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State of knowledge on breeding for durable resistance to soybean rust disease in the developing world

About this document:

This review document was prepared by Phinehas Tukamuhabwa and Mcebisi Maphosa,

Faculty of Agriculture, Department of Crop Science, Makerere University, Box 7062, Kampala, Uganda, for the Global Partnership Initiative for Plant Breeding Capacity Building.

State of knowledge on breeding for durable resistance to soybean rust disease in the developing world

A review prepared by
P. Tukamuhabwa and M. Maphosa
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About GIPB

The Global Partnership Initiative for Plant Breeding Capacity Building (GIPB) is a multi-party initiative of knowledge institutions around the world that have a track record in supporting agricultural research and development, working in partnership with country programmes committed to developing stronger and effective plant breeding capacity (http://km.fao.org/gipb/)

As a partnership of stakeholders from the public, private and civil society sectors, the initiative is aimed at catalyzing and supporting national, regional and global action among relevant international organizations, foundations, universities and research institutes, corporate and business sector, civil society associations, and national and regional bodies.

Mission

The Mission of GIPB is to enhance the capacity of developing countries to improve crops for food security and sustainable development through better plant breeding and delivery systems.

Objectives

A GIPB stakeholder consultation process has defined the following five longer-term specific objectives, aiming at the integrated enhancement of national plant breeding capacity building strategies:

Support for policy development on plant breeding and associated scientific capacity building strategy, to help allocate resources to strengthen and sustain developing countries' capacity to use plant genetic resources for food and agriculture.

Provision of education and training in plant breeding and related scientific capacities relevant to utilization of plant genetic resources.

Facilitate access to technologies in the form of tools, methodologies, know how and facilities for finding genetic solutions to crop constraints.

Facilitate exchange, from public and private breeding programmes, of **plant genetic resources** that can enhance the genetic and adaptability base of improved cultivars in developing countries.

Sharing of information focused on plant breeding capacity building to deliver newly available knowledge to national policy makers and breeders in developing country programmes.

About the authors

Dr Phinehas Tukamuhabwa has been a lecturer in Genetics and Plant Breeding in the Crop Science Department at Makarere University, Uganda since 2002. He is Leader of the Soybean Rust Project, in collaboration with the World Vegetable Research Center (AVRDC) and supported by the Regional Universities Forum for Capacity Building in Agriculture. He is dedicated to building capacity of students in Crop Science, Agricultural Economics and Extension.

Dr Tukamuhabwa has been Team Leader of the *Soybean Research and Development Project* sponsored by IFAD through the Vegetable Oil Development Project. In 2006 the project in which he was principal investigator won the Vice Chancellors award for innovations and academic excellence in recognition of two soybean varieties (Maksoy 1N and Namsoy 4M) which are resistant to soybean rust disease. Through the release these two soybean varieties, the soybean industry in Uganda which had collapsed due to soybean rust is steadily taking shape. The farmers have been greatly motivated to grow soybean extensively because of knowledge acquired about soybean's nutritive value and the ready market information, which were provided through this project. He has also lead a team of local and International Scientists in development of six climbing bean varieties widely grown in Uganda

Dr Tukamuhabwa has supervised several MSc students, several of whom did their research on soybean rust. He has published extensively, including several papers on soybean rust.

Mr **Mcebisi Maphosa** is a native of Zimbabwe. He received his MSc in Plant Breeding and Genetics from Makerere University, Uganda, and is currently a candidate for a PhD in Plant Breeding and Biotechnology at the same university. His thesis research is on enhancing durable resistance to soybean rust disease. Prior to his PhD studies he served as an intern at the Regional Universities Forum for Capacity Building in Agriculture (RUFORUM) Secretariat, Kampala, Uganda and was a Graduate Teaching Assistant at the University of Zimbabwe.

Executive summary

Soybean (*Glycine max* L.) is increasingly playing an important nutritive role in the food and feed industry in most developing countries. However the crop is currently threatened by Soybean rust disease (SRD) caused by *Phakopsora pachyrhizi*. This review provides general information on soybean rust, worldwide disease threats and case studies of widely used resistance breeding approaches. Currently, soybean rust is known to have spread from Asia to most developing countries in Africa and South America through continental movement of urediniospores.

At least four major genes have been deployed to control soybean rust in the orient, where the disease has been known for a long time, and in other areas of the tropics. However, genetic resistance has broken down due to several virulent races of soybean rust that are now prevalent. More resistant sources have been identified in Uganda and Brazil and are being used in various breeding programmes. Durable resistance is considered the most cost effective and sustainable means of controlling SRD in areas where it has become endemic. Durable resistance is theoretically effective against all races of the soybean rust pathogen, which is an important consideration as soybean rust is a complex of races, with multiple virulence factors. Different mechanisms can be used by breeders to control SRD: vertical and horizontal resistance, and tolerance. However, the utilization of each depends on the germplasm available to the breeder; resources and facilities available; time required to release the variety; soybean rust races present; and the targeted longevity of the resistance.

This review on approaches to breeding for resistance is complemented by suggested future research areas for breeders to improve the durability of resistance to SRD. These are conveniently classified into short, medium and long-term strategies. Emphasis is also put on pre-breeding through exploration of wild relatives of soybean to broaden the range of resistance sources. Various breeding strategies, ranging from conventional to molecular techniques, are suggested, including gene pyramiding, multi-line formation, combining ability studies, and molecular techniques such as marker assisted selection (MAS) and genetic transformation.

Contents

Introduction

Soybean (*Glycine max* (L) Merrill) (2n=40), family Fabaceae, sub-family Papilionoidae, has been cultivated in eastern Asia since the 11th century (Hymowitz and Shurtleff, 2005). *Glycine max* was domesticated from the wild soybean, *Glycine soja* Sieb. and Zucc., and is now grown under a wide range of climatic conditions in Latin America and Africa, ranging from temperate to humid tropics. Until the mid-1940s the major areas of soybean production were restricted to temperate regions of the world, after which production slowly to spread to tropical and sub-tropical regions (Franca Neto and Henning, 1994).

Soybean has increasingly become one of the most important and versatile leguminous crops, used as both a food and feed source. It has high protein content (40%) of good nutritional quality, high oil content (20%), together with numerous beneficial nutrients and bioactive factors, all of which combine to make soybean a highly desirable crop of choice, with the potential to improve the diets of millions of people in the developing countries (Singh *et al.,* 2008). Among crops, the unparalleled amino acid content and profile, and the high protein productivity per unit area mean that that soybean is a crop of great promise for most developing countries faced with rampant malnutrition and food insecurity. Moreover, in low-input farming systems, the crop is known to improve soil properties through nitrogen fixation and enhanced moisture retention (Graham and Vance, 2003). The combination of improved soil properties and the ability to break lifecycles of pests and diseases makes soybean an ideal crop in cereal rotation programmes (Waymark, 1997). Thus any constraints on or threats to soybean production have great potential for eroding the food and nutrition security of millions of people, especially in developing countries.

Soybean production and distribution in the developing world

Soybean production and utilization in developing countries is increasing rapidly and replacing the traditionally grown grain legumes in response to the demand for soybean products (Popelka, Terryn and Higgins, 2004). According to IITA (2008), 21 countries were engaged in soybean production within the African soybean region (Figure 1). The major soybean producing countries in Africa are Nigeria, South Africa, Uganda and Zimbabwe (FAOSTAT, 2009).

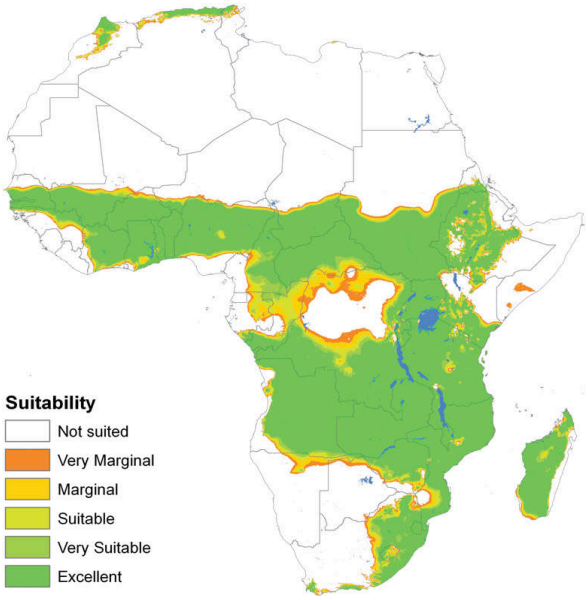


Figure 1. Soybean growing suitability map for Africa. Adapted from IITA, 2008.

Increased soybean production in a country usually implies that any constraints to soybean production would have a negative impact on the national economy. South America has a combined output that exceeds that of the United States of America. The major soybean producing countries in South America are Brazil, Argentina and Paraguay (Suenaga and Cattelan, 2008) (Table 1). The distribution of soybean production in South America is shown in Figure 2.

Soybeans are native to East Asia and 9 percent of world soybean production is from Asia. In Asia, the major soybean growing country is China, followed by India.

Figure 2. Major soybean producing areas in South America. Adapted from Global land use data (2000).

Table 1. Major developing country soybean production in 2007.

Country	**Production** (tonne)	**Area** (ha)	**Approx. yield** (t/ha)
Africa			
Nigeria	617 000	650 000	0.95
South Africa	430 000	245 000	1.75
Uganda	176 000	147 000	1.19
Zimbabwe	112 300	69 900	1.61
Egypt	33 030	16 500	2.00
Asia			
China	15 600 200	8 900 100	1.75
India	9 433 000	8 550 000	1.10
Korea DPR	345 000	300 000	1.15
Viet Nam	14 492	190 100	0.07
Thailand	217 870	139 278	1.56
South America			
Brazil	58 197 297	20 637 643	2.81
Argentina	45 500 000	16 100 000	2.82
Paraguay	3 900 000	2 300 000	1.69
Bolivia	1 595 947	958 279	1.66
Uruguay	779 920	366 535	2.13

SOURCE: FAOSTAT, 2009.

Among developing regions in 2007, the South American continent was the leading producer of soybean in terms of area and tonnage, while the African continent was least. Yields per unit area were higher in South America than Asia, which is a native soybean producer. Soybean production for the developing countries is shown in Table 2.

Table 2. World soybean production and acreage in 2007.

Region	**Production** (tonne)	**Area** (ha)	**Approx. Yield** (t/ha)	**As % of global production**
South America	110 464 799	40 449 396	2.73	50.00
Asia	19 388 071	27 757 024	0.69	8.79
Africa	1 485 650	1 261 950	1.17	0.67
World	220 532 612	90 199 626	2.44	100.00

SOURCE: FAOSTAT, 2009

The Soybean rust pathogen

Worldwide, several pathogens are known to attack soybean, but fungal pathogens cause relatively the greatest losses (Pivonia and Yang, 2004). Soybean rust caused by *Phakopsora* spp. fungi (Order: Uredinales; Family: Melampsoraceae) causes most damage, with potential yield losses of up to 90% in heavy infestations (Hartman, Sinclair and Rupe*,* 1999). Two obligate fungal species, *Phakopsora meibomiae* and *Phakopsora pachyrhizi*, cause soybean rust, but the latter—the Asian- or Australasian-type—is more aggressive and of most economic significance for soybean production (Bonde *et al.,* 2006). These two species cannot be distinguished by direct observation of an infested field, but only through using a polymerase chain reaction (PCR) assay that makes use of the 20% difference in nucleotides in the ribosomal internal transcribed region (Frederick *et al.,* 2002). *P. meibomiae* has been reported in the following American countries: Barbados, Belize, Bolivia, Brazil, Chile, Colombia, Costa Rica, Cuba, Dominican Republic, Ecuador, Guatemala, Mexico, St Thomas (United States Virgin Islands), Trinidad and Tobago, and Venezuela. However, both *P. meibomiae* and *P. pachyrhizi* occur in Argentina, Brazil and Paraguay. In Africa and Asia, the Asian type is the only confirmed *Phakopsora* species affecting soybean production (USDA, 2004).

Spread of Soybean rust in the developing world

Soybean rust disease (SRD) caused by *P. pachyrhizi* causes severe losses in most developing countries in Africa, Asia and South America (Ivancovich, 2008). The occurrence of SRD was first observed in Japan in 1902, devastating small-scale soybean production, and it spread to other Australasian countries, namely India, Indonesia, Nepal, Philippines, Peoples Republic of China, Taiwan Province of China, Thailand, Viet Nam and Australia (Bromfield, 1984). It was, however, restricted to South-East Asia, India and Australia before spreading to new geographical locations (Levy, 2004; Junior, 2008). According to Isard *et al.* (2006), Asian Soybean rust (ASR) has moved to new geographical locations through airborne movement of urediniospores: first from India to central Africa, then from Africa to South America. Air currents are considered responsible for local, regional and international movement of urediniospores and causing the spread of ASR to new locations. The arrival date of soybean rust in the African continent is unknown (Levy, 2005). However, in sub-Saharan Africa, the devastating effects of ASR were first observed in the late 1990s. In 1996, ASR was first observed in Uganda, and it then spread to Kenya and Rwanda, Zambia and Zimbabwe by 1998, Mozambique in 2000, and South Africa in 2001 (Levy, 2003). In Nigeria, it was observed in 2001 (Akinsanmi, Ladipo and Oyekan*,* 2001), Ghana in 2007 (Bandyopadhyay *et al.,* 2007), and Democratic Republic of Congo in 2007 (Ojiambo *et al.,* 2007). In South America, the first confirmed case of ASR was in Paraguay in 2001. Thereafter, the pathogen spread to Argentina and Brazil, becoming widespread in Paraguay by 2002 (Miles, Frederick and Hartman, 2003). Epidemiological studies are scarce in many developing countries because the disease is a recent introduction.

Soybean rust symptoms and effects

SRD is a polycyclic disease which, unlike other rust pathogens with narrow host ranges, has more than 100 functional host leguminous plants (Slaminko *et al.,* 2008). Common cultivated legumes, including common bean (*Phaseolus vulgaris*), scarlet runner bean (*P. coccineus*), lima bean (*P. lunatus*), cowpea (*Vigna unguiculata*), pigeon pea (*Cajanus cajan*), field pea (*Pisum sativum*) and lentil (*Lens culinaris*), act as inocula reservoirs and bridge hosts, which further exacerbates the problem of soybean rust (Anon., 2007; Schwartz, Steadman and Pastor-Corrales, 2005; Bennett, 2005; Hartman *et al.,* 2004). These crops play a crucial role in most cropping systems, particularly in developing countries, which makes the control of ASR a big challenge. The multiple host range of ASR can be explained by its unique ability to penetrate the cuticle directly in comparison with most fungi, which gain access to the plant through wounds and stomata (Miles, Frederick and Hartman, 2003). These factors imply that soybean rust has an accelerated invasion capability and can spread rapidly once the pathogen is established.

The signs and symptoms of ASR may be observed at any time during the cropping cycle, but losses are related to the phenological stage and severity of symptoms at the time of infection (Ivancovich, 2008). During the pod filling stage (R5–R6), disease severity increases greatly, causing substantial yield losses. This therefore has important implications in timing resistance evaluation by the breeder. Consideration needs to be given to early-stage resistance, as well as late-stage resistance. Carrying out resistance assessments at the two major developmental stages and combining the analyses provides a better guide for resistance breeding purposes (Ribeiro *et al.,* 2007).

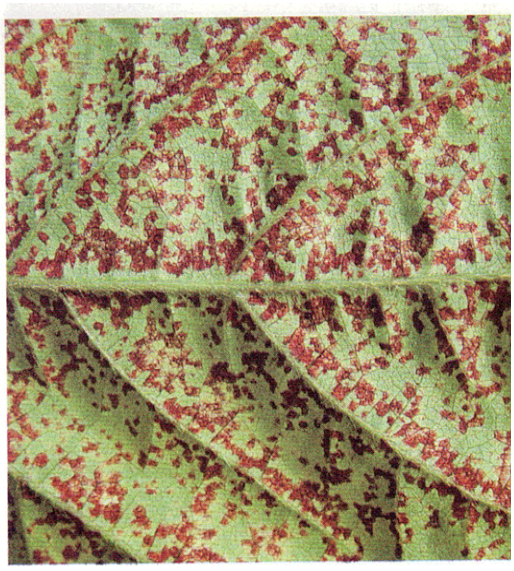
Soybean rust manifests on the petioles and sometimes on the stems of soybean plants (Yang, 1991) (Figure 3). It produces tan to red-brown polygonal pustules (2–5 mm^2) on the undersurface (abaxial surface), restricted by the vascular bundles, with urediniospores emerging from a circular ostiole and being disseminated by wind. Urediniospores are the only spores that have been extensively studied under field conditions; other spore types, such as teliospores and basidiospores, have only been induced under controlled laboratory conditions. The teliospore and basidiospore life cycle has not been characterized due to lack of suitable hosts (Snover-Clift and McKellar, 2004).

Early symptoms of ASR can often be confused with those of other pathogens, such as bacterial pustule (*Xanthomonas axopondis* pv *phaseoli*), bacterial blight (*Pseudomonas savastanoi* pv *glycinea*) and brown leaf spot (*Septoria glycines*). Hence accurate diagnosis during early stages of disease development requires the use of a hand lens (10–20×). Typical ASR manifests as 'volcano'-shaped erumpent uredinia, with several openings (ostioles) releasing urediniospores (Figure 4). Urediniospores, however, cannot be individually distinguished at these magnifications.

Symptoms can also manifest on the adaxial (upper) surface, in which case the disease will be in the advanced stages of development. Symptoms are first observed on the lower leaves as water-soaked lesions that change to small, chlorotic areas, which increase in size and change colour to either tan or red-brown. Genotypes with larger and darker red-brown lesions have less sporulation, while the small and lighter tan lesions are characterized by profuse sporulation. Immune genotypes have no visible sign of infection. Thus, based on the lesion types, resistance or susceptibility of a line can be assessed (Bromfield and Hartwig, 1980).

A.

B.



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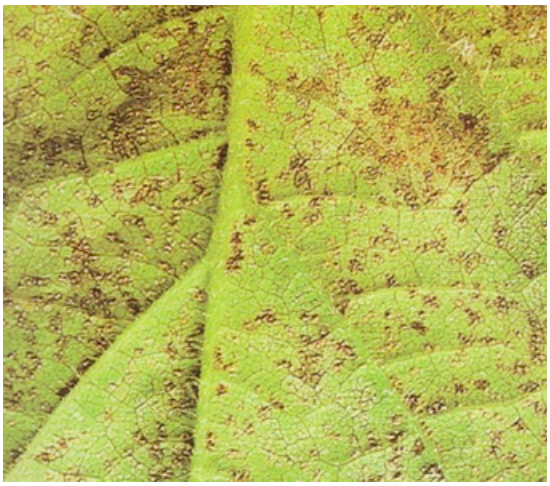


Figure 3. A. Typical soybean rust symptoms in a heavy infestation at Mubuku, Uganda. B. Resistant red-brown lesions with limited sporulation. C. Profusely sporulating tan lesions. Source for 3B and 3C: Yorinori, 2008.

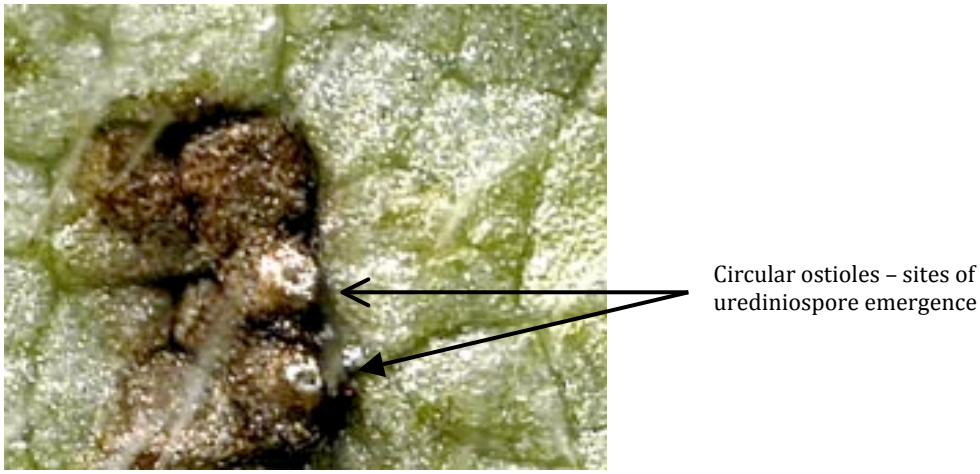


Figure 4. Close-up of uredinia on underside (abaxial surface) of leaf.

Ideal conditions for soybean rust proliferation

The major factors of epidemiological importance for ASR are the relative humidity of the soybean field, the number of rainy days, and the planting date. In general, conditions that promote vigorous plant growth and thick canopy cover promote the development of ASR. Disease incidence is pronounced in hot, humid environments, which results in severe disease attack that reduces photosynthetic area on the leaves and leads to premature defoliation (Anon., 2007). High relative humidity of between 75 and 80%, a temperature range of 15 to 28°C and 6 to 12 hours of moisture are required for spore germination and disease perpetuation (Hartman, Miles and Frederick, 2005). Once infection has occurred, uredinia are produced after 5 to 7 days and a new generation of spores is produced in 10 to 20 days (Yang, 2002). Yield losses due to soybean rust result from premature defoliation curtailing photosynthetic capacity, and hence a low number of filled pods per plant, pods per plant, seeds per plant, weight of seeds per plant and 1000-seed weight (Bennett, 2005).

Soybean rust assessment

All aspects of breeding for disease resistance depend on accurate disease diagnosis and screening of germplasm, irrespective of where the evaluation is done. Epidemiological and resistance breeding studies for soybean rust depend on reliable quantification methods that provide reproducible results. The International Working Group on Soybean Rust (IWGSR) developed a soybean rust rating system to guide breeders in the evaluation and selection process. In this three-digit scoring system, the first digit denotes the upper position of the most diseased leaves in the leaf canopy; the second digit denotes density of rust lesions on the most diseased leaves; and the third digit denotes infection type (Figures 5, 6 and 7). The rating scale is explained below.

Table 3. Relationship between disease reactions and IWGSR ratings for soybean rust.

Disease reaction	IWGSR rating
Immune	111
Resistance	122, 123, 132, 133, 222, 223
Moderately resistant	142, 143, 232, 233, 242, 243, 322, 323
Moderately susceptible	332, 333
Susceptible	343

A final classification is established based on all three parameters (Table 3).

Despite the fact that this assessment method takes into consideration all parameters necessary to evaluate for resistance, it is not extensively used by breeders. This is because of the qualitative nature of the evaluation, which cannot be subjected to appropriate statistical analysis. Thus other methods have been adopted to provide quantitative assessment and ease statistical analysis. Rust assessments developed to overcome the shortcomings of the three-digit system commonly use a 0–9 severity scale, where 0 = no disease and 9 = 90% disease severity with defoliation (Walla, 1979).

Soybean growth stage influences pathogen development, which calls for caution in conducting ASR assessments. Late maturing soybean is less affected by rust compared with early maturing varieties planted on the same date. Thus, to make valid comparisons, a relative lifetime (RLT) method was developed to compensate for the differences in days to host maturity (Wang and Hartman, 1992). RLT used as a time element from 0 to 100 indicates the percentage of lifetime that has been completed on a particular date. It is calculated using the formula:

$$\text{RLT} = \frac{\text{Days after planting} \times 100}{\text{Days to maturity}}$$

Closely related to RLT are the soybean growth stages described by Fehr and Caviness (1977), which standardize soybean growth phases (Table 4). Most assessments for soybean rust are better done after the R6 stage, when significant differences in rust severity can be identified between susceptible and partially resistant lines (Hartman, Wang and Tschanz, 1991). In addition, beyond the R6 stage soybean leaves of susceptible are more severely

affected by rust allowing for easy assessment of resistance (for soybean growth stages, see Table 4).

First digit (see Figure 5):
Upper position of most diseased leaves

1 = bottom third of the plant canopy

2 = middle third of the canopy

3 = upper third of the canopy

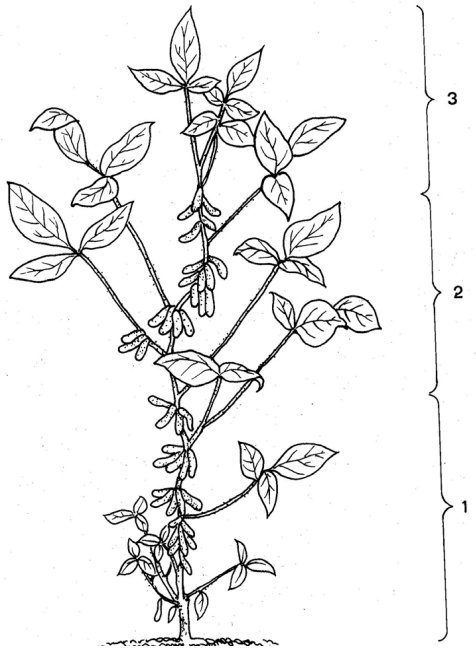


Figure 5. Leaf positions used in IWGSR scoring system (Yang, 1991)

Second digit (see Figure 6):
Density of rust lesions on most diseased leaves

1 = no lesions

2 = light lesion density
(<10 lesions per cm^2)

3 = medium lesion density
(11–50 lesions per cm^2)

4 = heavy lesion density
(>50 lesions per cm^2)

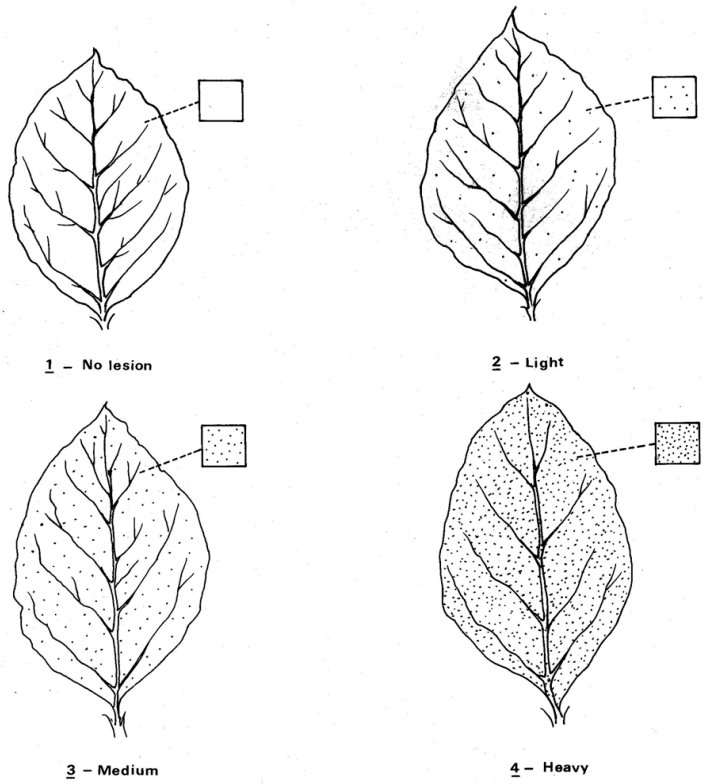


Figure 6. Soybean rust density scale for IWGSR rating system (Yang, 1991)

1.

2.

Third digit:
Infection type on the most diseased leaves

1 = no pustule
(Figure 7 – top left)

2 = non-sporulating pustules
(Figure 7 – top right)

3 = sporulating pustules
(Figure 7 – bottom)

3.

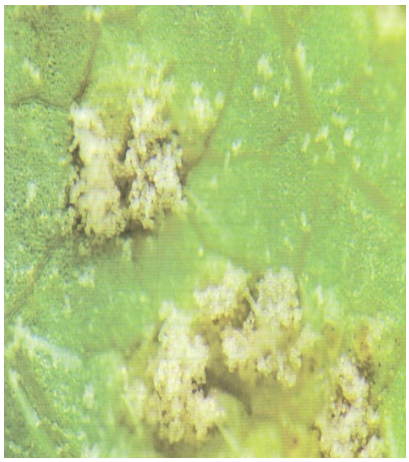


Figure 7. Sporulation levels of uredinia, where 1 = no pustules; 2 = non-sporulating pustules; 3 = sporulating pustules. Source: Morel *et al.*, 2008.

Table 4. Soybean growth stages using the scale of Fehr and Caviness (1977).

Growth Stage	Definition
VE	Emergence. Cotyledons are above the soil surface.
V1	Completely unrolled unifoliolate leaves.
V2	Completely unrolled leaf at the first node above the unifoliate node.
V3	Three nodes on the main stem with fully developed leaves, beginning with the unifoliate node.
V(n)	n^{th} trifoliolate.
R1	Beginning bloom.
R2	Full bloom.
R3	Beginning pod.
R4	Full pod.
R5	Beginning seeding.
R6	Full seed.
R7	Beginning maturity.
R8	Full maturity.

Yield losses due to ASR in developing countries

The rapid spread of ASR, coupled with its potential for causing severe yield losses, makes it an important disease in soybean growing countries. Information related to yield losses resulting from ASR is scanty, and has been mostly obtained from major growing areas where the disease is now endemic. Fungicide treatment experiments at AVRDC, Taiwan, have shown yield losses ranging from 23 to 50% (Yang, 1991). Similarly, in mainland China, losses of 30 to 50% were reported under heavy infestation (Yu, Tan and Sun, 1994). In India, losses of up to 80% were experienced in 1994 and 1995 in the state of Karnataka (Patil and Basavaraja, 1997). However, losses of up to 100% have been encountered in some areas in the absence of any form of chemical protection. In these countries, however, the extent of yield loss depends on prevailing weather conditions, varieties grown and physiological crop growth stage when the crop was infected. In Uganda, yield losses associated with soybean in three commercial varieties were in the ranges of 27–36% (Kawuki, Adipala and Tukamuhabwa*,* 2003) and 15–41% (Tukamuhabwa and Dashiell, 1999). In Zimbabwe, yield losses were in the range 60–80%; in South Africa losses were 10–80% in mixed cropping and 100% in monoculture systems (Caldwell and Laing, 2001). In Nigeria, according to Akinsanmi, Ladipo and Oyekan (2001), yield loss in some soybean lines ranged between 28 and 49%. In Paraguay and Brazil, yield losses of 60% and 30–75%, respectively, were experienced in 2001 (Yorinori *et al.,* 2005). In Argentina, direct field evaluation in some provinces showed yield losses of between 17 and 28% (Formento, 2008).

The area under soybean, particularly in the warmer regions of Africa and South America, continues to increase and soybean rust is expected to become a more severe problem as *P. pachyrhizi* has long been a member of the tropical and subtropical fungal flora (Shurtleff and Aoyagi, 2007; Travasso *et al.,* 2006; Yang, 1991). Losses to soybean rust are of great concern to soybean producers as climate change has the potential to further modify host plant physiology and resistance, and could affect the rate of pathogen development (Sivakumar, 2008). The covariant mix of climate change induced stresses implies that countries must adopt stress mitigating crop technologies, such as use of soybean varieties with durable resistance to ASR. Furthermore, the prediction of soybean rust survival zones suggest that places where rust has been observed are areas where it can persist year round, further exacerbating the potential losses in those areas (Pivonia and Yang, 2004). Thus, to achieve sustained productivity, soybean breeding programmes must be actively involved in identifying new sources of resistance or tolerance to ensure the breeding and release of new rust-resistant varieties. This can be achieved either through selection of landraces from farmers' fields, through classical conventional breeding, or through the use of modern molecular techniques.

Progress in breeding for host plant resistance to ASR

To control ASR, host genetic resistance remains the most economically viable, environmentally friendly and strategically important option for resource-constrained farmers in the developing world. Three approaches have been generally used to improve varieties for resistance to ASR, namely specific resistance, partial resistance, and yield stability or tolerance. These approaches have been used independently in most cases.

Screening soybean germplasm for resistance genes

Historically, identifying soybean rust resistance sources has been a major objective at AVRDC - The World Vegetable Center, with over 9 000 soybean accessions screened for specific resistance, rate reducing resistance and tolerance (Sinclair, 1989). Currently, such work is being undertaken by several breeding programmes worldwide, with most prominence in China and the United States of America. In addition, nearly 300 accession of wild perennial *Glycine* spp. have been evaluated for resistance (Kuchler *et al.,* 1984).

During 1986–1990, 6 687 accessions of soybean germplasm from southern China were screened for resistance to ASR. None of these was immune or highly resistant. Only 0.8% (56 accessions), including Da Jiangsidou, Gutian Linli baimou bou, Mashan Renfong huang dou and Tiandeng hei dou, were found to be moderately resistant (Anon., 1994). In the same report, the resistance in line PI 459025 was reported to be controlled by a single dominant gene, while the tolerance in lines AGS129 and AGS181 seemed to be controlled by multiple genes. In addition, the USDA germplasm collection is evaluating over 16 000 soybean accessions for resistance to soybean rust, but none has been found resistant to mixed isolates (Miles, Frederick and Hartman, 2003).

Specific resistance gene sources

To date, six race-specific genes have been identified: *Rpp1, Rpp2, Rpp3, Rpp4, Rpp5* and *Rpp?*(Hyuuga). Varieties with specific resistance genes produce immune reactions with no visible symptoms when inoculated with specific isolates, while some produce red-brown lesions with sparse uredinia. These six independent resistance genes—*Rpp1–5* and *Rpp?*(Hyuuga)—were identified in accessions PI 200492, PI 230970, PI 462312, PI 459025, PI 200456 and PI 506764, respectively. In addition, other resistance genes and their source material exist, though without specific names, such as in PI 398507, FT2, PI 407912, PI 424473 (Arias *et al.,* 2008) and UG5 (Tukamuhabwa, Dashiell and Assafo, 2001). The basis for identifying these resistance genes is phenotypic evaluation of disease severity, lesion type, sporulation degree and number of uredinia per lesion.

Soybean has a dense molecular map, comprising 20 linkage groups identified using SSR, RFLP, AFLP, RAPD, isozyme and classical trait markers (Song *et al.,* 2004). These markers have allowed the assignment of some identified resistance genes to the different linkage groups. The linkage groups of the six resistance genes are presented in Table 5.

Table 5. Resistance genes, linkage groups and their reference source.

Resistance gene	Linkage group	Source
Rpp1	G	Mclean and Byth, 1980
Rpp2	J	Bromfield and Hartwig, 1980
Rpp3	C2	Hartwig and Bromfield, 1983
Rpp4	G	Hartwig, 1986
Rpp5	N	Garcia *et al*., 2008
Rpp?(Hyuuga)	C2	Monteros *et al*., 2007

Recessive genes have also been reported to confer resistance in accessions PI 200456 and PI 224270, though not yet mapped to any particular linkage group (Calvo *et al.,* 2008). Both

dominant and recessive resistance genes that have been identified are only effective against specific races of ASR (Table 6). The resistance conferred by these single resistance genes is not durable, though it has been easier for breeders to introgress them to other varieties through backcrossing schemes.

Table 6. Original resistance gene sources and *P. pachyrhizi* isolates used in their identification.

Resistance gene	Accession	*Phakopsora pachyrhizi* isolate[(1)]	
		Resistant reaction	**Susceptible reaction**
Rpp1	PI 200492	IN 73-1	TW 72-1, TW 80-2
Rpp2	PI 230970	AU 72-1, IN 73-1, PH 77-1, TW 72-1	TW 80-2
Rpp3	PI 462312	IN 73-1	W 72-1, TW 80-2
Rpp4	PI 459025	IN 73-1, TW 72-1,	TW 80-2
Rpp5	PI 200456	BR[(2)]	N/A[(3)]
Rpp?(Hyuuga)	PI 506764	BR[(4)], Geo	N/A[(3)]

NOTES: (1) Origin of isolates: AU = Australia, IN = India, PH = Philippines, TW = Taiwan, BR=Brazil, Geo = Georgia. (2) Isolate from cv. BRSMS Bacuri from Cambé, P.R, Brazil (Garcia *et al*., 2008). (3) Not yet observed. (4) Mixed Brazilian isolate (Monteros *et al*., 2007).
SOURCE: Modified from Miles, Frederick and Hartman, 2003.

Breeding for vertical resistance to soybean rust disease

Most of the breeding work on soybean rust resistance has focused on vertical or specific resistance as the primary means of control, rather than on horizontal resistance. Race-specific resistance genes that confer hypersensitive responses and complete protection have been used in breeding for other resistance traits in soybean, as well as in other autogamous crops worldwide (Lillemo *et al.,* 2006; Long *et al.,* 2006; Mauro, Oliveria and Mauro*,* 1999). Specific resistance to soybean rust is manifested by extreme reduction in number and size of uredinia following inoculation with specific isolates (Bonde *et al.,* 2006).

Historically, single-gene resistance was used to control soybean rust in the Eastern Hemisphere, where the disease has been endemic for a long time. In Africa and South America, vertical resistance has also been the major control means against soybean rust. However, with time, most of the resistance-gene sources have become vulnerable to new or more aggressive soybean rust races (Pham *et al.,* 2009; Morel *et al.,* 2008). Thus the durability of such resistance is usually short since it is overcome by genetic changes in the pathogen populations in response to the selection pressure that results when a resistant cultivar is deployed on a large scale. The genetic plasticity of *P. pachyrhizi* pathogenicity factors makes breeding for durable resistance to soybean rust a challenge, especially in areas where the disease has become endemic (Twizeyimana *et al.,* 2009; Yorinori, 2008; Hartman *et al.,* 2004). In addition, soybean rust pathogens have been found to possess ancillary virulence genes, which enables them more easily to overcome single-gene resistance deployment. The presence of such multiple virulence genes in *P. pachyrhizi* is unusual since no soybean line is known to naturally possess more than one specific-resistance gene (Shanmugasundaram, Yan and Wang, 2004).

Soybean rust races

Soybean rust pathogen variability has been documented in different parts of the world, including Nigeria, by Twizeyimana *et al.* (2009); Brazil, by Kato and Yorinori (2008); Uganda, by Lamo (2004); Thailand, by Poonpolgul (2004); and generally in Asia, by Hartman and Wang (1992). In Taiwan, nine races of soybean rust were identified from 42 isolates using race differentials (Shanmugasundaram, Yan and Wang, 2004; AVRDC, 1985). According to Poonpolgul (2004), Thailand had 59 races that were identified from 69 isolates. In Uganda, Lamo (2004) identified three races from 45 pure isolates, using 19 race differentials. Twizeyimana *et al.* (2009) identified seven pathogen clusters using eight race differentials. Thus the four widely used sources of resistance (*Rpp1–4*) have rapidly become ineffective in different parts of the world due to pathogen variation and the presence of multiple virulence

factors. A classic example of multiple virulence factors is demonstrated by Taiwan 80-2A, which is known to have virulence factors that cause rust to overcome host plant resistance in PI 200492 (*Rpp1*), PI 230970 (*Rpp2*), PI 339871, PI 462312 (*Rpp3*) and PI 459025 (*Rpp4*) (Tschanz, Wang and Tsai*,* 1986).

In Uganda, evaluation of exotic germplasm identified *Rpp2* as the only effective source against soybean rust, whilst others succumbed and showed rust symptoms during three consecutive seasons, i.e. 2005A, 2005B and 2006A (Oloka *et al.,* 2008). In Paraguay, where the presence of soybean rust was detected in 2001, only cv. Bing Nang, the source of the *Rpp4* resistance gene, has not been overcome by the rust pathogens (Hartman, Miles and Frederick, 2005). All four resistance genes (*Rpp1–4*) were equally effective in Brazil soon after the detection of ASR in 2001, but *Rpp1* and *Rpp3* are now ineffective (Laperuta *et al.,* 2008). Due to the unstable nature of vertical resistance conferred by these genes, most soybean breeders have shifted their interest to other forms of resistance that are durable. This move—'disinterest' in vertical gene resistance—was reinforced by the observation that newer isolates of soybean rust from Africa and South America are more aggressive to lines with single-gene resistance (Hartman *et al.,* 2004).

Relevance of vertical resistance in controlling soybean rust

Despite the presence of different pathogen races in some areas, specific resistance is still valuable in controlling soybean rust, particularly in Africa and South America. There, soybean rust is a relatively new disease, so pathogen racial diversity is expected to be still low, and hence specific sources of resistance could be effective for a longer period (De Lucia *et al*., 2008). For example, in South Africa, where rust was first observed in 2001, resistance genes *Rpp2*, *Rpp3* and *Rpp4* were still effective against rust (Pretorius, Visser and du Preez*,* 2007). In Nigeria, Twizeyimana *et al.* (2009) reported that *Rpp1* and *Rpp4* were still moderately resistant. In Brazil, *Rpp2* and *4* were still effective against most rust pathogen races (Laperuta *et al.,* 2008). These genes have remained effective for six years following the appearance of ASR (Garcia *et al.*, 2008). Some single genes, such as *Rpp4,* have shown a lot of promise in sustaining resistance. For example, *Rpp4* is known to have lasted for approximately 20 years in Asia (Hartman, Miles and Frederick, 2005, cited by Garcia *et al.*, 2008). In addition, single genes are easier to work with, as they can be moved into elite breeding stock in a backcrossing scheme in a relatively short time without altering other desirable agronomic attributes. Dealing with single-gene resistance enables efficient selection in the early generations of a breeding programme and increases cost-effectiveness because of the ease of evaluation. Use of marker assisted selection (MAS) for these resistance genes would expedite the introgression process into various genetic backgrounds and increase selection efficiency.

Challenges associated with vertical resistance to ASR

In breeding for resistance to any particular pathogen, sustaining the resistance trait is of great interest. With time, disease ratings of individual plants with specific resistance increase, due to changes in pathogen populations. Reflecting this phenomenon of resistance erosion manifested by 'boom-and-bust cycles' of pathogen agressivity, breeding for durably effective resistance is necessary. Resistance is durable if it has remained effective for a long period in which it has been deployed on a large scale in an environment conducive to the pathogen (Niks and Lindhout, 2006). As noted earlier, resistance to soybean rust pathogens has not lasted for very long due to a combination of rapid pathogen evolution and presence of multiple virulence factors. Additionally, most countries where soybean rust has become endemic have bridge species and functional hosts that ensure that inoculum is always present, further promoting development of new races when resistant varieties are deployed (Anon., 2007). Durability of resistance will therefore largely depend on strategies that slow down pathogen evolution. Paradoxically, introduction of resistant varieties is well known as a mechanism that favours pathogen evolution, thereby complicating further the process of breeding for genetic resistance.

Durable resistance to ASR

Durable resistance is theoretically effective against all races of the ASR pathogen, which is an important consideration, primarily because ASR is a complex of races with multiple virulence factors. In this report, the term 'durable resistance' is used interchangeably with rate-reducing resistance, horizontal resistance, partial resistance and general resistance.

Partial resistance has been identified as a means of controlling soybean rust through production of 'slow rusting' cultivars. Partial disease resistance (PDR) is characterized by a reduced rate of epidemic development in a host population, a phenomenon attributed to various components of PDR that include lower infection frequency, longer latent period, smaller lesions and less spore production per uredinium. The latency period is the time between onset of the infection process and the reproduction of the pathogen. When breeding for resistance to ASR, it is important to have a long latent period as the pathogen has then less capacity to produce secondary infections. The number of ASR spores resulting in a reproducing infection measured per plant, per leaf or per cm^2 of tissue is a parameter of the partial resistance of a cultivar. This form of resistance is thought to be polygenic as it is effective against a broad spectrum of races having some degree of virulence (Long *et al.,* 2006). Though potentially beneficial, the utilization of this form of resistance has not been commonly applied in breeding for resistance to ASR due to the length of time required and difficulty in evaluating progenies for PDR (Hartman, Miles and Frederick, 2005).

In a report by Tschanz and Tsai (1983), lines with partial resistance or slow-rusting lines have been identified at AVRDC and characterized based on latent period and the number of uredinia per lesion. A major impediment in developing lines with rate-reducing resistance has been how to identify them within segregating populations or among accessions that have different maturities. Besides the physiological differences related to maturity, environmental conditions may vary as plants mature at different times. An evaluation method that partially corrects for differences in host maturities has been used (Tschanz, Wang and Tsai, 1983). The soybean relative lifetime (RLT) and the logit transformation of rust severity are used to determine the level of rate-reducing resistance by comparing the slopes of the regression lines.

Lines SRE-Z-11A, SRE-Z-11B and SRE-Z-15A have consistently low rates of rust development and low predicted rust severity. These lines represent the best available levels of rate-reducing resistances (Tschanz, Wang and Tsai, 1983). They have been used as parents in AVRDC's soybean improvement programme.

Characteristics of partial durable resistance

Partial resistance or rate-reducing resistance is quantitatively inherited and offers better potential for long-term control of soybean rust in comparison with control based on single-gene resistance. This form of resistance has a quantitative measure, is polygenic and non-race-specific (unlike single-gene, race-specific resistance) and is either red-brown, tan or has no symptoms. In soybean, this form of resistance has been detected for some diseases, including SRD (Bonde *et al.,* 2006), and *Phytophthora* root and stem rot (Ferro *et al.,* 2006). The occurrence of a wide spectrum of red-brown resistance phenotypes, variation in the number of uredinia per lesion, and varied average uredinia diameters suggests quantitative control of this form of resistance (Bonde *et al.,* 2006). This form of resistance is, however, confounded in most breeding programmes due to the focus on specific-gene resistance (Arias *et al.,* 2008). Moreover, no universally acceptable measure for partial resistance exists, and to date no soybean cultivar with partial resistance to ASR has been released, though this form of resistance is potentially more durable.

In instances where partial resistance has been investigated, the quantitative nature of such resistance implies advanced-stage assessment of adapted lines is to be recommended. Multi-locational testing is crucial in assessing partial resistance, due to the role played by interaction of genotype and environment in evincement of quantitative traits. The segregation of many loci in this type of resistance may also reduce the efficiency of the selection process, which also calls for delaying selection until most progenies have acquired homozygosity at all loci. A greater challenge lies in the identification of partial resistance, since evaluation is time

consuming and requires periodic assessment in the field, making it difficult to incorporate into a breeding programme (Hartman, Miles and Frederick, 2005). The challenges associated with partial and vertical resistance have led to a search for better methods of combating SRD, such as tolerance.

Selection procedure for durable resistance to ASR

Tschanz (1982) made suggestions for selection for rust resistance based on observations that assessing rust severities of single plants collected once or twice during the season is laborious and time consuming, especially for large, non-replicated, early generation populations. The best method of differentiating levels of rate-reducing resistance is to test homozygous or nearly homozygous lines in replicated plots (usually 3×5 m or 4×6 m in size). With this method, rust severity data needs to be collected at least weekly from the onset of the epidemic so that the rate of rust development can be accurately determined. The disadvantage of this method is that relatively few selections can be evaluated and land area requirements are large, particularly if levels of tolerance are to be determined.

A method that seems to be both practical and capable of dealing with large populations involves early-generation advance without selection; mid-generation selection for tolerance; and late-generation selection for rate-reducing resistance, tolerance and agronomic characters. Early-generation advance can be accomplished by either a bulk or single-seed descent method, depending on desired population size and diversity. Plants in the F_4 and F_5 generations would be selected for their level of tolerance, and their seed would be bulked within families. Line selection would occur in the F_6 generation and would be based on desired levels of tolerance and resistance. The F_7 generation would be used to determine the homozygosity of the lines and their levels of rate-reducing resistance, as well as for multiplying seed for the next series of tests, which would more precisely determine levels of rate-reducing resistance.

The rate of rust development is best calculated by regressing the logit of percent-rust-severity on relative time (RT) (Tschanz, Wang and Tsai, 1983). Relative time is used instead of days after planting to partially compensate for the differences in maturity duration between cultivars, and is calculated using the formula:

$$RT = \frac{\text{Days after planting (DAP)} \times 100}{\text{Days to full maturity (DFM)}}$$

The available information indicates that variation in levels of rate-reducing resistance exists even in resistant cultivars that are not specifically selected for rate-reducing resistance. The rate-reducing resistance to soybean rust is apparently inherited quantitatively because the variation in levels of rate-reducing resistance in a population appears to have a continuous distribution. Previous observations of cultivar × environment interaction, when rust development is evaluated on cultivars grown in different locations and seasons, also indicate that rate-reducing resistance is quantitatively inherited (Gillett, 1986). These observations suggest that recurrent selection can be used to concentrate reducing-resistance genes from different sources into one genotype.

Tolerance to ASR

Ineffectiveness of race-specific resistance and difficulties associated with selecting for partial resistance prompted AVRDC to develop new methods for improving the yield of rust-affected soybean cultivars, including selection for tolerance to ASR. Tolerance is defined as the relative yielding ability of soybean cultivars grown under severe rust stress. Tolerance to SRD has been identified and used to minimize yield losses due to ASR, especially in the Orient, where the disease has been endemic for a long time. Yield gains of 30–60% over control cultivars (AVRDC, 1992) have been achieved when using tolerant varieties.

Sinclair and Hartman (1995) reported that tolerance to ASR is best estimated by yield comparisons between the same genotypes planted in a fungicide-protected plot and a non-

fungicide-protected plot. Although it requires additional field space, tolerance is assessed once per season, unlike the effort required to obtain data for disease progress curves, for defoliation, and for pustule counts when assessing rate-reducing resistance (Shanmugasundaram, Yan and Wang, 2004). Based on this selection procedure, lines have been selected and screened in rust tolerance trials in Taiwan and Thailand (Yang *et al.,* 1999), leading to advanced materials with good levels of tolerance or characterized by lower yield loss and better 100-seed weight than control treatments. Tolerance as a selection criterion for breeding soybean rust-resistant lines has thus led to the development of rust resistant high yielding lines.

Consequently, breeding effort has shifted towards selecting for tolerance as a means of sustaining soybean productivity. To exploit tolerance in breeding programmes, soybean lines at advanced stages of development need to be evaluated in various agro-ecological zones where adequate disease pressure is assured. Superior tolerant genotypes can then be released for commercial production or used in crosses to create populations with variability for the trait. Tolerance has great potential since it does not promote selective reproduction of soybean rust, thus curtailing pathogen evolution. Selection of accessions for tolerance involves a number of approaches, but a common feature is that the material has to be evaluated in a soybean crop with and without fungicide application, in different seasons and locations. Kawuki, Adipala and Tukamuhabwa (2003) described two approaches that could be used in the process of evaluating soybean genotypes for tolerance. The first approach is percentage yield loss, that uses the formula:

$$\text{Tolerance} = \frac{\text{Yield of rust protected plot - yield of unprotected plot}}{\text{Yield of rust-protected plots}} \times 100$$

A second approach involves the use of a rust tolerance index (RTI), which is computed by:

$$\text{RTI} = \text{yield of unprotected plots} / \text{yield of rust protected plots}$$

Similar to RTI, Shanmugasundaram, Yan and Wang, (2004) used a stress tolerance index (STI), using a three-dimensional plot to select rust tolerant, high yielding lines. In this procedure, the x–y plane is divided into four segments by drawing intersecting lines through the midpoints of the x and y planes. The z-axis indicates the level of stress tolerance (STI) that a line has in any one of the four groups (Figure 8). Rust severity and percentage yield loss will be plotted on the x and y axes, respectively. The z-axis will thus enable selection of rust-tolerant, high yielding lines. Potential yield represents a fungicide-sprayed environment, and the mean potential yield is the average of several fungicide-treated plots.

STI is estimated as:

$$\text{STI} = (Y_s \times Y_p) / (Y_p)^2$$

where Y_s is yield in a soybean rust environment (x-axis), Yp is the yield from a rust-protected field (y-axis), and Y_p is mean yield from a rust-protected field.

The genotypes are then grouped into four categories based on their performance in rust and non-rust environments. Group A genotypes perform equally well in rust and non-rust environments; Group B genotypes perform well only in a no-rust environment; Group C genotypes yield relatively better in rust environments; and Group D genotypes perform poorly in environments with or without rust. Using the STI method, researchers from AVRDC have been able to identify a number of rust-tolerant lines.

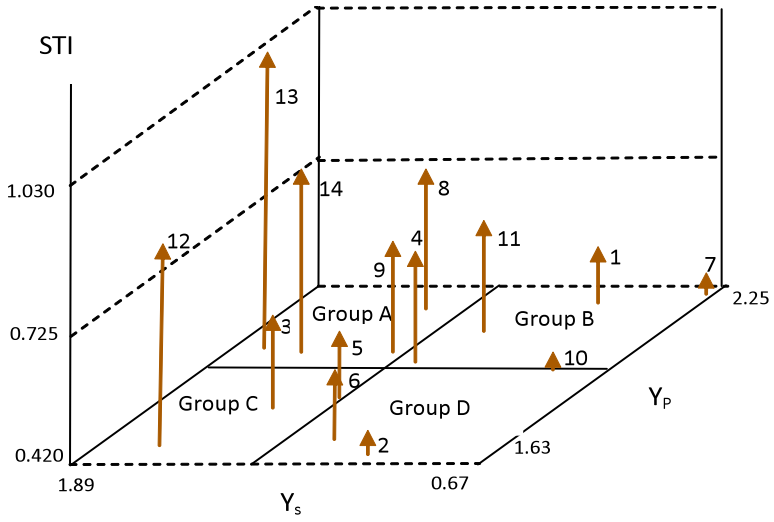


Figure 8. Three-dimensional plot for stress tolerance index (STI) determination (Modified from Shanmugasundaram, Yan and Wang, 2004).

Figure 9. An advanced yield trial evaluation soybean lines for tolerance to ASR in Uganda. On the left is cv. Duiker, which is susceptible to ASR; on the right is line MNG 8.10 [released as cv. Maksoy 2N], which shows tolerance to ASR.

Breeding for tolerance to ASR

Owing to the shortcomings of vertical and partial resistance mechanisms, researchers from AVRDC shifted their focus to tolerance (Shanmugasundaram, Yan and Wang, 2004; Hartman, Wang and Tschanz, 1991; Wang and Hartman, 1992). A desirable attribute of this form of 'resistance' is that it does not impose selection pressure on the ASR pathogen, and hence does not provoke the appearance of new races (Arias *et al.,* 2008). It is important to note that tolerance is quantified in terms of yield, and therefore is dependent on various yield components. Soybean yield components that can be easily determined in the field under experimental conditions are number of pods per plant, number of filled pods per plant, and 100-seed weight. These can then be used to compare different lines for their ASR tolerance levels.

According to Kawuki, Adipala and Tukamuhabwa (2003), there is great variation in tolerance among soybean cultivars, which is highly desirable as variation forms the basis of selection for trait improvement. Thus, Shin (1986) reported yield losses of 22% in tolerant cultivars compared with 69% in susceptible cultivars. Superior tolerant and non-tolerant

genotypes can be used in crosses to generate populations with variability for tolerance. Furthermore, (Arias *et al.,* 2008) have suggested the existence of additive gene effects, implying that selection is likely to be effective for the development of new tolerant soybean varieties. To exploit tolerance, high yielding advanced generation lines need to be evaluated through multi-locational testing, using any one of the three methods discussed in the section above on *Tolerance*. Initial early generation selections can be based on other desirable agronomic traits, such as pod and seed development, and undesirable individuals discarded. In later generations, such as F_5, selection can be based on number of fully filled pods without any abnormalities despite high rust severity (Tschanz and Wang, 1987).

In Uganda, a similar strategy has been implemented by the soybean breeding programme through collaborative effort by Makerere University and the National Agricultural Research Organization (NARO) to develop tolerant line Maksoy 2N (MNG 8.10), released in 2008. Using RTI, a number of lines were selected based on mean RTI (Table 7), where the closer the value to 1 the less the yield loss and the more tolerance; greater than 1 implies a decrease in yield due to fungicide application. Based on the RTI and other criteria, MNG 8.10 was released as Maksoy 2N.

Research in Uganda has consistently shown that genotypes resistant to ASR show a reduction in yield once fungicides are applied (Tukamuhabwa, Dashiell and Assafo*,* 2001; Kawuki, Adipala and Tukamuhabwa, 2003; Oloka, 2007). These observations confirm the superiority and effectiveness of host plant resistance. The mechanism that reduces performance of resistant genotypes once sprayed needs further exploration.

Table 7. Mean yields and RTIs of test genotypes over two seasons in Uganda.

Genotype	**Mean yield** (kg/ha)		**RTI**		
	Unprotected	**Rust protected**	**2006A**	**2006B**	**Mean RTI**
MNG 8.24	1727	1866	0.89	0.96	0.94
MNG 8.22	1554	1877	1.01	0.68	0.86
MNG 10.3	1693	1939	1.04	0.73	0.90
MNG 8.6(B)	1548	1840	1.00	0.72	0.87
Maksoy 1N(1)	1759	1434	1.13	1.32	1.26
Nam 1	1254	1404	0.84	0.94	0.91
Namsoy 4M(1)	1656	1621	0.98	1.04	1.03
MNG 3.26	1785	1822	1.00	0.96	0.99
MNG 4.19	1790	2087	0.87	0.85	0.86
MNG 9.17	1258	1589	1.01	0.71	0.89
MNG 8.10 [Maksoy 2N]	1702	1775	0.92	0.98	0.96
MNG 1.15	1175	1658	0.74	0.68	0.73
MNG 14.1-12	1523	1915	1.06	0.61	0.84
MNG 5.12	1626	1722	0.99	0.89	1.01
MNG 11.2	1940	1932	1.02	0.99	1.02
Mean	1599	1765	0.97	0.89	0.94
LSD5%	371	466	NS	0.31	0.27
CV%	20.2	23.0	25.8	21.0	25.0

NOTES: (1) = commercial cultivar. NS = not significant. SOURCE: Adapted from Oloka, 2007.

Evaluation of wild species and hybridization with Glycine max

Sinclair and Hartman (1996) reported the genus *Glycine* Willd. to be divided into two subgenera, *Glycine* and *Soja* (Moench) F.J. Herm. (Table 8). The subgenus *Soja* includes the cultivated soybean *G. max* (L.) Merr. and the wild soybean, *G. soja* Siebold & Zucc. Both species are annual, diploid with 2n=40, and hybridize readily. Soybean grows only under cultivation, while *G. soja* grows wild in China, Japan, Korea, Taiwan and Russia. *G. max* and *G. soja* form the primary gene pool for the cultivated soybean (Kingsolver, Melching and Bromfield, 1983). *G. soja* is the wild ancestor of the soybean (Hartman, Wang and Hymowitz, 1992; Melching, Bromfield and Kingsolver, 1983).

All of the perennial species related to soybeans are found in Australia. The range of *G. tabacina* extends also to mainland China, parts of Oceania, the Rukyu islands and Taiwan. The range of *G. tomentella* also extends beyond Australia into southern China, Papua New Guinea, the Philippines and Taiwan. *G. soja* and the perennial *Glycines* are potential sources of genes for resistance to rust (Sinclair and Hartman, 1996). Testing of current germplasm holdings of wild Glycine species and the collection of additional germplasm, particularly from the Asian-Oceania-Australian centre of *Glycine* diversity, is needed. At present, the USDA soybean germplasm collection has 888 accessions, with representatives of all wild *Glycine* taxa.

Table 8. Species in the genus *Glycine* Willd. and their three-letter code, ploidy, standard, genome symbol and distribution (Hymowitz, 1996).

Species	Code	2n	Standard	Genome	Distribution
Subgenus *Glycine* J.C.Wendl.					
G. albicans Tind. and Craven	ALB	40	—	—	Australia
G. arenaria Tind.	ARE	40	505204	—	Australia
G. argyrea Tind.	ARG	40	505151	A2A2	Australia
G. canescens F.J.Herm	CAN	40	440932	AA	Australia
G. clandestina J.C.Wendl.	CLA	40	440948	A1A1	Australia
G. curvata Tind.	CUR	40	505166	C1C1	Australia
G. cyrtoloba Tind.	CYR	40	440963	CC	Australia
G. falcata Benth.	FAL	40	505179	FF	Australia
G. hirticaulis Tind. and Craven	HIR	40	—	—	Australia
G. hirticaulis Tind. and Craven		80			
G. lactovirens Tind. and Craven	LAC	40	—	—	Australia
G. latifolia (Benth.) Newell and Hymowitz	LAT	40	378709	B1B1	Australia
G. latrobeana (Meisn.) Benth.	LTR	40	483196	A3A3	Australia
G. microphylla (Benth.) Tind.	MIC	40	440956	BB	Australia
G. pindanica Tind. and Craven	PIN	40	—	—	Australia
G. tabacina (Labill.) Benth.	TAB	40	373990	B2B2	Australia
G. tabacina (Labill.) Benth.		80	—	Complex	Australia, West Central South Pacific Islands
G. tomentella Hayata	TOM	38	440998	EE	Australia
G. tomentella Hayata		40	—	DD2	Australia, Papua New Guinea
G. tomentella Hayata		78	—	Complex	Australia, Papua New Guinea
G. tomentella Hayata		80	—	Complex	Australia, Papua New Guinea, The Philippines, Taiwan
Subgenus *Soja* (Moench) F.J.Herm					
G. soja Siebold and Zucc.	SOJ	40		GG	China, Russia, Taiwan, Japan, Korea (wild soybean)
G. max (L.) Merill	MAX	40		GG	Cultigen (soybean)

The potential use of wild perennial *Glycine* species in plant improvement programmes has been discussed in Australia and the United States of America (Hymowitz, 1996). The wild perennial *Glycine* present a potentially rich source of germplasm for soybean breeders, yet these species have been relatively little studied or exploited in plant breeding programmes. *Glycine* accessions from Australia were screened for resistance to soybean rust in Taiwan, and high levels of resistance were found in accessions of *G. argyrea, G. clandestina, G. tabacina* (2n=80) and *G. tomentella* (2n=40, 80). Over three years, 294 accessions, representing 12 perennial *Glycine* spp., were screened for resistance to *P. pachyrhizi* (Kuchler *et al.,* 1984), with 23% found resistant, 18% moderately resistant and 58% susceptible. Of the *G. tabacina* (2n=80) accessions, 59 (40%) were resistant in two experiments. Resistance to *P. pachyrhizi* was found in accessions of *G. argyrea, G. canescens, G. latifolia, G. microphylla, G. clandestina* and *G. tomentella*, but not in accessions of *G. arenaria, G. cyrtoloba, G. curvata,* and *G. falcata*.

Both race-specific and race-non-specific genes have been reported in some perennial *Glycine* spp. Single resistance genes were detected in lines of *G. canescens*, at four distinct loci, and a single major gene for resistance was found in *G. argyerea*. However, the usefulness of these resistant genes will depend on how easy it is to transfer them to soybean, and their stability over time and against all races of *P. pachyrhizi* that occur in the various geographical areas. In *G. canescens*, each group may have several resistant genes or loci. There are two groups of wild soybeans containing between 10 and 12 resistant genes (Tan, Yu and Yang*,* 1995).

Challenges of wide crosses

The hybrids from intra-subgeneric crosses with *G. max* have high levels of resistance but have not been exploited in soybean breeding programmes. Incorporating rust resistance from the perennial species into cultivated soybean through wide hybridization has been largely ineffective because of the problems associated with sterility of the resulting hybrids. There has also been a lack of effort by the scientific community, probably because of pod abortion, which is a post-fertilization problem (Sinclair, 1989). However, concerted efforts to obtain wide hybrids have resulted in only a few sterile F_1 hybrids. Of the 16 wild perennial *Glycine* spp. currently identified taxonomically, only four species (*G. argyrea*, *G. canescens*, *G. clandestina* and *G. tomentella* (2n=78, 80)) have been hybridized successfully with soybean.

Singh, Krishna and Hymowitz (1996) produced for the first time fertile lines with 2n=40, 41, 42, 43 or 44 chromosomes from an amphidiploid (2n=118) of *G. max* (2n=40) × *G. tomentella* (2n=78), which opened up the feasibility of gene introgression from wild perennial *Glycine* spp. to broaden the soybean genetic base. However, the current utilization by breeders of this resistance, or the genes for this resistance present in several *Glycines*, is not known (Bromfield, 1984).

The way forward

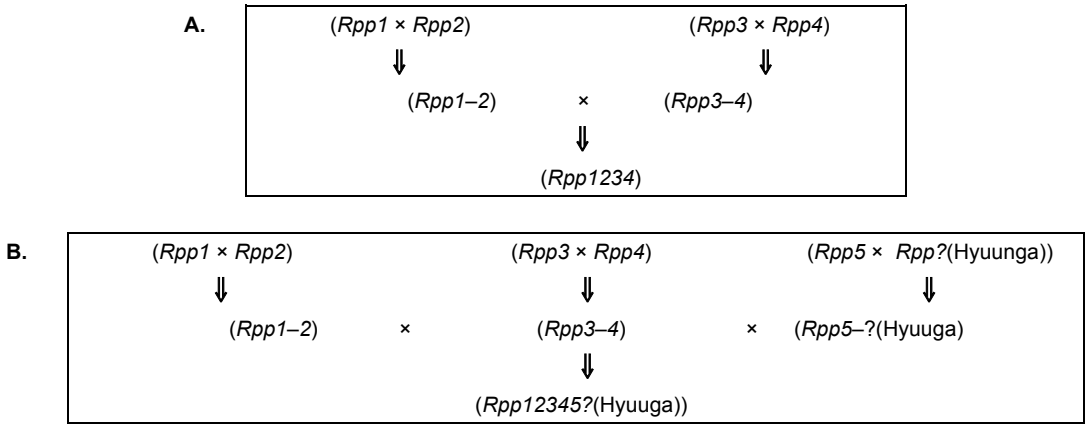
Breeding for durable resistance against the highly variable ASR deserves high priority among rust mitigation strategies. Soybean remains under threat and urgent steps need to be taken to ensure sustainable soybean production in developing countries. These mitigation strategies can be broadly divided into three: short-, medium- and long-term. However, these may vary depending on the status of breeding programmes, but we have decided to conveniently divide them into these three broad groups.

Short-term strategies

Single-gene resistance

Single-gene resistance will remain a key method in the control of ASR, though in many cases it has proved not to be durable. However, because of the relative ease with which it is identified, evaluated and introgressed, most of the breeding programmes in their infancy or seeking immediate remedies to ASR will use the available resistance genes as a means of ASR control. A number of researchers have suggested using various gene combinations as a way of enhancing durability of the resistance (Ribeiro *et al.,* 2008; Hartman, Miles and Frederick, 2005). Gene pyramiding (stacking) of the various genes into one genetic background, has also been suggested by Garcia *et al*., (2008) as a means of enhancing the longevity and effectiveness of the resistance. In the interim, this could be a feasible approach. Moreover, the availability of a dense molecular map makes the prospects of implementing MAS possible (Song *et al.,* 2004). To date, the simple sequence repeat markers for the four widely used genes have been mapped: *Rpp1* on linkage group G (Hyten *et al.,* 2007); *Rpp3* on linkage group C2 (Hyten *et al.,* 2009); and *Rpp2* and *Rpp4* on linkage groups J and G, respectively, by Garcia *et al.* (2008). The primers, repeat motifs and SSR loci of the specific loci are available from Soybase – the Soybean data bank (See: http://soybeanbreederstoolbox.org). A proposed pyramiding scheme for the four resistance genes is illustrated in Figure 10. As new sources of resistance are mapped and primers designed, this scheme can be modified accordingly to suit the genes present. For pyramiding to be an effective tool, monitoring of ASR virulence patterns has to be done and new resistance genes introgressed to provide resistance to emerging races.

Figure 10. Possible crossing schema for pyramiding resistance genes (A), and its possible extension (B) to incorporate additional genes.



Limited research has gone into the exploration of the avenues of specific gene pyramiding for SRD resistance. DNA markers can be used as a precise and efficient tool for multiple gene identification and selection (Yamanaka *et al.,* 2008; Peleman and van der Voort, 2003). Breeders can therefore select for specific genes of interest at an early stage, even in the absence of the Soybean rust pathogen. This is particularly important due to the dependence on weather conditions for rust to be expressed. When weather conditions are not conducive for rust development, the crop remains clean and selection is not practical. Research is needed to understand how these genes interact in one genetic background and how they affect the overall agronomic performance and acceptability of a new cultivar. Repeatability of MAS will need to be established in different genetic backgrounds to fully exploit the potential of molecular markers. This will promote use of these markers in different germplasm sources.

Need to characterize new sources of gene resistance

Not all resistance genes have been characterized. Some resistant genotypes have been identified, such as UG5, that is resistant to all isolates in Uganda and Nigeria (Tukamuhabwa, Dashiell and Assafo, 2001; Twizeyimana *et al.,* 2009); or PI 417125, PI 203398, PI 416764, PI 417115, PI 416819, PI 340050 and PI 417503, identified by Miles, Frederick and Hartman (2006) as resistant to SRD in Brazil. However, the nature of the resistance in such lines and others is not known and cannot be matched with the genes already characterized.

In many breeding programme, the absence of high levels of resistance necessitates the search for new sources of resistance. Identifying new forms of resistance will be particularly useful if the identified genes are different from those already known. Thus there is need to characterize all new sources of resistance and determine their allelic relationship. For example, several allelic experiments by Pierrozi *et al.* (2008) and Laperuta *et al.* (2008) in Brazil have contributed towards identifying new resistance sources, thus making their genetic potential available for management of ASR worldwide. Based on allelic tests for *Rpp2* and *Rpp4,* which are still effective against ASR, 23 new sources of resistance were identified (Table 9) (Laperuta *et al.,* 2008). These tests analysed the F_2 segregation pattern of bi-parental progeny from *Rpp2* and *Rpp4* testers with the resistant sources, using a Chi square test. Using a single, pure isolate that overcame the resistance in *Rpp1* and *Rpp3,* characteristic segregation ratios were assessed. Allelic tests depend on the availability of pure isolates to prevent ambiguity in interpretation. Where races in the inoculum are mixed, two reaction phenotypes can be expressed on the leaves, complicating interpretation. To ensure purity of the isolates, three cycles of single spore isolation and propagation on a susceptible host are recommended.

The identification of new sources of resistance implies that breeders can have a wider range of genes to utilize in breeding, rather than having to depend on the widely used *Rpp1–4* genes. Breeders can also collaborate with farmers through participatory research to identify landraces that could be sources of resistance. Inheritance studies for the new sources of resistance are also important to rationalize the variety development process (Arias *et al.,* 2008). Based on allelic test and inheritance studies, new sources of resistance can be identified, together with mechanisms of gene control.

Need for effective race differentials

In most developing countries it is difficult to predict the performance of varieties due to lack of information on the genetic diversity of the rust pathogen. Knowledge of pathogen variability in the different soybean growing areas is vital if resistance is to be an effective tool in the management of SRD. So far, most of the limited work on determining pathogen variability has involved race differentials. A major hurdle to overcome has been the lack of universally valid race differentials. For example, AVRDC recommended race differentials that succumbed to ASR in South Africa (Caldwell, Govender and Laing, 2003). Thus seeking effective race differentials will play a critical role in race identification.

Table 9. Segregation ratios from the *Rpp2* and *Rpp4* testers, and conclusion drawn.

Source	Ratio with *Rpp2*	Ratio with *Rpp4*	Conclusion
PI 197182	1:0	15:1	Gene *Rpp2*
PI 230971	1:0	13:3	Gene *Rpp2*
PI 417125	1:0	15:1	Gene *Rpp2*
GC 84058-21-4	15:1	15:1	New gene
PI 408251	15:1	15:1	New gene
PI 379618 TC1	15:1	15:1	New gene
Nova Santa Rosa	15:1	15:1	New gene
PI 203398 (Abura)	15:1	15:1	New gene
PI 423966	15:1	15:1	New gene
PI 416764	15:1	15:1	New gene
PI 417115	15:1	15:1	New gene
PI 416819	15:1	15:1	New gene
GC 84058-18-4	15:1	15:1	New gene
PI 398526	13:3	13:3	New gene
PI 339866	13:3	15:1	New gene
PI 340050	13:3	15:1	New gene
PI 417503	13:3	15:1	New gene
PI 417421	13:3	15:1	New gene
PI 203406	13:3	15:1	New gene
FT 87-17893	13:3	15:1	New gene
PI 417074	13:3	15:1	New gene
PI 408205	13:3	15:1	New gene
GC 84051-9-1	15:1	13:3	New gene
PI 416810	15:1	13:3	New gene
PI 200487 (Kinoshita)	15:1	13:3	New gene
PI 423962 (Hyuuga)	15:1	13:3	New gene

SOURCE: Laperuta *et al*., 2008.

Another approach that could be used is to characterize the ASR races using molecular tools. This offers great promise due to the potentially unlimited polymorphisms that can be revealed by DNA markers. Thus breeding programmes engaged in race characterization have to evaluate the potential of molecular markers, such as simple sequence repeats (SSRs), in assessing pathogen variability. From this information, the level of genetic diversity and evolutionary relationships can be determined, which are fundamental factors in breeding for disease resistance. Inventories of pathogen races can enable targeted breeding, resulting in resistance gene deployment. Molecular techniques will also be valuable tools to monitor virulence patterns of pathogen populations to manage SRD.

Inventories of dominant races have been undertaken in countries such as Taiwan (Wang and Hartman, 1992), Thailand (Poonpolgul, 2004), Nigeria (Twizeyimana *et al.,* 2009), and Uganda (Lamo, 2004); De Lucia *et al.*, 2008). However, the pace and consistency with which this has been done implies that breeding efforts have lagged behind the rate of pathogen evolution. In addition, race identification has been confusing because there is no standard method in use by all breeders.

Need for a network to address ASR

Concerted effort is necessary to counter the SRD threat, given the potential of urediniospores to migrate across national boundaries. Soybean rust information networks for disseminating and sharing information can be formed across various developing countries to facilitate integrated research through interdisciplinary expertise. A soybean rust network is necessary to guide development of standard methods for race identification, to identify

worldwide collections of sources of resistance and isolates, especially in support of developing countries.

Medium-term strategies

Determining parental lines with additive gene effects

The observation by Kato and Yorinori (2008) that genetic background plays a crucial role in the expression of resistance might suggest that combining-ability analyses could contribute towards the quest for effective durable resistance. Soybean breeding has largely been dependent on the generation of bi-parental crosses and advancement of segregating progenies to homozygosis. Combining-ability studies provide a guide that can be used to formulate systematic breeding (Awan, Malik and Siddique, 2005). Due the aggressiveness of African and other New World isolates towards accessions with single-gene resistance, it is imperative to determine effective gene combinations (Hartman *et al.,* 2004). Such analyses can be done using either locally available germplasm or widely used resistant genotypes, or both. Appropriate mating designs should be employed in generation of populations for analysis.

Partial resistance and tolerance

A focus on breeding for partial resistance and tolerance is likely play a crucial role in the foreseeable future. However, the success of utilizing partial resistance will depend on the establishment of precise methods for evaluating this rate-reducing resistance. This is a challenge, given the time-consuming nature of evaluation, and the non-availability of standard approaches for selecting for such a form of resistance. Novel approaches, such as histological assays (Bonde *et al.,* 2006) or evaluation and modelling with linear models could help in the prediction of partial resistance (Wagner, Carmer and Wilkinson*,* 1992). Histological assays are more critical measures that are able to detect subtle differences between genotypes arising from partial resistance. This technique involve inoculating leaves with soybean rust, excising the leaves from the plant, removing chlorophyll pigmentation and staining uredinia for better visualization (Bonde *et al.,* 2006).

Other breeding methods, such as recurrent selection, will be valuable in developing resistant cultivars. This is important as rate-reducing resistance expressing additive gene effects has been observed to be dispersed in different parental genotypes. Thus, to concentrate these genes, crosses involving genotypes need to be done pending the release of cultivars with rate-reducing resistance (Ribeiro *et al.,* 2007). Tolerance to ASR will similarly provide a medium-term strategy towards containing SRD. However, in some Asian countries where vegetable soybean is grown, this type of resistance may reduce the market value for the fresh pods. In instances where soybean is grown as a grain crop this method is the most strategically important method. This, combined with the fact that tolerance does not promote development of new races, will be welcome in all countries grappling with multiple races of the pathogen.

Long-term strategies

Pre-breeding for resistance against ASR

The increase in the number of species in the subgenus *Glycine* has been the result of extensive plant exploration. Exploitation of the wild progenitors is a reasonable approach since a cultigen (e.g. the soybean) and its wild progenitor (*G. soja*) are genetically members of the same species and gene transfer between them is a relatively easy task. Use of other wild species, such as those belonging to the secondary or tertiary gene pools of soybean (Kingsolver, Melching and Bromfield, 1983), is much more difficult, since various types of isolating mechanisms that prevent gene flow between them and soybean must first be overcome.

Genetic diversity is the foundation for sustainable development of improved varieties. However, given the narrow genetic base of modern soybean cultivars, new sources of resistance can also be sought from closely rated *Glycine* species that have been shown to contain resistance genes against a number of fungal pathogens (Hartman *et al.,* 2000). Related perennial species, such as *G. tomentosa* (2n=78) have been observed to possess high levels of resistance, greater than *Rpp1–4* (Patzoldt *et al.,* 2007). The narrow genetic base—attributed to the self-pollinated nature of soybean—and stringent quality requirements by processors and consumers make exploitation of wild relatives a necessity to generate more genetic variation. Variability studies by Nichols *et al.* (2007) identified a greater number of alleles in *G. soja* than in *G. max,* suggesting that the former could be a potential source of novel alleles, given that the two species have the same chromosome number and are cross compatible. Wild, un-adapted lines may possess desirable alleles for quantitative traits that might not be present in elite breeding material (Tanksley and McCouch, 1997). Hence, genetic improvement through pre-breeding can benefit both qualitative and quantitative forms of soybean rust resistance.

Most breeding programmes are profit oriented and therefore unwilling to invest in pre-breeding due to the uncertainty in results. Pre-breeding research is faced with challenges of linkage drag and differences in ploidy levels between wild relatives such as *G. tomentosa* and domesticated *G. max*. Breeding efforts in this area require coordinated and sustained effort to ensure continuity because of long duration and the substantial investment needed to achieve an agronomically acceptable genotype. To expedite pre-breeding, efforts should be directed at biotechnological approaches such as MAS and genetic transformation. Given the precision and efficiency of MAS and genetic transformation through linkage drag reduction, the goal of pre-breeding can be realized. Gene discovery and isolation studies for transformation also hold promise, considering that they can be transferred irrespective of the source of gene construct once a suitable gene is identified. Cassettes of unique pyramids of disease resistance genes can also be incorporated through genetic transformation, expediting the resistance breeding process (McDonald and Linde, 2002).

Breeding for diverse pathogen population

In the long term, breeding efforts can focus on breeding for resistance to diverse pathogen populations to safeguard against any changes in pathogen races. In Africa, IITA has been involved in breeding soybean varieties for diverse pathogen rust populations and has recently released TGX 1835-10E, which is resistant to pathogen races in central, eastern, western and southern Africa. In Nigeria, this line is resistant to all known races of soybean rust (IITA, 2010). In Uganda, genotype TGX 1835-10E was released in 2004 as a rust resistant cultivar ‘Maksoy 1N’ by Crop Science Department of Makerere University. South America could adopt a similar strategy, which would make it possible for a genotype to be cultivated irrespective of the prevalent soybean rust pathogen race.

Role of multi-lines in ASR resistance breeding

Horizontal resistance is known to be durably effective in controlling many plant diseases, including SRD. It is, however, a challenge to manipulate this form of resistance in breeding programmes. Given the diversity of resistance genes—*Rpp1–5*, *Rpp?*(Hyuuga) and others—multi-lines could be constituted to buffer the soybean varieties against different pathogen populations. Multi-lines are mixtures of isolines in a given proportion, each with a single gene controlling different forms of the same character. A highly desirable attribute of multi-lines is the reduced selection pressure challenge to pathogens. Based on current observations, no variety is resistant to all races of ASR, so this approach could stabilize yield in rust endemic areas. However, the effectiveness of a multi-line is dependent on the knowledge of existing races to ensure inclusion of lines that match prevailing pathogen races. Moreover, soybean can fit well in the multi-line arrangement, since the cream seed colour is preferred in most markets. Multi-line development would focus more on synchronizing maturity dates and seed size.

Developing countries can also champion breeding, using novel techniques such as micro-array analyses, which represent the latest front in agricultural research. Most of the research on soybean rust resistance has focused at the DNA level. A wealth of information and insights can be gained through expression profiling studies to identify other candidate genes and proteins expressed in resistant soybean plants challenged by rust. Studies on ASR-soybean molecular interactions can help future efforts to breed for durably effective resistance (van de Mortel *et al.,* 2007). Such research, however, will require collaborative efforts between developing countries and established institutions. Better insights on mechanisms can be obtained from model plants and alternative hosts to assist in breeding for durable resistance.

Conclusions

Whereas breeding for durable resistance to soybean rust is important to soybean producing developing countries, overemphasis on such resistance breeding may have a yield penalty. Reliance on a few sources of resistance narrows genetic variability and limits progress in breeding for other desirable attributes, such as yield. Thus, utmost care needs to be taken during the evaluation and selection process so as not to compromise on yield, since it is the ultimate goal when breeding for resistance.

Soybean breeding programmes in developing countries need also to establish networks to share interdisciplinary expertise, knowledge and technology.

Conventional breeding techniques have so far had a significant impact in reducing the devastating impact of SRD; many other new opportunities remain to be explored. Due to limited financial resources, such conventional techniques will continue to play a significant role in improving soybean germplasm for resistance to SRD.

Adequate financial and human resources would enable developing countries to use molecular plant breeding techniques. Such techniques hold great promise for the genetic improvement of various traits, and even more so with the availability of a dense molecular marker map of soybean.

The potential inherent in the wild relatives of soybean is likely to be unlocked by the use of molecular markers, reflecting their ability to reduce linkage drag from these unadapted species.

Finally, to achieve any meaningful results, breeding for durable resistance must be an ongoing process, focusing on all forms and sources of resistance.

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State of knowledge on breeding for durable resistance to soybean rust disease in the developing world

This publication was the result of a competitive call for papers to review the state of knowledge on breeding for durable resistance, and prospects for improvement of resistance to wheat (*Triticum aestivum* L.) and soybean (*Glycine max* L.) rusts. The purpose of these studies was to support efforts directed to climate change adaptability and mitigation through enhanced and sustainable use of genetic variability. Topics covered include: 1. worldwide rust threats with high impact to food security (current and potential); 2. general approaches to breeding for resistance to these diseases; 3. relevance of vertical resistance approaches; 4. relevance of horizontal, durable resistance; and 5. the way forward.

GIPB is pleased to present the review papers that resulted from this initiative: Sustainable wheat rust resistance - Learning from history by P. S. Brennan (Plant Production and Protection Paper Series 203) and State of Knowledge on Breeding for Durable Resistance to Soybean Rust Disease in the Developing World by P. Tukamuhabwa and M. Maphosa (Plant Production and Protection Paper Series 204).