soybeans. *Crop Sci.* 23, 237–239.
- Kawuki, R., Adipala, E., Tukamuhabwa, P., 2003. Yield loss associated with soya bean rust (*Phakopsora pachyrhizi* Syd.) in Uganda. *J. Phytopathol.* 151, 7–12.
- Kawuki, R., Tukamuhabwa, P., Adipala, E., 2004. Soybean rust severity, rate of rust development, and tolerance as influenced by maturity period and season. *Crop Prot.* 23, 447–455.
- Keyser, H.H., Li, F., 1992. Potential for increasing biological N fixation in soya bean. *Plant Soil* 141, 119–135.
- Kiryowa, M., Tukamuhabwa, P., Adipala, E., 2005. Inheritance of resistance to soybean rust. *Afr. Crop Sci. Conf. Proc.* 7, 257–260.
- Levy, C., 2005. Epidemiology and chemical control of soybean rust in southern Africa. *Plant Dis.* 89, 669–674.
- McKevith, B., 2005. Nutritional aspects of oilseeds. *Nutr. Bull.* 30, 13–26.
- Ogoke, I.J., Carskey, R.J., Togun, A.O., Dashiell, K.E., 2003. Maturity class and P effects on soya bean grain yield in the moist savanna of west Africa. *J. Agron. Crop Sci.* 189, 422–427.
- Oloka, H.K., Tukamuhabwa, P., Sengooba, T., Shanmugasundram, S., 2008. Reaction of exotic soybean germplasm to *Phakopsora pachyrhizi* in Uganda. *Plant Dis.* 92, 1493–1496.
- Pataky, J.K., Raid, R.N., du Toit, L.J., Schueneman, T.J., 1998. Disease severity and yield of sweet corn hybrids with resistance to northern leaf blight. *Plant Dis.* 82, 57–63.
- Rossi, R.L., 2003. First report of *Phakopsora pachyrhizi*, the causal organism of soybean rust in the province of Misiones, Argentina. *Plant Dis.* 87, 102.
- Schneider, R.W., Hollier, C.A., Whitam, H.K., Palm, M.E., McKemy, J.M., Hernandez, J.R., Levy, L., DeVries-Paterson, R., 2005. First report of soybean rust caused by *Phakopsora pachyrhizi* in the continental United States. *Plant Dis.* 89, 774.
- Shanmugasundram, S., Yan, M.R., Wang, T.C., 2004. Breeding for soybean resistance in Taiwan. In: Moscardi, et al. (Eds.), *Proc. VII World Soybean Research Conf., IV International Soybean Processing and Utilization Conference, III Congresso Brasileiro de Soja* (Brazilian Soybean Congress), Embrapa Soybean, Londrina, pp. 456–462.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry, the Principles and Practice of Statistics in Biological Research*, third ed. W.H. Freeman and Company, New York, pp. 419–422.
- Tukamuhabwa, P., Dashiell, K.E., Assafo-Adjei, B., 2001. Determination of yield loss caused by soybean rust (*Phakopsora pachyrhizi* Syd.) in four genotypes of soybeans. *Afr. Crop Sci. Conf. Proc.* 5, 423–426.
- Wang, T.C., Hartman, G.L., 1992. Epidemiology of soybean rust and breeding for host resistance. *Plant Prot. Bull.* 34, 109–124.