Adaptability evaluation of US-developed soybean recombinant inbred lines in Rwandan conditions

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About 70% of the Rwandan population live on agriculture-related activities. Soybean is among the selected priority crops that are supported by the government through the agriculture sector subsidy program. However, the national production and yields per hectare remain very low compared to other countries such as the USA. Yet demand for soybean products and byproducts is increasing. On the list factors limiting soybean production, the narrow germplasm is ranked first. We introduced and tested a US-developed soybean population of 115 recombinant inbred lines segregating for yield among other factors. The lines were tested during the cropping seasons B2019 and A2020 where they were grown at two research stations using a randomized complete block design (RCBD) with three replications. At one of the stations in the low altitudes the top yielder from the US-developed RIL outperformed the high-yielding local check by almost 1.2 MT/ha. A total of 32 RILs yielded more than the local check. At the other station, the general performance of the RIL population was in the range of the top performing local check. In general, our data suggest that the US-developed population, though from a temperate zone, can easily adapt in some agroecological zones of Rwanda.

Key words: soybean, introduction, yield, cropping seasons.

INTRODUCTION

Soybean [Glycine max (L.) Merrill], is among the oldest crop introductions in Rwanda, having been introduced by the Belgians in early 1920’s (Niyibituronsa et al., 2018; Shurtleff and Akiko, 2010). However, the crop gained a relatively low interest among farmers until recently, after the government’s efforts to boost soybean production. In fact, the area under soybean production in Rwanda, moved from an estimated area of 1640 ha in 1973 to a total of 46695 ha in 2019 (NISR, 2019), after the efforts of the government to include soybean among priority crops.

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under the crop intensification program (a subsidy scheme that supports farmers’ access to improved seeds and fertilizers).

In terms of production, recent statistics report annual production of 24,525 MT is equivalent to around 0.5 tons/ha in yield. Put in context of the local cropping calendar, with two major soybean cropping seasons, namely season A (September-January) and B (February-June), the yield per ha is comparable to almost 50% of the reported annual production (World Bank, 2015).

This yield remains very low compared to the yields obtained in other parts of the world such as the USA where the average yield was 3.3 tons/ha in 2018 (American Soybean Association, 2018). However, despite the government efforts to promote soybean production, the country’s productivity does not increase proportionally to the deployed efforts. This may be due to the poor germplasm leading to lack of high yielding and adapted varieties, poor soil fertility, climatic variability, pests and diseases, poor access to quality seeds, and limited application of best agronomic practices (Mugabo et al., 2014). However, among these factors, the poor germplasm and lack of high yielding varieties remain the most important limiting factors to soybean production as the country counts only 11 varieties on its official variety list (GoR, 2023).

In the livestock industry, recent reports ranked the unaffordability of quality feeds as the major limiting factor in the sector (Mbuza et al., 2017; Mutimura et al., 2013). More appallingly, nutrition statistics have reported high levels of chronic malnutrition of up 45%, especially in children under the age of five (NISR, 2019), yet in addition to being a major ingredient for making fortified foods, soybean remains a critical component of animal feed formulations, thus critical to the availability of animal-based proteins, which are paramount to sustainably fix malnutrition issues (Biningwaho et al., 2011).

Though soybean has been selected as a priority crop, overall, the local production does not meet the national demand. The national soybean grain demand of the two main soybean processing plants, on their own, is estimated at 62,000 MT/year which is almost double the current national annual production (MINAGRI, 2018).

In terms of seed quality (amino acids, fatty acids, protein and oil), there are no reported data about seed quality traits for the local varieties. On the other hand, the US soybeans were among the best worldwide in terms of seed quality with the average protein and oil content of 35.7 and 19.5%, respectively, on a 13% moisture basis in 2014 (Assefa et al., 2019). These data suggest that, the US varieties could be an asset to the soybean industry in Rwanda both in terms of production and seed quality. In fact, previous studies proved that soybean meal was the most affordable way to fill the protein gap in animal feed (Hishamunda et al., 1998) and could even be the best replacement to commercial feeds (Nyina-Wamwiza et al., 2007).

Soybean breeding has generally been the core strategy used to mitigate the aforementioned challenges that reduce production and negatively affects not only the agriculture sector but livestock rearing equally. Unfortunately, in Rwanda, the lack of varieties (germplasm), make soybean research in general, and breeding in particular, almost nonexistent. Therefore, there is a need to increase the genetic diversity of the local soybean germplasm through introduction and breeding programs for future research initiatives intended to find practical solutions to the identified soybean production problems. In the present study, we tested in Rwandan conditions, the adaptability of a population of soybean recombinant inbred lines (RILs) belonging to maturity group V developed by the soybean breeding program at the University of Tennessee, USA, with the overall goal of improving the local germplasm pool for high yield and seed quality (oil and protein content).

**MATERIALS AND METHODS**

**Study sites and edaphoclimatic conditions**

The trial was set up in four row plots of 5 m × 1.60 m in two locations at Muyumbu research site (MRS) and Rubona research site (RRS) representing the low and mid altitudes agroecological zones, respectively (Ndahimbaje et al., 2014). The Muyumbu site is located between the administrative boundaries of Muyumbu and Nyakaliro sectors of Rwamagana district in the Eastern province of Rwanda. The Rubona site is located in Rusatira sector of Huye district in the Southern province.

The MRS is located at 30° 14' 35E and 1° 59' 44.8S at an elevation of 1361 masl. The average annual rainfall from 1983 to 2021 is 1100 mm while the average annual temperature over the same period is 27°C (agrometeorology data extracted from Meteo Rwanda Map room: http://maproom.meteorwanda.gov.rw/maproom/). The site’s soils are classified in humid oxeromixambrihumult of the Acrisols domain with clay loam texture (soils characteristics extracted from the Rwanda Soil Information System platform Rwasis: https://www.cabi.org/projects/rwanda-soil-information-services-rwandasis/).

Rubona research site (RRS) is located at 29° 45' 35E and 2° 27' 36" S with an elevation of 1706 masl. The average annual rainfall (from 1983 to 2021) is 1150 mm with an average annual temperature of 23°C (http://maproom.meteorwanda.gov.rw/maproom/). Soils are typic Sombrihumult of the Alisols domain and Sandy clay loam texture (https://www.cabi.org/projects/rwanda-soil-information-services-rwandasis/).

**Plant**

A total of 120 US-developed soybean lines were tested in two different research stations in Rwanda over two agricultural seasons. Among them, 115, F2:7 RILs derived from a cross between TN09-029 and NCC05-1168 at the University of Tennessee, Soybean Breeding and Genetics Program. These lines were in the range of late IV-V maturity groups (MG). Line TN09-029, is a late IV MG, highly resistant to SCN race 2, 3 and 5 (Gillen and Shelton, 2012) while Line NCC05-1168, is an early V MG, resistant to stem canker and SCN race 3 (Gillen and Shelton, 2011). In addition, standards...
Field experiments establishment and follow up

The trial were set up in four row plots of 5 m × 1.60 m in two locations at Muyumbu research station (MRS) and Rubona research station (RRS) representing the low and mid altitudes agroecological zones, respectively (Ndayambaje et al., 2014). The experiments were conducted in Season B2019 in MRS and Season A2020 in RRS. In season B2019, planting was done from 20th to 21st March at MRS and from 4 to 5th April at RRS. In season A2020, the planting was done from 11 to 12th October 2020 at RRS and from 14 to 15th October 2020 at MRS. The trials were set up in a randomized complete block design (RCBD) in 3 replications. The first and the second ploughing were conducted to prepare land. Before sowing, 10 cm deep rows were drawn using a 4-rows digging fork and tapes for making straight rows. A well-decomposed farm yard manure (FYM) was applied in the rows at a rate of 15 ton/ha. The FYM was covered by a layer of DAP (18-46-0) basal dressing fertilizer at a rate of 100 kg/ha. Sowing was done at a rate of 60 kg ha⁻¹ with a spacing of 10 cm between seeds within the row and 40 cm between the rows. For all the entries, seeds were inoculated with *Bradyrhizobium japonicum* USDA 110 at a rate of 40 g/kg of seeds. Earthing up was done using a hoe, for all the entries, at V3 stage. In average, 4 rounds of weed control were manually conducted during the entire crop cycle. A systemic fungicide, Benomyl (benzimidazole) was applied times to all entries to provide a preventive protection to a wide range of fungal diseases as a routine practice in seed production at the stations. At maturity, harvesting was manually done for the two middle rows, with one entry harvested at one go to avoid any mixture among entries. Threshing and winnowing were manually done after sun drying of the entries. Additional sun drying was done after cleaning up the seeds in order to reach the required moisture content level (13%). It is worth to note that no irrigation was provided in all stations both seasons in order to assess the performance of the introduced genotypes under normal farmers’ field conditions.

Measurements

For each entry, at flowering, flower color and pubescence color notes were taken. The flower color was either recorded as White (W), Purple (P) or Segregating (S). Pubescence color was recorded at maturity as grey (G), Tawny (T), Light Tawny (LT) or Segregating (S) with reference to their respective 2018 field notes from The University of Tennessee (UTK), Soybean breeding program. The plant height measured from the ground to the highest node in cm was recorded at maturity using a scale ruler. Plant lodging notes were measured at maturity by the scale of 1 = upright position to 5 prostrate position. Date to maturity was recorded in days after germination to maturity. The seed yield at 13% moisture content was weighed by an electronic scale and moisture content was determined using electronic moisture meter.

Rainfall data were provided by Meteo Rwanda from the closest automated Meteo stations to monitor the variability of seasonal precipitation at both stations.

Data analysis

Agronomic and seed quality data were recorded using field note books and later on in Microsoft Excel files for proper management and further analysis. The analysis of agronomic traits was performed using SAS 9.4 statistical software (SAS institute, Cary, NC). The analysis of variance (ANOVA) was drawn using the GLIMMIX procedure (PROC GLIMMIX) to obtain the treatment means, standard deviation, and p-values using the least significant difference of 0.05 (p<0.05).

RESULTS

Rainfall distribution at MRS (B2019) and RRS (A2020)

Rainfall distribution during the soybean growing season is a critical parameter for maximizing grain yields as grain yield is affected by the rainfall during growing season (Mandic et al., 2017).

During cropping season B2019, RRS was characterized by rain shortage towards the end of the season (end May - July). Daily rainfall reached almost 0 mm per day during the last two months of the season (approximately 60 - 115 days after planting) (Figure 1) while during cropping season A2020, the closest meteorology station recorded a very high cumulative rainfall of 236.5 mm (Figure 2).

Seasonal and locational agronomic performance

In situations of climatic and microclimatic diversity like in Rwanda, testing newly developed and/or introduced genotypes across multiple environments and cropping seasons is a requirement in order to identify the best adapted and stably performing lines across or for specific environments.

The RILs population were tested in two year-locations. Seasons consisted of season B2019 and season A2020 according to local agriculture season naming (Ndayambaje et al., 2014; Nahayo et al., 2018). Locations were the Rwanda agriculture board research stations in Muyumbu research station (MRS) representing the low altitudes and Rubona research station (RRS) representing the medium altitudes. During the season B2019 at MRS the yields ranged from 771 to 3426 kg ha⁻¹ with a population mean of 2033 kg ha⁻¹ (Table 2). A total of 32 US-developed lines including Ellis have higher yields than the top-yielding Rwandan check, Peka-6 (Figure 3). Population wise, the high yielding local check (Peka-6) belonged to the group of middle-class yielders (Figure 4). The earliest line matured at 102 days whereas the latest matured at 120 days and in general plants were resistant to lodging with a lodging score of 1.6. Plant height ranged from 38.3 to 65.7 cm with an average of 51.2 cm.

The Pearson correlation analysis between traits at MRS during season B2019 (Table 3, below the diagonal) revealed a highly significant (p<0.001) and positive correlation between yield and height (r=0.61), lodging (r=0.24) and maturity (r=0.43). Plant height and lodging...
(r=0.3) and maturity (r=0.39) were positively correlated. The correlation between lodging and maturity was non-significant.

The performance at RRS during season A2020 was low compared to that at MRS but higher than RRS season B2019. The performance of the population and the entire trial at RRS was not as high as at MRS. In fact, the yield of the best performing line SCN-031 was only 714 kg ha\(^{-1}\) (Figure 5) due a shortage of rains at critical stages of the vegetative growth and maturation (Figure 1).

The local check Peka-6 was the highest performer with
Table 2. Significant differences among genotypes (G), (P=0.05), for yield, plant height, maturity date, lodging at MRS during season B 2019.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Genotype P value</th>
<th>Mean</th>
<th>Min</th>
<th>Max</th>
<th>Std. Dev.</th>
<th>LSD value</th>
<th>Resid. Var.</th>
<th>Coeff. Var. b</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yield (Bu/Acre)</td>
<td>0.0021</td>
<td>2033.0</td>
<td>771.6</td>
<td>3426.2</td>
<td>357.0</td>
<td>786.9</td>
<td>1</td>
<td>0.05</td>
</tr>
<tr>
<td>Height (cm)</td>
<td>0.0446</td>
<td>51.2</td>
<td>38.3</td>
<td>65.6</td>
<td>6.0</td>
<td>14.9</td>
<td>0.9</td>
<td>1.94</td>
</tr>
<tr>
<td>Maturity (Days After Planting)</td>
<td>0.0454</td>
<td>107.3</td>
<td>101.6</td>
<td>120.3</td>
<td>2.0</td>
<td>4.9</td>
<td>0.9</td>
<td>0.89</td>
</tr>
<tr>
<td>Lodging</td>
<td>0.7908 NS</td>
<td>1.6</td>
<td>1.6</td>
<td>1.6</td>
<td>1.6</td>
<td>0.3</td>
<td>0.05</td>
<td>14.15</td>
</tr>
</tbody>
</table>

a. Std. deviation of LSMEANs
b. (Root MSE × 100)/mean
NS: Non-significant.

Figure 3. Thirty-three (33) top yielders at MRS during season B 2019.

Figure 4. Frequency distribution for seed yield. Checks are shown on the top of their yield class.

1630 kg ha⁻¹ (Table 4). A number of the US-developed lines such as Ellis, SCN-138, SCN-006, SCN-072, and SCN-038 consistently came in the top yielders. The earliest lines matured at 120 days whilst the latest was 130 days. Plant height ranged from 27.4 to 43.5 while the resistance to lodging was at mean of 1.2.

For the relationships between agronomic traits at RRS (Table 3, above the diagonal), all traits were positively
Table 3. Pearson correlation between traits at MRS during season B2019 (below the diagonal) and at RRS during season A2020 (above the diagonal).

<table>
<thead>
<tr>
<th>Correlation</th>
<th>Yield</th>
<th>Height</th>
<th>Lodging</th>
<th>Maturity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yield</td>
<td>0.21***</td>
<td>0.18**</td>
<td>-0.09NS</td>
<td></td>
</tr>
<tr>
<td>Height</td>
<td>0.61***</td>
<td>0.4***</td>
<td>0.023***</td>
<td></td>
</tr>
<tr>
<td>Lodging</td>
<td>0.24***</td>
<td>0.3***</td>
<td>0.28***</td>
<td></td>
</tr>
<tr>
<td>Maturity</td>
<td>0.43***</td>
<td>0.39***</td>
<td>0.04NS</td>
<td></td>
</tr>
</tbody>
</table>

NS: Non-significant, (**): significant at p<0.001, (***): significant at p<0.05.

Across seasons and environments performance

Multi-environment trials help to evaluate the performance of cultivars in a given environment by quantifying G x E effects and determining cultivar stability (Gurmu et al., 2010). We analyzed the performance of the US-developed lines by combining data from the first season (B2019) at MRS and second (A2020) season at RRS (Table 1). Data from B2019 at RRS were excluded due to the very apparent effect of drought on the overall performance. Similarly, no data from A2020 at MRS were collected after the whole trial was swept out by
inundations (the station is located in the valley). The combined performance of the RIL revealed a significant G×E effect for yield and lodging (Table 4). The average mean yield was 1393.7 kg ha⁻¹ while the maximum yield was 2239.4 kg ha⁻¹. The days to maturity ranged from 113 to 125. The mean recorded plant height was 31.5 cm while the average plant lodging was 1.4.

**DISCUSSION**

In this study, we investigated the general performance of a US-developed population of recombinant inbred lines introduced into Rwandan conditions. The population consisted of 115 lines plus 1 of its parental lines, 2 elite checks, and 2 local checks. They were tested against two popular local checks over 2 consecutive agricultural seasons. Due to environmental effects, trials at some locations completely or partly failed and data were not included. Here we discuss the main findings from the collected data.

The yield potential could be doubled

Yield is the primary breeding objective pursued by breeders in potentially successful varieties. At MRS during the B2019 season, the RIL population outperformed the local checks and the top yielders could double the standard average yields obtained by the farmers locally. In fact, official data from the institute of statistics reports the country’s annual average yields as around 0.5 Mt ha⁻¹ (NISR, 2010; 2018a; National Institute of Statistics of Rwanda, 2020). The same performance was reached by Rurangwa et al. (2018) only after applying rhizobia and different types of fertilizers including manure and potassium (Rurangwa et al., 2018). Our yields were generally higher than those obtained in farmers’ field after applying only rhizobia inoculation and urea (Nsengiyumva et al., 2017) and even those obtained during the pan-African soybean variety trials across three environments (Soybean Innovation Lab, 2019). Thus, the average mean yield of our population was in the range of what was reported earlier (Nsengiyumva et al., 2017) and even still higher than what were obtained during the pan-African soybean variety trials (Soybean Innovation Lab, 2019).

Days to maturity is an important consideration while deciding on the right genotypes to grow. On one hand, early maturity may result from premature flowering causing short stature of the plants and hence reducing yields (Sinclair and Hinson, 1992; Miranda et al., 2020). This short stature was reported to be the result of very short days (~12 h of photoperiod) during the vegetative stage also called juvenile stage when temperate genotypes are introduced to the tropics (Miranda et al., 2020). Soybean breeders could overcome this natural constraint and maintain high yields through the genetic exploitation of the long juvenile (Lj) trait (Miranda et al., 2020; Hartwig and Klöhl, 1979; James and Lawn, 2011). In fact, the J gene allows the plant to delay flowering and have longer vegetative growth even when exposed to reduced photoperiods of 12 h (Bäurle and Dean, 2006). This could be another area of future research with the US-developed population in a bid to manipulate its yield components and adaptability in Rwanda. Similarly, it is generally assumed that maturity is positively correlated with yield estimates in soybeans and later maturing cultivars will mostly out-yield earlier maturing cultivars (Moreira et al., 2019). On the other hand, early-maturing may be preferred over late-maturing varieties, especially in areas experiencing harsh environmental conditions. Soybean breeders are then called upon to develop early maturing varieties while maintaining acceptable level of yields (Yamaguchi et al., 2015; Chigeza et al., 2019). Therefore, breeders often make a tradeoff between high yields and early maturity especially in semi-arid areas that experience rain shortage and prolonged droughts.

The positive correlations were previously reported between yield and plant height (Li et al., 2020; Gawęda et al., 2020), lodging (Mansur et al., 1996) and days to maturity (Abugalieva et al., 2016; Balla and Ibrahim, 2017; Moreira et al., 2019). Plant height was higher in
MRS probably due to more vegetative growth which may explain higher yields obtained at MRS. In fact, this positive relationship between yield and vegetative growth was reported previously (Wang et al., 2020; Diondra et al., 2008; Ruiz-vega, 1984). However, in other studies no correlation was found between yield and height, as both traits are polygenic and complex traits (Diondra et al., 2008; Shree et al., 2018). As for the relationship between yield and plant lodging, the latter was found to only affect yield negatively depending on the stage of the crops or management options (Shapiro and Flowerday, 1987; Ramli et al., 1980; Wilcox and Sediyama, 1981; Leffel, 1961; Xiang et al., 2013). Elsewhere, lodging was found to have no effect on seed yield (Kabelka et al., 2004; Tefera et al., 2009). This could be due to the polygenetic nature of resistance to lodging (Chen et al., 2017). The positive correlation between yield and days to maturity could be phenologically explained by the production of more branches/plant and/or number of pods/plant (Akram et al., 2014). Overall, our data showed that a selection of US-developed top yielders may offer the best varieties for the lowlands of Rwanda. Equally, some lines could be grown in the middle altitudes, considering their early maturity and comparable yields to the currently available variety options.

The genotype × environment (G×E) significantly affect the overall performance

The combined performance revealed a significant G×E effect for yield and lodging (Table 4). The maximum yields were comparable to the yields obtained in previous studies (Rurangwa et al., 2018). The latest maturing line of our population matured only two days after the earliest maturing lines, ‘Caviness’ from the pan-African soybean variety trial (Soybean Innovation Lab, 2019). However, the population members would be classified in the class of medium to late maturing varieties (Chigeza et al., 2019). Surprisingly, the combined cross environments trials did not reveal a significant G×E z value for days to maturity, suggesting that maturity date was less influenced by environmental cues. Yet, according to Mourtzinis and Conley (2017), maturity group, a direct controller of maturity date in the temperate zone, is determined by two abiotic factors, namely photoperiod and temperature (Mourtzinis and Conley, 2017). This could be an indication that the concept of maturity groups does not apply in sub Saharan Africa (Miranda et al., 2020) or, at least, needs to be continuously monitored (Mourtzinis and Conley, 2017) since temperate varieties, when grown in the tropics, flower too early to allow for optimum vegetative growth, regardless of maturity group (Miranda et al., 2020). Alternatively, this could be explained by a strong involvement of the E genes that control time to flowering and maturity, but this should be confirmed by the investigation of the RILs E locus.

Taken together, the cross-environments and seasons data analysis suggest that in general the US-developed may lines fit better in the low altitudes of Rwanda than the medium altitudes. That is, the same RIL population revealed an equivalent performance as the local checks in the medium altitudes.

Conclusion

Soybean is becoming a priority crop in Rwandan agriculture. The current soybean yields, and production nationwide do not satisfy the existing market given the growing demand for soybean-based products and by-products. The Rwandan soybean program is characterized by a narrow germplasm with a low yield potential that cannot provide enough and stable production to meet the national demand. Considering the challenge of adaptation of the temperate soybean lines when taken to the tropics, we introduced and tested the performance of US-developed maturity group V lines in Rwandan conditions. The lines were tested in two major soybean growing areas; the low and medium altitude and tested them over two consecutive cropping seasons (A and B). The study showed that the US-developed population could outperform the local checks and double the current yield potential. It showed further that the US-developed lines perform better in the low altitudes than the middle altitudes. There was a highly significant G×E effect on yield. The US-developed lines matured in the same range as the earliest local check and could be classified as medium-to-late maturing lines. For a better insight to the adaptation and stability of these lines, they should be tested in more environments and over many seasons. Quality traits should be also investigated in future research in order to get a comprehensive profile of the US-developed population in Rwandan conditions. Further, it would be important to investigate the effect of maturity (E) and long juveniles (J) genes on the adaptation of this population.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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