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Soybean rust severity, rate of rust development, and tolerance as influenced by maturity period and season

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Abstract

Studies were conducted in Uganda for three consecutive seasons to evaluate soybean lines of different maturation periods against rust. All the lines were highly susceptible to rust with only two lines graded as moderately resistant: TGx 1835-10E (early maturing) and TGx 1838-5E (late maturing). These two lines were consistently associated with non-sporulating lesions. Within each maturation group, soybean lines differed significantly in rates of rust development (RRDs), rust severities at R6 growth stage, and yielding ability under rust stress. Most of the lines had RRDs higher than the local check. However, it was only the early maturing lines that yielded higher than the local check. Higher levels of rust tolerance were observed in the early maturing lines (yields >1000 kg/ha), and lowest in late maturing lines (yields <500 kg/ha). Most variation in yields was due to differences among soybean lines, except the late and medium maturing lines were it was due to seasonal variation. Most variation in RRDs was due to the seasons and not soybean lines, and rust severity increased with crop age.

Keywords: Maturity period; Rust tolerance; Soybean; Uganda

1. Introduction

Soybean rust (*Phakopsora pachyrhizi* Sydow) has been known in the Orient since 1914 (Baker, 1914), where it has caused significant yield reductions (Bromfield, 1984). To date, soybean rust is the most devastating disease of soybean in tropical and sub-tropical areas (AVRDC, 1992). Soybean plants are susceptible to the fungus at all growth stages (GSs) (Hsu and Wu, 1968; Bromfield, 1976). However, attack at flowering (Ogle et al., 1979) and pod filling stage (Shin, 1986), which is commonly observed in soybean fields, is more yield reducing. Currently, Uganda is experiencing a soybean rust epidemic. The disease was first observed in 1996 on experimental plots at Namulonge Agricultural and Animal Production Research Institute (NAARI), and thereafter on farmers' fields throughout the country. All commercial varieties are highly susceptible recording yield losses as high as 40% (Kawuki et al., 2003). Unfortunately, even the few breeding lines available in the local germplasm are highly susceptible to rust (Tukamuhabwa et al., 2001).

Elsewhere, host plant resistance has been used to control soybean rust (AVRDC, 1992). Both rate-reducing and race-specific resistances have been identified, but with no immune cultivars developed so far (Tschanz et al., 1985; AVRDC, 1992). Specific resistance to soybean rust is characterized by limited pathogen development and sporulation (Singh and Thapliyal, 1977). Unfortunately, the identified sources of specific resistance are known to be challenged by at least one known isolate of *P. pachyrhizi* (Hartwig and Bromfield, 1983; Bromfield, 1984), thus making it unsustainable. Rate-reducing resistance to soybean rust was identified and confirmed at the Asian Vegetable Research and Development Centre (Tschanz and Wang, 1980); rate-reducing resistance slows down the rate of disease development and is usually effective against most races of the pathogen. However, quantification of rate-reducing resistance is somewhat difficult, and thus limits its identification and usage (Bromfield, 1984).

Difficulties associated with both race-specific and rate-reducing resistances have led to identification of new methods (rust tolerance) that can be used to

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minimize yield losses. Tolerance to rust, defined as relative yielding ability of soybean under rust stress (Tschanz et al., 1985), has been identified and used to minimize yield losses associated with soybean rust (Tschanz and Tsai, 1983). Considering the increasing threat of soybean rust in Uganda and eastern African region at large, and the apparent lack of resistant or tolerant soybean cultivars in the country, it is necessary to screen soybean materials from elsewhere for possible sources of resistance or tolerance. Thus, the objective of this study was to screen introduced soybean lines against rust.

2. Materials and methods

The trials were set up at NAARI in central Uganda, where severe rust epidemics have been experienced (Kawuki et al., 2003). The trials were conducted for three consecutive seasons, second rains 2000 (October–January 2001), first rains 2001 (March–June), and second rains 2001 (October 2001–January 2002). During the growing seasons, maximum (27.5 ± 1°C) and minimum (15.5 ± 0.6°C) temperatures were similar. Within each season total rainfall amounts were similar, but with varying peak periods. During 2000B and 2001B highest rainfall amounts were in September with corresponding totals of 141 and 210 mm, respectively. However, during 2001A highest rainfall amounts were in May with a total of 225 mm. The test lines were 51 advanced selections from the International Institute of Tropical Agriculture (IITA), and comprised 21 early maturing (85–99 days to maturity), 22 medium maturing (100–110 days to maturity), and 8 late maturing (110–121 days to maturity) lines. Pedigree information of these materials is presented in Table 1. These soybean lines were not bred specifically for rust, they were bred and selected for adaptability in tropical Africa by the IITA, and this was their first evaluation against rust in Africa. Nam 2, which is highly susceptible to rust, was included as a local check.

The experiment layout was a randomized complete block design with three replicates. Spacing between and within rows was $60\times5\,\text{cm}^2$, respectively, with a plot size of two rows measuring 5 m. Two rows of Nam 2 were sown between test lines to increase the air-borne inoculum. All the test lines were planted on the same date, and were kept weed-free by regular hand hoeing. Rust was established by natural epidemics.

At on-set of the disease (reproductive phase) disease assessments were made using both the three digit International Working Group of Soybean Rust scale (IWGSR), and a 0–9 percentage severity scale, where 0 = no disease and 9 = 90% disease plus defoliation (Walla, 1979; cited by Sinclair, 1982). The 0–9 scale was used to determine quantitative scores for computation of rates of rust development (RRDs). For each assessment the GS of the crop was determined following Fehr and Caviness (1977) to guard against the variation in crop susceptibility arising from the variation in the crop physiological age. Since rust severity varies across the plant canopy positions (Kitani, 1952; Omar and Ismail, 1982), each assessed plant was divided into three canopy positions (top, middle and bottom), with approximately the same number of nodes. A unifolioliate leaf at each of these plant positions was assessed for rust severity (percentage of leaf surface occupied by rust lesions). This was done on six randomly selected plants. Where unifolioliates were missing due to defoliation, 90% severity was recorded. The mean leaf severities at the top, middle and bottom canopy positions were then computed. All rust assessments were done on the lower leaf surface where lesions are abundant and very clear. A hand lens ($\times 20$) was used to distinguish between sporulating and non-sporulating lesions. The assessed leaf was considered sporulating when over 50% of the observed lesions were sporulating, and it was considered non-sporulating when over 50% of the observed lesions were not sporulating. In total four rust severity assessments were made each season.

RRDs were computed by a linear regression using the logits (transformed mean rust severity at top, middle, and bottom plant canopy positions), and the relative lifetime (RLT) of the crop as the time element:

$$\text{RLT} = \frac{\text{DAP}\times 100}{\text{DTFM}},$$

where DAP are the days after planting; DTFM the days to full maturity.

The RLT was used instead of the DAP to partially compensate for the differences in maturation dates of the lines, which influences their rust susceptibility (AVRDC, 1992). The RLT indicates the percentage of soybean cycle that has been completed on a particular date. The regression coefficient (slope) is the RRD (Tschanz et al., 1985).

At GS R6 lines were categorized as immune, moderately resistant, moderately susceptible, or highly susceptible basing on their rust reaction; the IWGSR scale was used grade the lines. The description of the rust reaction grade is presented in Table 2. GS R6 corresponds to time when soybean leaves are severely infected by rust (AVRDC, 1988a), and when significant differences in rust severity are observed between susceptible and partially resistant soybean cultivars (Hartman et al., 1991). Therefore, rust reaction at this stage is indicative of its level of resistance or susceptibility. Days to maturity (R8) were recorded for each line. At harvest, 1 m was measured off from both ends of the plots, and thereafter, all the plants in the remaining 3 m rows were harvested, sun-dried, and manually threshed. For each plot, seed moisture content (MC)

Table 1
Pedigree of soybean germplasm used in the study

Entry	Cross	Origin
TGx 1740-2E	TGx 539-5E × Sibley	IITA-Nigeria/USA
TGx 1897-17F	TGx 1809-12E × TGx 1740-6F	IITA-Nigeria/IITA-Nigeria
TGx 1485-1D	TGx 316-024D × TGx 813-11D	IITA-Nigeria/IITA-Nigeria
TGx 1805-8F	TGx 1486-1D × TGx 1492-99D	IITA-Nigeria/IITA-Nigeria
TGx 1830-20E	TGx 1483-3D × TGx 1448-1E	IITA-Nigeria/IITA-Nigeria
TGx 1835-10E	TGx 1213-1D × TGx 1445-3E	IITA-Nigeria/IITA-Nigeria
TGx 1876-4E	TGx 1660-19Fx TGx 1740-6F	IITA-Nigeria/IITA-Nigeria
TGx 1895-4F	TGx 1814-3E × TGX 1740-6F	IITA-Nigeria/IITA-Nigeria
TGx 1831-32E	TGx 1566-2E × TGx 1446-3E	IITA-Nigeria/IITA-Nigeria
TGx 1895-6F	TGx 1814-3E × TGX 1740-6F	IITA-Nigeria/IITA-Nigeria
TGx 1871-12E	TGx 1740-6F × TGx 1660-15F	IITA-Nigeria/IITA-Nigeria
TGx 1895-23F	TGx 1814-3E × TGX 1740-6F	IITA-Nigeria/IITA-Nigeria
TGx 1892-10F	BR 839240 × TGx 1740-6F	Brazil/IITA-Nigeria
TGx 1895-19F	TGx 1814-3E × TGX 1740-6F	IITA-Nigeria/IITA-Nigeria
TGx 1895-22F	TGx 1814-3E × TGX 1740-6F	IITA-Nigeria/IITA-Nigeria
TGx 1888-15F	TGx 1786-6F × BR 839240	IITA-Nigeria/Brazil
TGx 1894-3F	TGx 1814-3E × TGx 1740-6F	IITA-Nigeria/IITA-Nigeria
TGx 1882-2F	TGx 923-2E × TGx 1479-1E	IITA-Nigeria/IITA-Nigeria
TGx 1869-31E	TGx 1448-2E × TGx 1660-15F	IITA-Nigeria/IITA-Nigeria
TGx 1880-3E	TGx 1681-3F × TGx 1479-1E	IITA-Nigeria/IITA-Nigeria
TGx 1842-1E	TGx 1458-2E × TGx 1440-1E	IITA-Nigeria/IITA-Nigeria
Medium		
TGx 1805-31F	TGx 1486-1D × TGx 1492-99D	IITA-Nigeria/IITA-Nigeria
TGx 1895-50F	TGx 1814-3E × TGX 1740-6F	IITA-Nigeria/IITA-Nigeria
TGx 1888-15F	TGx 1786-6F × BR 839240	IITA-Nigeria/Brazil
TGx 1873-16E	TGx 1681-3F × TGx 1448-2E	IITA-Nigeria/IITA-Nigeria
TGx 1802-3F	TGx 1213-1D × TGx 1483-3D	IITA-Nigeria/IITA-Nigeria
TGx 1878-7E	TGx 1681-3F × TGx 1740-6F	IITA-Nigeria/IITA-Nigeria
TGx 1893-7F	TGx 1814-3E × TGx 1740-6F	IITA-Nigeria/IITA-Nigeria
TGx 1019-2EN	TGM 1551 × TGx 536-100C	IITA-Nigeria/IITA-Nigeria
TGx 1890-7F	TGx 1740-6F × BR 839240	IITA-Nigeria/Brazil
TGx 1802-1F	TGx 1213-1D × TGx 1483-3D	IITA-Nigeria/IITA-Nigeria
TGx 1866-33F	TGx 1447-1D × TGx 1479-2D	IITA-Nigeria/IITA-Nigeria
TGx 1891-3F	TGx 1660-19F × BR 839240	IITA-Nigeria/Brazil
TGx 1893-10F	TGx 1814-3E × TGx 1740-6F	IITA-Nigeria/IITA-Nigeria
TGx 1893-6F	TGx 1814-3E × TGx 1740-6F	IITA-Nigeria/IITA-Nigeria
TGx 1896-3F	TGx 1807-19E × TGx 1740-6F	IITA-Nigeria/IITA-Nigeria
TGx 1844-18E	TGx 1449-2D × TGx 1440-1E	IITA-Nigeria/IITA-Nigeria
TGx 1440-1E	TGx 536-02D × TGx 814-27D	IITA-Nigeria/IITA-Nigeria
TGx 1448-2E	TGx 824-18D × TGx 814-27D	IITA-Nigeria/IITA-Nigeria
TGx 1889-12F	TGx 1674-3F × BR 839240	IITA-Nigeria/Brazil
TGx 1866-12F	TGx 1447-1D × TGx 1449-2D	IITA-Nigeria/IITA-Nigeria
TGx 1895-33F	TGx 1814-3E × TGX 1740-6F	IITA-Nigeria/IITA-Nigeria
TGx 1895-49F	TGx 1814-3E × TGX 1740-6F	IITA-Nigeria/IITA-Nigeria
Nam 2 Local Check	87D-668	Nigeria
Late maturing		
TGx 1869-13E	TGx 1448-2E × TGx 1660-15F	IITA-Nigeria/IITA-Nigeria
TGx 1886-38F	TGx 180912E × BR 839240	IITA-Nigeria/Brazil
TGx 1844-4E	TGx 1449-2D × TGx 1440-1E	IITA-Nigeria/IITA-Nigeria
TGx 1866-7F	TGx 1447-1D × TGx 1449-2D	IITA-Nigeria/IITA-Nigeria
TGx 1848-10E	TGx 1479-1E × TGx 1449-2D	IITA-Nigeria/IITA-Nigeria
TGx 1895-35F	TGx 1814-3E × TGX 1740-6F	IITA-Nigeria/IITA-Nigeria
TGx 923-2E	TGx 17-2GE × TGx 849	IITA-Nigeria/IITA-Nigeria
TGx 1838-5E	TGx 1213-1D × TGx 1489-1D	IITA-Nigeria/IITA-Nigeria

Note: Most of the lines were derived from the same population/crosses. For example, TGx 1895 lines have the same parents; the numeric numbers that follow indicates the chronological order in which the lines were selected. The alphabetic letters indicate filial generation when lines were selected.

Table 2
Rust reaction grade at full seed formation

Reaction grade	Description[a]
I = immune	No lesions on leaves
MR = moderately resistant	No lesions on top leaves, few sporulating lesions on middle and bottom leaves Medium to heavy non-sporulating lesions on all leaves
MS = moderately susceptible	Medium number of sporulating lesions on top leaves, coupled with a heavy sporulating lesion density on middle and bottom leaves Defoliation limited to bottom leaves
HS = highly susceptible	Heavy sporulating lesion density on the leaves, coupled with extensive defoliation of middle and bottom leaves

[a] B basing on second digit IWGSR scale: 1.1–1.9 = few lesions; 2–2.9 = medium lesion number; >3 = heavy lesion number.

was determined from a 100 g sample using a Steinlite moisture tester (Steinlite model 400-G tester, Stein Laboratories Inc., Kansas), and thereafter yields adjusted to 13% (MC) using the formula:

$$\text{yield (kg/ha)} = \frac{\text{plot yield (kg)} \times 10,000}{\text{harvested area (m}^2\text{)}} \times \frac{100\%\ \text{MC}}{87}.$$

Disease and yield data were analyzed separately per season. Combined analysis of variance over the three seasons was also done to get the season × genotype interaction. For each maturation group, pooled rust severity (across the three seasons) at R6 were regressed on pooled yield data (across the three seasons). Means were separated using the least significant difference. These analyses were done using Genstat Computer software (Lawes Agricultural Trust, 1995). To compare the performance of the three maturity groups, which differed in number of entries, data were subjected to generalized linear modelling using Statistical Analysis System (SAS, 1993).

3. Results

3.1. Rates of rust development, severity and reaction at full seed formation

Results of rust reaction, percentage rust severity and RRDs on soybean germplasm are presented in Table 3. At R6 GS, only two lines, TGx 1835-10E (early maturing) and TGx 1838-5E (late maturing), were graded as moderately resistant. All the other lines were either moderately susceptible (MS) or highly susceptible (HS). Most lines were however graded as highly susceptible during 2001A, when they were severely defoliated (Table 3). A few lines: TGx 1485-1D, TGx 1831-12E (early maturing); TGx 1844-18E, TGx 1866-12F, TGx 1802-3F (medium maturing); and TGx 1844-4E, TGx 923-2E (late maturing), were consistently graded as highly susceptible.

Within each maturation group, percentage rust severities significantly differed among the soybean lines (Table 3). Lowest rust severities within early, medium, and late maturation groups were recorded on TGx 1835-10E (29.4%), TGx 1893-7F (42.1%), and on TGx 1838-5E (42.6%), respectively (Table 3). However, the highest severities were recorded TGx 1485-1D (69.2%), TGx 1844-18E (76.8%), and TGx 923-2E (77.4%), respectively. Results further showed that early and medium maturing soybean lines only registered significantly lower rust severities than the late maturing during 2000B and 2001A (Table 4). On average, early maturing lines registered the lowest severity (54%), followed by medium maturing lines (61%), and then the late maturing lines (65%) (Table 4). Results also indicated that season, genotypes and their interactions significantly influenced rust severities and accounted for variation equivalent to (36.7%, 37.4%, and 9.0%) in early; (38.5%, 35.5%, and 15.2%) in medium; and (38.3%, 35.2%, and 17.3%) in the late maturing lines, respectively.

Within each maturation group, results consistently showed significant differences in RRDs among the soybean lines, except for the late maturing lines during 2001A (Table 3). Within the early, medium and late maturation groups, the lowest RRDs were recorded on TGx 1895-22 (0.105), TGx 1889-12F (0.111), and TGx 1848-18E (0.134), respectively. Highest RRDs were recorded on TGx 1835-10E (0.184), TGx 1440-1E (0.176), and TGx 923-2E (0.196), early, medium and late maturing lines, respectively (Table 3). Clearly, most of the lines had higher RRDs than that of the local check Nam 2 (Table 3). Just like the rust severities, RRDs varied significantly between the maturation groups, except perhaps during 2000B when no significant differences were observed between early and late maturing soybean lines (Table 4). On average, early maturing lines registered the lowest RRDs (0.07),

Table 3
Rust reaction, rates of rust development, and yielding ability of 51 soybean lines when naturally infected with *Phakopsora pachyrhizi* at Namulonge

Entry	Rust severity (%)[a]			Rates of rust development[b]			Yield (kg/ha)		
	2000B[c]	2001A	2001B	2000B	2001A	2001B	2000B	2001A	2001B
(a) Early maturing									
TGx 1740-2E	52.2 (MS)	67.1(HS)	54.4 (MS)	0.084	0.176	0.134	1450	1410	1597
TGx 1897-17F	47.7 (MS)	56.9(MS)	42.0 (MS)	0.103	0.152	0.119	1308	1277	833
TGx 1485-1D	65.5 (HS)	74.8 (HS)	67.3 (HS)	0.090	0.162	0.159	611	697	793
TGx 1805-8F	60.2 (HS)	58.4 (MS)	41.8 (MS)	0.054	0.134	0.138	1411	1322	1019
TGx 1830-20E	64.1 (HS)	72.2 (HS)	46.9 (MS)	0.113	0.204	0.123	602	698	1019
TGx 1835-10E	19.4 (MR)	41.5 (MR)	27.5 (MR)	0.250	0.186	0.115	1244	1879	1482
TGx 1876-4E	44.4 (MS)	72.8 (HS)	50.6 (MS)	0.055	0.174	0.151	1310	1113	1551
TGx 1895-4F	57.7 (MS)	80.2 (HS)	57.1 (MS)	0.081	0.180	0.118	1296	977	1620
TGx 1831-32E	68.8 (HS)	82.2 (HS)	66.2 (HS)	0.071	0.178	0.159	865	652	1319
TGx 1895-6F	55.3 (MS)	80.6 (HS)	58.9 (MS)	0.101	0.189	0.175	841	719	995
TGx 1871-12E	46.1 (MS)	80.3 (HS)	53.3 (MS)	0.048	0.201	0.135	1259	975	1458
TGx 1895-23F	40.5 (MS)	54.9 (MS)	30.5 (MS)	0.072	0.145	0.133	939	1183	1597
TGx 1892-10F	44.9 (MS)	53.5 (MS)	32.2 (MS)	0.066	0.197	0.113	924	1162	1250
TGx 1895-19F	44.2 (MS)	65.3 (HS)	33.1 (MS)	0.065	0.135	0.148	653	951	764
TGx 1895-22F	49.7 (MS)	75.1 (HS)	54.9 (MS)	0.052	0.151	0.112	1295	955	181
TGx 1888-29F	39.3 (MS)	68.8 (HS)	38.2 (MS)	0.056	0.174	0.097	759	1254	1134
TGx 1894-3F	53.6 (MS)	65.6 (HS)	52.4 (MS)	0.042	0.170	0.162	1082	537	671
TGx 1882-2F	47.0 (MS)	73.3 (HS)	54.4 (MS)	0.051	0.152	0.169	1366	863	1065
TGx 1869-31E	48.3 (MS)	73.5 (HS)	62.8 (HS)	0.053	0.224	0.194	1047	629	1389
TGx 1880-3E	55.5 (MS)	67.7 (HS)	55.3 (MS)	0.075	0.161	0.190	1020	789	2060
TGx 1842-1E	57.5(MS)	75.5 (HS)	55.1 (MS)	0.073	0.171	0.213	1066	493	231
LSD	14.4	8.8	15.0	0.042	0.043	0.046	413.6	337.0	417.2
CV (%)	17.4	7.7	18.5	33.5	15.1	19.8	21.2	21.1	30.6
(b) Medium maturing									
TGx 1805-31F	46.4 (MS)	67.5 (HS)	49.7 (MS)	0.073	0.199	0.198	1175	404	1389
TGx 1895-50F	32.7(MS)	68.0 (HS)	40.2 (MS)	0.018	0.136	0.188	1286	931	1319
TGx 1888-15F	72.5 (MS)	79.7 (HS)	47.3 (MS)	0.081	0.163	0.187	328	218	856
TGx 1873-16E	58.1 (MS)	81.1 (HS)	65.3 (HS)	0.066	0.184	0.229	647	419	764
TGx 1802-3F	65.3 (HS)	82.4 (HS)	64.1 (HS)	0.067	0.149	0.203	891	435	1348
TGx 1878-7E	41.8 (MS)	73.3 (HS)	52.0 (MS)	0.073	0.190	0.202	809	516	1366
TGx 1893-7F	31.2 (MS)	62.2 (HS)	33.1 (MS)	0.049	0.191	0.184	812	448	1042
TGx 1019-2EN	38.8 (MS)	68.9 (HS)	53.1 (MS)	0.045	0.100	0.178	874	418	1319
TGx 1890-7F	74.9 (HS)	77.0 (HS)	56.7 (MS)	0.084	0.168	0.165	550	178	995
TGx 1802-1F	53.7 (MS)	79.9 (HS)	63.7 (HS)	0.031	0.176	0.162	536	339	916
TGx 1866-33F	60.1 (HS)	75.1 (HS)	46.0 (MS)	0.080	0.196	0.202	539	217	417
TGx 1891-3F	72.0 (HS)	73.3 (HS)	47.8 (MS)	0.065	0.133	0.255	923	470	948
TGx 1893-10F	44.2 (MS)	77.1 (MS)	54.0 (MS)	0.056	0.196	0.207	1075	632	1481
TGx 1893-6F	49.1 (MS)	69.3 (HS)	33.5 (MS)	0.051	0.152	0.147	864	311	1158
TGx 1896-3F	68.6 (HS)	84.8 (HS)	69.5 (HS)	0.080	0.163	0.102	588	46	486
TGx 1844-18E	68.8 (HS)	85.3 (HS)	76.4 (HS)	0.066	0.223	0.170	1229	69	1111
TGx 1440-1E	71.0 (HS)	77.1 (HS)	66.2 (HS)	0.103	0.236	0.190	812	0	880
TGx 1448-2E	51.0 (MS)	82.4 (HS)	72.4 (HS)	0.033	0.203	0.181	951	139	926
TGx 1889-12F	47.9 (MS)	76.2 (HS)	60.8 (HS)	0.042	0.138	0.154	1076	139	1146
TGx 1866-12F	62.9 (HS)	81.2 (HS)	71.3 (HS)	0.053	0.193	0.159	1173	23	1160
TGx 1895-33F	47.9 (MS)	68.0 (HS)	43.5 (MS)	0.144	0.168	0.147	826	653	1759
TGx 1895-49F	46.9 (MS)	72.6 (HS)	39.1 (MS)	0.070	0.163	0.120	1146	673	1227
Local check (Nam 2)	65.7 (HS)	78.5 (HS)	68.5 (HS)	0.084	0.158	0.108	988.5	763.9	995
LSD	13.0	6.9	10.8	0.040	0.052	0.062	326.6	242.2	400.8
CV (%)[d]	22.2	5.6	12.2	38.5	18.9	21.3	23.1	42.3	22.5
(c) Late maturing									
TGx 1869-13E	62.9 (HS)	84.2 (HS)	59.1 (MS)	0.101	0.176	0.172	478	23	1047
TGx 1886-38F	66.6 (HS)	82.4 (HS)	55.3 (MS)	0.072	0.224	0.174	343	23	467
TGx 1844-4E	66.2 (HS)	81.8 (HS)	72.2 (HS)	0.062	0.209	0.157	340	0	708
TGx 1866-7F	63.3 (HS)	86.6 (HS)	66.7 (HS)	0.080	0.209	0.171	141	0	491
TGx 1848-10E	42.9 (MS)	86.6 (HS)	66.6 (MS)	0.063	0.188	0.152	771	23	1148
TGx 1895-35F	57.7 (MS)	82.3 (HS)	44.0 (MS)	0.073	0.196	0.147	174	0	745

Table 3 (*continued*)

Entry	Rust severity (%)[a]			Rates of rust development[b]			Yield (kg/ha)		
	2000B[c]	2001A	2001B	2000B	2001A	2001B	2000B	2001A	2001B
TGx 923-2E	77.5 (HS)	86.7 (HS)	68.0 (HS)	0.130	0.265	0.193	216	0	425
TGx 1838-5E	31.9 (MR)	73.5 (MR)	22.5 (MR)	0.128	0.131	0.179	981	535	1296
LSD	15.9	3.9	10.4	0.056	0.068	0.058	199.2	38.8	413.2
CV (%)	35.8	3.0	11.3	39.9	21.4	21.5	31.9	33.5	31.6

[a] Rust reaction in parenthesis.
[b] Rates of rust development is the slope of the linear regression of logits on relative lifetime of the crop (Tschanz et al., 1985).
[c] A and B correspond to first (March–June) and second (October–January) seasons.
[d] Coefficient of variation.

Table 4
Rust severity, rates of rust development and yielding ability of soybean germplasm naturally infected with *Phakopsora pachyrhizi* at Namulonge, central Uganda

Maturity group	Rust severity at R6			Rates of rust development			Yielding ability (kg/ha)		
	2000B	2001A	2001B	2000B	2001A	2001B	2000B	2001A	2001B
Early maturing soybean	49.1	68.5	45.9	0.087	0.170	0.133	1040.9	1030.6	1272.2
Medium maturing soybean	54.6	75.5	54.1	0.067	0.174	0.179	864.9	354.8	1087.7
Late maturing soybean	58.6	82.4	54.6	0.060	0.198	0.167	430.4	9.91	824.2
LSD	6.35	3.94	7.0	0.019	0.018	0.018	140.2	137.6	178.4
CV (%)	26.9	12.0	30.9	54.6	22.7	24.4	36.8	52.0	34.0

followed by medium maturing lines (0.15), and then the late maturing lines (0.17).

Genotype × season analysis indicated that RRDs were significantly influenced by the season, soybean lines, and by the season × genotype interaction. Of the total variation in RRDs, seasons, soybean lines and their interactions, respectively, accounted for: (49.4%, 11.0%, and 23.7%) for the early maturing; (63.1%, 8.0% and 12.9%) for the medium maturing; and (56.9%, 8.3% and 10.5%) for the late maturing lines. Thus, most variation in RRD was due to seasonal influences. Results further indicated that higher RRDs, or conversely, lower rates are not consistently associated with higher rust susceptibility and/or lower rust susceptibility, respectively. For instance, TGx 1835-10E which was moderately resistant had surprisingly higher RRDs, and TGx 1895-22F which was moderately susceptible had low RRDs (Table 3). However, some lines like TGx 1896-3F, TGx 1889-12F, TGx 1893-6F, and the local check had low RRDs, but were highly susceptible. Nevertheless, other lines TGx 1440-1E and TGx 923-2E, were highly susceptible, also had high RRDs.

3.2. *Yield performances of soybean germplasm under rust stress*

Within each maturation group the results indicated significant differences in seed yield among the soybean lines with yields being significantly lower ($P < 0.001$) during 2001A (Table 3). In fact, during 2001A, most medium maturing lines yielded less than 500 kg/ha, with almost all late maturing lines yielding no grain. On average, highest yields within early maturing lines (1534 kg/ha), medium maturing lines (1179 kg/ha), and late maturing lines (938 kg/ha) were, respectively, obtained from lines TGx 1835-10E, TGx 1895-50F, and TGx 1838-5E. Lowest yields in early (597 kg/ha), medium (347 kg/h), and late (211 kg/ha) were obtained from lines TGx 1842-1E, TGx 1896-3F, and TGx 1866-7F (Table 3). Results further indicated that the yielding ability of the lines varied significantly among the maturation groups (Table 4); early maturing lines registered the highest yields (1114 kg/ha), followed by medium maturing lines (778 kg/ha), and then the late maturing lines (415 kg/ha). Genotype × season analysis indicated that the seasons, soybean lines, and the season × genotype interaction significantly influenced the yielding ability of the soybean lines. Of the total variation in yield, seasons, soybean lines, and their interactions accounted for: (5.6%, 41.2%, and 31.8%) for the early, (49.4%, 24.6%, 12.4%) for the medium maturing, and (48.6%, 32.2%, 7.2%) for the late maturing lines, respectively. Thus, the results indicate that for the early maturing lines most variation in yield was due to soybean lines while for the medium and late maturing lines most variations in yield were due to seasonal influences. Results also indicated that low

RRDs were not necessarily associated with higher yields. For instance, soybean line TGx 1896-3F, which had an extremely low RRD, had surprisingly low yield. Linear regression of soybean yield on rust severity at R6 revealed a significant relationship between these two parameters: early maturing lines ($R^2 = 0.25, P > 0.001; y = -6.7x + 1480.5$), medium maturing lines ($R^2 = 0.31, P > 0.001; y = 15.5x + 1722.6$), and for the late maturing lines ($R^2 = 0.46, P > 0.001; y = -15.4x + 1441.7$).

4. Discussion

All the soybean lines succumbed to rust, but to different degrees. Most of these lines were derived from the same crosses and/or populations, and thus their reaction to rust was not expected to vary considerably. At the Asian Vegetable Research and Development Centre where over 9000 soybean accessions have been screened against rust, no immune cultivars were identified (Tschanz et al., 1985). Limited pathogen development and/or sporulation is characteristic of rust-resistant soybean cultivars (Singh and Thapliyal, 1977). From our study, only two lines (TGx 1835-10E and TGx 1838-5E) were associated with limited sporulation, and were thus denoted as moderately resistant. Studies conducted elsewhere (Hartman et al., 1991) indicated that at R6 GS, percentage leaf area infected by rust differed significantly between genotypes, with 14–95% and 0–34% leaf area affected on susceptible and resistant genotypes, respectively. Observations from our study have also indicated that at R6, late maturing lines have higher rust severities as compared to early and medium maturing lines. Comparable results were reported in Nepal (Manandhar and Joshi, 1983) and Brazil (do Vale et al., 1985), where late maturing cultivars were more severely affected by rust and showed higher yield losses. The seasonal influence on rust severity at R6 GS justify the need for rust evaluations to be done over seasons, so as to identify soybean lines with stable resistance to rust.

The study has also showed that low RRDs are not consistently associated with lower rust severities (moderately resistant lines), and that high RRDs are also not necessarily associated with higher rust severities (moderately susceptible or highly susceptible lines). Earlier studies (Tschanz et al., 1985) also established that low RRDs or high RRDs are not always associated with lower predicted rust severity or with higher rust predicted rust severity, respectively, when 70% of the soybean life cycle is completed. This phenomenon strongly illustrates that utilization of RRDs alone in a soybean breeding program does not precisely determine rust resistance within soybean lines or accessions.

It is therefore necessary that while screening soybean germplasm for rust resistance, RRDs must be used along side other epidemiological parameters for acceptable resistance to be identified. Tschanz and Wang (1987) have further pointed out that the interaction between RRDs and predicted rust severity at a latter crop GS (i.e., when 70% of crop life cycle is completed) are indicative of differences in levels of resistance at different plant GSs.

Thus, soybean lines with low RRDs and a high predicted rust severity may have a higher level of susceptibility in the early reproductive stages, when natural infection begins. On the other hand, lines with high RRDs and a low predicted rust severity may have higher levels of resistance in the early reproductive stages, and higher levels of susceptibility at latter GSs. Our study has indicated that line TGx 1835-10E (moderately resistant, with high RRDs) had extremely low rust severities at R4 GS (4.0%), but relatively higher rust severities (29.4%) at R6 GS. In contrast, genotypes (TGx 1895-50F, TGx 1805-8F, TGx 1895-23F and TGx 1895-49F) consistently had low RRDs and lower rust severities at GS R6, while other soybean lines (TGx 923-2E and TGx 1440-1E) consistently had higher RRDs and higher rust severities. These lines could therefore have similar levels of susceptibility at the different GSs during the epidemic.

Significant differences in the yielding ability of soybean lines under rust stress is an indicator of variation in tolerance. Politowski and Browning (1978) pointed out that cultivars that have susceptible reaction, and an equivalent level of infection and reproduction of the pathogen, but have significantly higher yield than other susceptible cultivars are tolerant. The association between higher yields (>1t/ha) and high rust predicted severities especially for early maturing lines is testimony to this fact. Tolerance to rust and its variation among soybean cultivars has been reported (Tschanz and Tsai, 1983; Tschanz et al., 1985). Basing on the results here, early maturing lines appear to be more tolerant, followed by medium maturing, and then the late maturing.

These differences can be explained by variation in duration of the reproductive stages, from full bloom (R2) to full maturity (R8), the period when the epidemic is underway during the growing season in Uganda. Elsewhere, rust severity has been reported to increase from pod formation to pod filling stage (Handaningsih et al., 1986), and that attack during these stages is more yield reducing (Shin, 1986). The early maturing lines spend a shorter time in this stage, and thus suffer less from the epidemic. On the other hand, the late maturing lines spend a longer time in this phase, and are consequently hit hardest by the disease.

Bromfield (1984) pointed out that early maturing cultivars, which have a short pod filling stage, suffer less from the epidemic, and can therefore be utilized to minimize yield losses attributable to soybean rust. For the early maturing lines, most variation in yield is attributed to the soybean lines (genotypes), while for the late and medium maturing lines, most variation in yield was attributed to the season. Basing on these results, its most likely that for the late maturing and medium maturing lines, the prevailing weather conditions (specifically temperature and rainfall intensity), which determine the rust pressure, considerably determine their performances as compared to the early maturing lines whose yields are relatively stable. This explains the extremely low yields of medium and late maturing lines obtained during 2001A. It was also shown that most variation in RRDs was due to seasonal influence and not the soybean lines. This finding seems to suggest that under favorable conditions for rust development (optimum temperatures and rainfall), susceptibility among soybean cultivars is more or less the same. For instance, during 2001A (associated with higher rainfall amounts), most of the soybean lines were graded as highly susceptible at GS R6. This finding further demonstrates the key role of climatic factors especially rainfall (during mid-growth period of the crop), on rust epidemics.

The study has identified a few early maturing and rust tolerant lines (yielding > 1200 kg/ha), but these yields are lower than other rust tolerant lines identified at the Asian Vegetable Research Development Centre in Taiwan with average yields of 2000 kg/ha (AVRDC, 1988b). Thus, there is a need to screen more soybean germplasm for rust tolerance. Its also likely that soybean lines TGx 1445-3E and TGx 1489-1D, which were used, respectively, in crosses of TGx 1835-10E and TGx 1838-5E, are responsible for conferring the observed resistance in these lines.

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