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REVIEW

Soybean production in eastern and southern Africa and threat of yield loss due to soybean rust caused by *Phakopsora pachyrhizi*

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Soybean is a major source of oil and proteins worldwide. The demand for soybean has increased in Africa, driven by the growing feed industry for poultry, aquaculture and home consumption in the form of processed milk, baked beans and for blending with maize and wheat flour. Soybean, in addition to being a major source of cooking oil, is also used in other industrial processes such as in the production of paints and candle wax. The demand for soybean in Africa so far outweighs the supply, hence the deficit is mainly covered through imports of soybean products such as soybean meal. The area under soybean production has increased in response to the growing demand, a trend that is expected to continue in the coming years. As the production area increases, diseases and insect pests, declining soil fertility and other abiotic factors pose a major challenge. Soybean rust disease, caused by the fungus *Phakopsora pachyrhizi*, presents one of the major threats to soybean production in Africa due to its rapid spread as a result of the ease by which its spores are dispersed by the wind. Disease control by introducing resistant soybean varieties has been difficult due to the presence of different populations of the fungus that vary in pathogenicity, virulence and genetic composition. Improved understanding of the dynamics of rust ecology, epidemiology and population genetics will enhance the effectiveness of targeted interventions that, in turn, will safeguard soybean productivity.

Keywords: control, epidemiology, genetic composition, pathogenicity, soybean demand, virulence

Soybean: its general use and economic importance

Soybean (*Glycine max*) is an important legume plant that is cultivated all over the world, not only as a major source of oil and protein in livestock feeds but also for human consumption, soil fertility improvement and, amongst others, for producing industrial products such as soy inks, non-toxic adhesives, candles and paints (Hartman *et al.*, 1999, 2011b). Soybean is produced on about 6% of the world's arable land, representing an estimated total area of more than 92·5 million ha, giving 217·6 million tonnes of production each year. Soybean has a high protein content (about 40%) of good nutritional quality, and a high oil content (about 20%) which, together with numerous beneficial nutrients and bioactive factors, make soybean the crop of choice for improving the diets of millions of people in developing countries (Ali, 2010). Soybean can be used blended with maize and wheat flour as a source of protein, or as soymilk, but soybean is also eaten as baked beans or in the form of soy paste or fermented soybean curd (tofu). Full-fat soy flour is used in bakery and dietetic foods and in novel products, such as tofu-based ice cream and soybean yogurt. Due to its protein content it can help to reduce malnutrition among children and nursing mothers when incorporated into other meals, hence enhancing nutrition in the developing world. Additionally, soybean plays a major role in improving soil fertility due to its ability to fix in the range of 44–103 kg of atmospheric nitrogen per hectare per year, thereby alleviating the need to apply large amounts of nitrogen fertilizer (Sanginga *et al.*, 2003). This advantage is especially important for crop production in Africa due to the economic limitations in the use of fertilizers. Soybean and its derivatives are among the most important agricultural products traded in the world market.

Global soybean production rose nearly 10-fold, from 27 million tonnes in 1961 to 276 million tonnes in 2013

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(FAOSTAT, 2013). The USA is the leading producer of soybean, accounting for about 32% of the global production, followed closely by Brazil (29%) and Argentina (17%) (FAOSTAT, 2013). The USA is also the main exporter of soybean, accounting for 44% of global exports, followed by Brazil with 34%. China accounts for nearly 59% of the total world import of soybean, followed by the EU (16%). The world trade for the six major legumes was estimated to be more than $21·8 billion in export, with soybean accounting for 84% of the total, followed by common bean (8·8%), groundnut (4·9%) and chickpea (2·4%) (Abate *et al.*, 2012). As a major source of oil and protein, soybean accounts for about 56 and 67% of the total global oilseed production and world supply of protein to be consumed, respectively (USDA, 2014).

Soybean diseases, such as bacterial pustule, frogeye leaf spot, red leaf blotch, soybean rust and bacterial blight have been reported to cause massive yield losses in sub-Saharan Africa (SSA) (Kawuki *et al.*, 2003). Soybean rust is rapidly spreading and establishing in the eastern and southern African region, thereby threatening soybean production (Murithi *et al.*, 2014). Soybean resistance is difficult to obtain, due to the high degree of genetic variability of the pathogen (Levy, 2005; Yorinori, 2008; Yamaoka *et al.*, 2014). Currently, different pathotypes of the fungus have been described across the major soybean growing regions worldwide (Lin, 1966; Yeh, 1983; Bromfield, 1984; Twizeyimana *et al.*, 2009; Akamatsu *et al.*, 2013). With the current massive increase of the area under soybean production, soybean rust is an important disease that cannot be ignored. This review highlights the current trends concerning soybean production and developments concerning soybean demand in the eastern and southern African region. Here, the status of soybean rust and its diversity at a global and regional level are also reviewed. Furthermore, the current research being performed on soybean rust is described, together with the control measures that can be implemented to secure soybean yields in the eastern and southern African region.

Soybean production and use in Africa

Soybean production in Africa occupies 1·3% of the total world area under soybean production representing 0·6% of the total production. In 2011, soybean was planted on 1·1 million ha of land in SSA, which is approximately 1% of the total arable land. Major production is concentrated in South Africa, which is the leading producer in Africa, contributing about 35% of the total production, followed by Nigeria (27%) and Uganda (8·5%) (FAOSTAT, 2013). Zambia, Zimbabwe and Malawi also produce substantial amounts of soybean. About 6·8 million households in SSA, representing about 28·6 million people, grow soybean. Soybean production in this area is projected to grow from about 1·5 million tonnes in 2010 to about 2 million tonnes in 2020, representing a growth rate of 2·3% per annum, to meet the predicted demand (Abate *et al.*, 2012).

The major factors that are expected to drive soybean production include land availability, the investment by private equities, international developmental organizations and banks into corporate farms, growth of the poultry market and the development of household consumption (Technoserve, 2011b). Soybean production in SSA has doubled in a period of 15 years, driven by significant increases in the land planted with soybeans over the years. The soybean market has also grown rapidly over the last decade, driven by the rapid growth of the poultry market and demand for household consumption. The demand outweighs the production, leading to increases in imports of soybean and soybean products from India, Argentina and Brazil. Imports of soybean into SSA in 2011 were estimated at nearly 1·6 million tonnes, valued at $1·22 billion. South Africa, Nigeria and Kenya account for nearly 43, 21 and 18% of the total import volume in this region, respectively. Other countries, including Ethiopia, Zambia, Zimbabwe, Seychelles, Botswana, Tanzania and Gabon also import significant amounts of soybean each year. Exports from Uganda and Zambia to the neighbouring countries are about 29 000 tonnes per year (Abate *et al.*, 2012).

Soybean production and use in eastern and southern Africa

Soybean has now been identified as the most preferred legume across eastern and southern Africa, as compared to common bean and cowpea, based on its preference by growers (Rusike *et al.*, 2013). Uganda is the leading producer of soybean in eastern Africa, with an increase in production from 158 000 tonnes in 2005 to 213 300 tonnes in 2011. During the same period, the area under production increased from 144 000 to 150 000 ha (FAOSTAT, 2011). The upward trend in production is attributed to improved soybean research by the government, learning institutions and developmental organizations, which has resulted in the release of high-yielding varieties with increased tolerance to diseases such as frogeye leaf spot, bacterial pustule and soybean rust. Uganda is now among the key exporters of soybean products at the regional markets. Furthermore, dissemination of soybean processing and cooking methods by non-governmental organizations among women's groups has facilitated the adoption of soybean among smallholder households. This has led to an increase in the use of soymilk and soy flour among households in Uganda.

There is a substantial demand for soybean and soybean products, amounting to about 150 000 tonnes per year, in Kenya where production is dominated by smallholder farmers (Chianu *et al.*, 2009). This is mainly attributed to an increasing demand for human consumption and from the rapidly growing feed manufacturing industry (Rusike *et al.*, 2013). Production increased from 2000 tonnes in 2009 to about 4500 tonnes in 2012 (FAOSTAT, 2012). The climatic conditions in Kenya are suitable for soybean production; however, the potential for soybean production is not maximized because cultivation takes place only in a few areas in the west and east, and in the Rift Valley only on a small scale (Chianu *et al.*, 2009). Efforts by the government, developmental organizations and the private sector have led to an increase in interest in the crop among small-scale farmers and processors, especially in the western region.

In Rwanda, soybean is planted in an area of over 47 000 ha, producing about 37 000 tonnes (FAOSTAT, 2011). Here, about 62% of all households producing soybean consume their total harvest. Consumption is mainly through blending with maize, sorghum and cassava flour, as roasted beans, soymilk and as a paste mixed with local vegetables. A large-scale investment in a soybean oil extraction plant (now under construction in Rwanda), with a capacity of 36 000 tonnes of oil per year, is expected to further increase the demand for soybean in the region (Rusike *et al.*, 2013).

In the past, a lack of links between producers and buyers in Tanzania resulted in production of soybean being abandoned. Recent efforts by developmental organizations to increase soybean productivity and to link farmers to the market have seen an increase in the number of farmers producing soybean (Wilson, 2015). A total of 4000–8000 tonnes of soybean is now produced annually, with production concentrating mainly in the Southern Highlands. Rising incomes and urbanization have contributed to the growing demand, with the feed industry accounting for about 150 000 tonnes annually. The demand far outweighs the supply, which is met by imports from neighbouring countries such as Zambia and Uganda. Soybean meal is also imported from India and Argentina (Rusike *et al.*, 2013).

The soybean industry is well established in the southern African region, with a total production of 861 000 tonnes in 2010 and a demand of 2 million tonnes (Technoserve, 2011a). In this region the demand for soybean for human consumption is usually in the form of flavoured textured soy protein (TSP), made from edible grade defatted soybean flour containing 50% protein (Ali, 2010). UNICEF and the World Food Programme (WFP) purchase corn soya blend (CSB), which normally forms part of feeding programmes and is supplied to vulnerable groups such as children and nursing women. More than 600 tonnes of CSB produced monthly in South Africa comprises 75% maize and 24% extruded soybean, supplemented with vitamins. The growing demand for soybeans offers a significant opportunity for smallholder farmers to increase incomes (Lubungu *et al.*, 2013). South Africa dominates both production and demand in the southern African region, with production expanding rapidly over the past 5 years and with the area under production more than doubling compared to other major cereal and oilseed crops (NAMC report, 2011).

Zambia is the second largest producer in the southern African region with a total production of about 260 000 tonnes and an estimated growth of 14% per annum (FAOSTAT, 2013). Soybean production is largely concentrated in the eastern, central and northern zones. Zambia is a net exporter of soybean, with about 45% exported to Zimbabwe and 10% to Botswana. Malawi and Mozambique have had rapid increases in soybean production as well, due to the involvement of the government, international research organizations and NGOs in these countries. Since 1997, soybean production has diffused into smallholder farming communities in Zimbabwe, helping to diversify cropping systems and to overcome soil fertility constraints. The rapidly expanding local and regional markets for soybean provide an opportunity for value addition and product diversification that can lead to better livelihoods and nutrition (Giller *et al.*, 2011). Overall, increase in soybean production and demand in eastern and southern Africa will continue with the rising of incomes, increased urbanization and expansion of the livestock sector to cater for the increasing demand of poultry and other livestock products.

Constraints to soybean production

Numerous biotic and abiotic constraints affect soybean production all over the world. Abiotic factors related to poor soil fertility, poor nodulation and seed longevity are the major problems in the tropics. Biotic factors, particularly diseases, insect pests and weeds, have consistently contributed to severe yield losses and affected the quality of soybeans. Among the important soybean diseases known worldwide are bacterial blight (*Pseudomonas savastanoi* pv. *glycinea*), bacterial pustule (*Xanthomonas axanapodis* pv. *glycines*), wild fire (*Pseudomonas syringae*), anthracnose (*Colletotrichum truncatum*), brown spot (*Septoria glycines*), charcoal rot (*Macrophomina phaseolina*), downy mildew (*Peronospora manshurica*), frogeye leaf spot (*Cercospora sojina*), red leaf blotch (*Phoma glycinicola*), soybean rust (*Phakopsora pachyrhizi)* and rhizoctonia foliar blight (*Rhizoctonia solani*) (Wrather *et al.*, 1997). Among them, soybean rust, bacterial pustule, frogeye leaf spot, red leaf blotch and bacterial blight have been identified as the major soybean diseases in SSA (Kawuki *et al.*, 2003).

Soybean rust particularly has been singled out as a major threat to soybean production globally, and its entry and establishment in Africa has caused major yield losses (Levy, 2005; Oloka *et al.*, 2008; Dean *et al.*, 2012). As experienced in Brazil, Argentina and Paraguay, spread and further establishment of soybean rust is expected to increase as soybean production intensifies (Yorinori *et al.*, 2005). Yield losses ranging from 10 to 90% have been reported across the globe (Akinsanmi *et al.*, 2001; Levy, 2005; Yorinori *et al.*, 2005; Oloka *et al.*, 2008). This impact is linked to the high specialization and significant variation that exists in the population of this obligate pathogen, concerning its virulence on soybean cultivars carrying specific resistance genes. Soybean cultivars available so far lack durable resistance and growers are left with using fungicides to control the pathogen as the only option for disease control.

The impact of soybean rust is similar to that exhibited by wheat stem rust (*Puccinia graminis* f. sp. *tritici*) races, in which virulence evolves so rapidly that host race-specific resistance genes generally exploited in plant breeding are usually overcome within 5 years after introduction of a resistant cultivar (Singh *et al.*, 2011). The spread of soybean rust spores through wind currents (Isard *et al.*, 2007) facilitates its movement and the pathogen can easily enter new soybean production areas, while the high variability of pathogenicity of this fungus makes it difficult to control by specific culture methods.

Spread, establishment and host range of soybean rust

Soybean rust can be caused by two obligate biotrophic basidiomycete fungi: *Phakopsora meibomiae* and *P. pachyrhizi*. *Phakopsora pachyrhizi* is more aggressive than *P. meibomiae* and has established in the eastern and western hemisphere due to its ability to sporulate profusely, thereby enhancing its dispersal (Bromfield, 1984; Miles *et al.*, 2003). The less invasive fungus *P. meibomiae* has not been reported outside the Americas. Under favourable conditions, with a temperature in the range of 15–28°C and the presence of moisture on the leaf surface for a period of 6–12 h, uredinia develop 5–7 days after infection, while urediniospores can be produced 2 days later (Marchetti *et al.*, 1979; Melching *et al.*, 1989). A relative humidity of 75–80% is necessary for spore germination and leaf infection. A single pustule can produce hundreds of urediniospores continuously for about 3 weeks after the onset of sporulation. The urediniospores are then dispersed by wind, resulting in new infections near the initial disease focus. The urediniospores can also be transported over long distances by the wind and may remain viable in the air for many days, as long as they are protected from ultraviolet radiation by a cloud cover, resulting in new infections outside the local area (Goellener *et al.*, 2010). The disease cycle continues until the plant is defoliated or environmental conditions no longer favour disease development. Teliospores have been reported on kudzu (*Pueraria* spp.), as well as on soybean (Yeh *et al.*, 1982; Harmon *et al.*, 2006). Teliospores are generally over-seasoning structures and have been germinated under laboratory conditions to produce basidiospores (Saksirirat & Hoppe, 1991). The importance of the telial stage in the development of soybean rust in the field is unknown. They are not generally considered the primary source of inoculum and are not often observed in the field (Ono *et al.*, 1992; Tan *et al.*, 2001).

Symptoms due to soybean rust infection may be observed at any developmental stage of the plant, but losses are mostly associated with infection at the flowering (R1) stage through to pod filling (R6) stage (Hartman *et al.*, 1991). Symptoms that manifest on the lower side of the leaf are usually grey-green, tan to dark brown, or reddish brown lesions with one or many yellowish brown to cream uredinia (Fig. 1; Ono *et al.*, 1992; Hartman *et al.*, 1999). Soybean rust infection lowers yields mainly through reducing the photosynthetic activity of the infected leaves. This is caused by a reduction in green leaf area due to lesion formation and premature defoliation, resulting in reduced dry matter accumulation, a decreased number of filled pods and a reduced size and weight of the seeds (Kumudini *et al.*, 2008).

Phakopsora pachyrhizi has an exceptionally broad host range, comprising more than 150 species in about 53 genera of the legume family, the largest family of flowering plants (Ono *et al.*, 1992; Hartman *et al.*, 2011a). Wild hosts include kudzu (*Pueraria lobata*) and beggar weed (*Desmodium tortuosum*) (Isakeit *et al.*, 2006; Sconyers *et al.*, 2006). Common cultivated legumes that serve as hosts include *Phaseolus vulgaris* (common bean), *Phaseolus coccineus* (scarlet runner bean), *Vigna unguiculata* (cowpea), *Cajanus cajan* (pigeon pea), *Pisum sativum* (field pea), *Lens culinaris* (lentil) and the fodder legume *Neonotonia wightii* (Lynch *et al.*, 2006; Nunkumar *et al.*, 2008). These legumes are widely cultivated throughout the year as a major source of food in developing countries. Due to their cultivation at different periods throughout the year, *P. pachyrhizi* may overwinter on these hosts, which may later act as sources of primary inoculum that may be available to infect soybean fields at the start of the growing season (Tukamuhabwa & Maphosa, 2012). Recent reports of new hosts of *P. pachyrhizi* include 12 new genera of legumes in the USA (Slaminko *et al.*, 2008) and black rosewood (*Afzelia xylocarpa*) in Thailand (Seemadua *et al.*, 2012).

Since the first report of its occurrence on yam bean (*Pachyrhizus erosus*) in Japan in 1902, subsequent reports of the occurrence of *P. pachyrhizi* in China, Taiwan, Australia (1934), India (1951) and Hawaii (1994) have followed. The earliest, unconfirmed, report (Fig. 2) of soybean rust in Africa was in 1978 in Zambia (Javaid

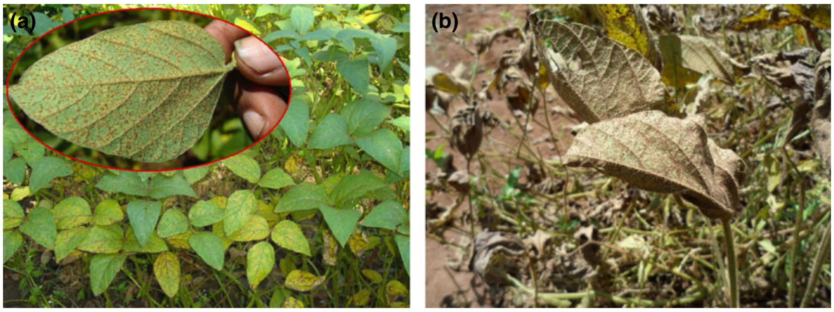
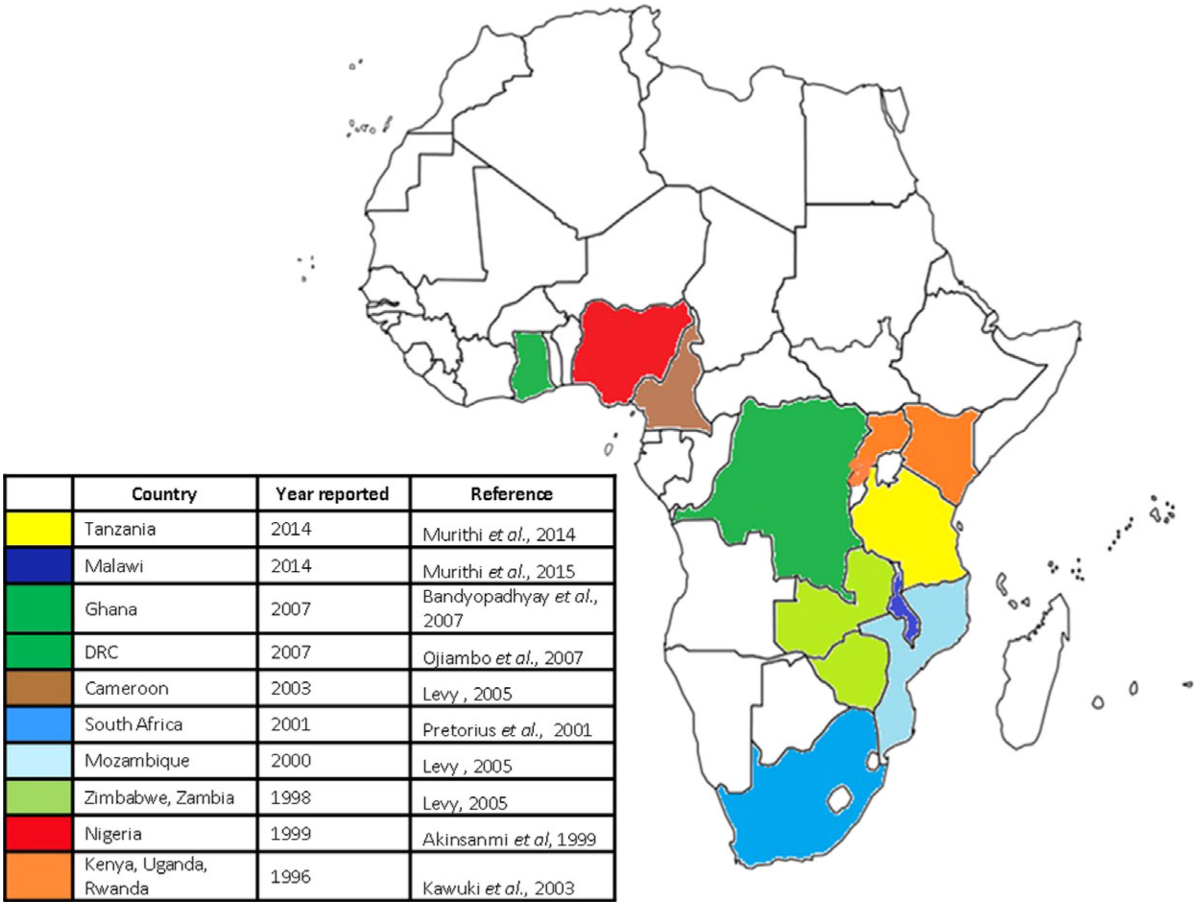


Figure 1 *Phakopsora pachyrhizi* symptoms as observed on soybean leaves. (a) Sporulation of *P. pachyrhizi* from uredinia on the lower side of the leaves. (b) Severely infected soybean leaves.



	Country	Year reported	Reference
🟨	Tanzania	2014	Murithi *et al.*, 2014
🟦	Malawi	2014	Murithi *et al.*, 2015
🟩	Ghana	2007	Bandyopadhyay *et al.*, 2007
🟩	DRC	2007	Ojiambo *et al.*, 2007
🟫	Cameroon	2003	Levy , 2005
🟦	South Africa	2001	Pretorius *et al.*, 2001
🟦	Mozambique	2000	Levy , 2005
🟩	Zimbabwe, Zambia	1998	Levy, 2005
🟥	Nigeria	1999	Akinsanmi *et al*, 1999
🟧	Kenya, Uganda, Rwanda	1996	Kawuki *et al.*, 2003

Figure 2 Year of the first reports on *Phakopsora pachyrhizi* on soybean in various countries in Africa.

& Ashraf, 1978; Miles *et al.*, 2003) on soybean plants, and on bambara nut (*Vigna subterranea*) in Tanzania in 1981 (Teri & Keswani, 1981). Its introduction into Africa was proposed to have occurred through urediniospores blowing from western India to the east African coastal areas by moist northeast monsoon winds (Levy, 2005). The disease became prevalent in Africa in 1996 when it was first confirmed in Uganda on experimental plots and thereafter on farmer's fields throughout the country. All commercial cultivars were found to be susceptible (Kawuki *et al.*, 2003). Within the same period (1998), the disease was reported in the major soybean growing regions in Kenya, Rwanda, Zimbabwe (Jarvie, 2009) and Zambia (Levy, 2005), in Nigeria in 1999 (Akinsanmi *et al.*, 2001), in Mozambique in 2000, in South Africa in 2001 (Pretorius *et al.*, 2001) and in Cameroon in 2003 (Levy, 2005). Other reports of the disease on soybean followed in 2007 in Ghana and the Democratic Republic of Congo in central Africa (Bandyopadhyay *et al.*, 2007; Ojiambo *et al.*, 2007), and recently in Tanzania and Malawi (Murithi *et al.*, 2014, 2015; Fig. 2). The American continent was free of rust until the 2000/1 season, when it was reported in Paraguay in 2001 (Yorinori *et al.*, 2005), and was established in Brazil and Argentina in 2002 and in Uruguay in 2004 (Rossi, 2003; Stewart *et al.*, 2005). The disease was reported in the USA in Louisiana in 2004 (Schneider *et al.*, 2005) and in Cuba in 2009 (Perez-Vicente *et al.*, 2010); however, it was put on check in the USA through regular monitoring using sentinel plots, spore traps and variety screening. Strobilurin and triazole fungicides are widely used in the Americas for controlling soybean rust, but their use leads to high production costs and environmental concerns in addition to increasing tolerance of the fungus to some fungicides (Mueller *et al.*, 2009). In 2003 Brazil used more than $590 million to control soybean rust on more than 18 million ha, with an average of two different fungicides per application (Yorinori *et al.*, 2005).

Pathogenic variation of *P. pachyrhizi*

Being restricted to a parasexual cycle only may limit the variability and plasticity of a pathogen. However, significant variability in the pathogenicity on various hosts and virulence on susceptible plants has been observed in *P. pachyrhizi* populations, known for having asexual reproduction only (Akamatsu *et al.*, 2013). *Phakopsora pachyrhizi* infection produces different infection types, depending on resistance or susceptibility of the soybean genotypes (Bromfield & Hartwig, 1980; Pham *et al.*, 2009). Generally the reddish brown (RB)-infection type, consisting of reddish brown lesions showing meagre or no sporulation and the immune (IM)-infection type, characterized by the absence of visible symptoms, imply the presence of an incompatible interaction in which the pathogen is avirulent and the plant is resistant. Compatible interactions are characterized by a TAN-type of infection, consisting of tan coloured lesions with multiple actively sporulating uredinia. In this case the host genotype is considered to be susceptible and the pathogen virulent. Pathotypes and races of *P. pachyrhizi* have traditionally been assessed based on the infection types caused by different isolates on various host differentials.

Genes conferring resistance to *P. pachyrhizi* have been identified as *Rpp1* (for resistance to *P. pachyrhizi*) (McLean & Byrth, 1980), *Rpp2* (Bromfield & Hartwig, 1980), *Rpp3* (Bromfield & Melching, 1982), *Rpp4* (Hartwig, 1986), *Rpp5* (Garcia *et al.*, 2008) and *Rpp6* (Li *et al.*, 2012). The genes have been mapped on the various soybean chromosomes; *Rpp1* is located on chromosome 18, *Rpp2* on 16, *Rpp3* on 6, *Rpp4* on 18, *Rpp5* on 3 and *Rpp6* on 18 (Hyten *et al.*, 2007, 2009; Garcia *et al.*, 2008; Silva *et al.*, 2008). Significant progress has been made to characterize these genes using virus-induced gene silencing (VIGS), in which soybean is challenged with recombinant *Bean pod mottle virus* (BPMV) targeting endogenous genes (Pandey *et al.*, 2011; Morales *et al.*, 2012).

The earliest report of pathogenic variation in *P. pachyrhizi* was from Taiwan in 1966, when different infection phenotypes were observed on six different soybean genotypes and an additional five different legumes, in response to inoculation with nine different *P. pachyrhizi* isolates (Lin, 1966). In Australia two pathotypes were identified, with one being virulent on a particular soybean accession but avirulent on another one, while the other isolate was virulent on both soybean accessions (McLean & Byrth, 1976). Since then, different pathotypes encompassing different isolates of *P. pachyrhizi* have been identified globally (Table 1). The durability of the *Rpp* genes has already been challenged, because they confer resistance to only a limited set of specific *P. pachyrhizi* isolates, and these single-gene sources have not been durable when used in commercial cultivars (Yeh, 1983; Bromfield, 1984; Hartman *et al.*, 2005; Miles *et al.*, 2011). For instance, cultivar PI 230970 (*Rpp2*), identified as resistant in field evaluations from 1971 to 1973, exhibited some TAN lesions in the field in 1976, indicating a loss of full resistance. By 1978, most of the lesions found on the plants were TAN-type lesions. Soybean cultivar PI 200492 (*Rpp1*), identified as resistant from 1961 to 1963, had become susceptible by the mid-1970s (Bromfield, 1984). Similarly, the *Rpp3* gene, present in cultivar PI 462312 and identified early in the 1970s, had become ineffective in the late 1970s (Bromfield, 1984). Cultivar PI 459025B (*Rpp4*) is known to still show resistance, but field trials have revealed susceptibility to some *P. pachyrhizi* isolates (Hartman *et al.*, 2005). In Brazil, *Rpp1* to *Rpp4* were effective against rust in 2001; however, both *Rpp1* and *Rpp3* succumbed to the pathogen within 2 years of their introduction (Yorinori, 2008).

The virulence of *P. pachyrhizi* populations differs based on the geographical regions from where they are collected (Twizeyimana *et al.*, 2009; Yamanaka *et al.*, 2010; Akamatsu *et al.*, 2013; Table 1). Furthermore, the responses of the host genotypes differ (Bromfield, 1984) and there are differences between new and old isolates (Bonde *et al.*, 2006). Concerning the latter, a comparison between isolates collected from different geographical locations in different periods in Asia, Australia, Africa and South America in 2001 and older isolates collected in the 1970s, revealed that the isolates collected in 2001 were more virulent. Newer isolates caused a lower frequency of RB reactions and in most cases there was a complete absence of immune reactions on the various host differentials (Bonde *et al.*, 2006).

Comparison of the pathogenicity profiles of 59 different rust populations obtained from Brazil, Argentina and Paraguay, which were tested on 16 soybean differentials, revealed a significant variation in pathogenicity among the populations. Only two pairs among the 59 *P. pachyrhizi* populations displayed identical pathogenicity profiles, indicating substantial variation in the rust populations studied (Akamatsu *et al.*, 2013). Brazilian isolates exhibited a higher virulence, reflected by higher levels of sporulation when tested on four varieties carrying *Rpp1*, as compared to Japanese isolates. Fungal virulence can also vary over time, as was demonstrated by two Brazilian rust populations that showed a similar virulence on a set of differentials in 2005, but exhibited a different virulence spectrum on another set of differentials in 2008 (Yamanaka *et al.*, 2010). In the USA, isolates collected from Florida in 2006, 2009 and 2011/12 were compared for their virulence on two soybean accessions PI 200492 (*Rpp1*) and PI 567102B (*Rpp6*). More sporulation was observed on the genotypes inoculated with the isolates that were collected in 2011/12, as compared to the ones collected in earlier years, suggesting the appearance of a pathotype that had become more virulent towards the normally resistant genotypes, as compared to the *P. pachyrhizi* pathotypes present among earlier populations (Paul *et al.*, 2013).

A high level of virulence among several isolates of *P. pachyrhizi* has further been demonstrated by production of mixed reactions of RB and TAN lesions on particular soybean genotypes. One isolate, 72-1 from Australia, induced both RB and TAN lesions on the same leaflets of eight different soybean accessions (Bromfield *et al.*, 1980). Other studies have reported mixed reactions in different rust populations, especially when using a bulk pathogen population or a mixture of isolates (Miles *et al.*, 2006; Yamanaka *et al.*, 2010; Maphosa *et al.*, 2013). These reactions could result from a mixture of races in the inoculum (Bonde *et al.*, 2006) that may imply more diverse virulence of the different isolates in a given population.

Table 1 Characterization of the virulence spectrum of *Phakopsora pachyrhizi* isolates from different geographical regions on differential sets of soybean

Country	Year of collection	No. of isolates tested	Lines used	Pathotypes/ races identified	Reference
Taiwan	1966	9	11 legume accessions, 6 accessions of soybean and 5 *Phaseolus* species	6	Lin (1966)
Australia	1976	2	Cultivar Willis and PI 200492 (*Rpp1*)	2	McLean & Byth (1976)
Australia, India, Puerto Rico & Taiwan	Multiple	4	PI 200492 (*Rpp1*), PI 230970 (*Rpp2*), PI 462312 (*Rpp3*)	4	Bromfield *et al.* (1980)
Taiwan	1983	50	PI 200492 (*Rpp1*), PI 462312 (*Rpp3*), PI 230971, TK 5 and TN 4	3	Yeh (1983)
Taiwan	1983	42	AVRDC differential lines: PI 200492 (*Rpp1*), PI 230970 (*Rpp2*), PI 462312 (*Rpp3*), PI 230971, PI 239871A, PI 239871B, PI 459024 and PI 459025B, TK-5, TN-4 and Wayne	9	AVRDC (1983)
Australia	1984	8	257 accessions of *Glycine* spp; *G. canescens, G. clandestine, G. tabacina* and *G. tomentella*	6	Burdon & Speer (1984)
China	1989	7	PI 200492 (*Rpp1*), PI 462312 (*Rpp3*), PI 459025B (*Rpp4*) and 5 other accessions	4	Tan & Sun (1989)
Japan	1993–7	45	AVRDC differential lines	18	Yamaoka *et al.* (2002)
South Africa	2004	1 composite population	AVRDC differential lines	1	Caldwell & McLaren (2004)
USA	Multiple	12 international	PI 200492 (*Rpp1*), PI 230970 *(Rpp2*), PI 462312 (*Rpp3*) and PI 459025B (*Rpp4*)	6	Bonde *et al.* (2006)
USA	2001	4 bulked international	PI 200492 (*Rpp1*), PI 230970 (*Rpp2*), PI 462312 (*Rpp3*) and PI 459025B (*Rpp4*)	2	Miles *et al.* (2006)
Paraguay	2006	1 composite field population	PI 462312 (*Rpp3*), PI 459025B (*Rpp4*) and 528 other accessions	2	Miles *et al.* (2008)
USA	2006–7	6	PI 200492 (*Rpp1*), PI 594538A (*Rpp1b*), PI 462312 (*Rpp3*), 459025B (*Rpp4*) and 23 other accessions	2	Paul & Hartman (2009)
USA	Multiple	10 international	PI 200492 (*Rpp1*), PI 230970 (*Rpp2*), PI 462312 (*Rpp3*), PI 459025B (*Rpp4*) and 16 others	8	Pham *et al.* (2009)
Uganda	2004	19 lines	AVRDC differential lines	3	Tukamuhabwa & Maphosa (2012)
Nigeria	2005	116	PI 200492 (*Rpp1*), PI 230970 (*Rpp2*), PI 462312 (*Rpp3*), PI 459025B (*Rpp4*), PI 594538A, UG-5, TGx 1485-1D and TGx 1844-4F	7	Twizeyimana *et al.* (2009)
USA	2009	8 international	PI 200492 (*Rpp1*), PI 594538A (*Rpp1b*), PI 587866 and PI 587880A	3	Ray *et al.* (2009)
Vietnam	2010	1 composite field population	PI 200492 (*Rpp1*), PI 594538A (*Rpp1b*), PI 462312 (*Rpp3*), PI 459025B (*Rpp4*) and 85 other accessions	7	Pham *et al.* (2010)
Brazil	2007–8	3	13 accessions including sources of *Rpp1–Rpp5*	3	Yamanaka *et al.* (2010)
USA	Multiple	8	PI 462312 (*Rpp3*), Hyuuga (*Rpp3, Rpp5*) and 12 other accessions	6	Kendrick *et al.* (2011)
USA	2001	4	34 accessions, including resistance sources *Rpp1–Rpp4*	nc	Miles *et al.* (2011)
USA	2006–8	Field populations	PI 200492 (*Rpp1*), PI 230970 (*Rpp2*), PI 462312 (*Rpp3*), PI 459025B (*Rpp4*) and over 500 other accessions	2	Walker *et al.* (2011)
USA	2006–9	72	PI 200492 (*Rpp1*), PI 230970 (*Rpp2*), PI 462312 (*Rpp3*), PI 506764 (*Rpp3*-Hyuuga), PI 459025B (*Rpp4*), and PI 200526 (*Rpp5*); UG-5	3	Twizeyimana *et al.* (2011)
Japan	2007–9	26	9 soybean accessions, including resistance sources *Rpp1–Rpp5* and kudzu (*Pueraria lobata*)	6	Yamaoka *et al.* (2014)

PI, plant introduction; AVRDC, Asian Vegetable Research and Development Centre; *Rpp*, resistance to *P. pachyrhizi;* nc, not classified.
Table adapted from Hartman *et al.*, 2011b by kind permission of CAB Reviews.

Virulence variation of *P. pachyrhizi* isolates in Africa

In Africa, the pathogenicity and virulence of soybean rust has only been tested for a limited number of soybean rust isolates. *Phakopsora pachyrhizi* isolates collected from Zimbabwe in 2001 produced a TAN-type of infection on all soybean differentials carrying resistance genes (*Rpp1*–*Rpp4*), as compared to isolates originating from Taiwan, India and South America. In contrast, an isolate from South Africa in the same study produced RB infection types on *Rpp2*, *Rpp4* and *Rpp1*+, suggesting the presence of different pathotypes in Africa (Bonde *et al.*, 2006). In Uganda, none of the 196 soybean varieties that were screened for resistance against soybean rust between 1996 and 1998 were found to be immune. Furthermore, eight of the varieties initially found to be resistant succumbed to rust in the subsequent seasons (Kawuki *et al.*, 2003).

Three virulent races were identified out of 45 different isolates that were tested on 19 soybean lines from the Asian Vegetable Research and Development Center (AVRDC) in Uganda in 2004 (Tukamuhabwa & Maphosa, 2012). In the 2005 and 2006 growing seasons, 25 different soybean accessions, four among them bearing *Rpp1* to *Rpp4*, were found to be susceptible to rust populations originating from Uganda, except for accession PI 230970 (*Rpp2*) (Oloka *et al.*, 2008). However, TAN-type lesions were recently observed on PI 230970 (*Rpp2*) when inoculated with five isolates of *P. pachyrhizi* in field trials in Uganda (Maphosa *et al.*, 2013), suggesting a change in virulence of Ugandan rust populations within a period of less than 10 years. In other studies, Twizeyimana *et al.* (2009) identified seven different pathotypes out of 116 representative isolates collected in three different agro-ecological zones in Nigeria and inoculated on eight different accessions, some of which had resistance genes *Rpp1* to *Rpp4*.

Recently, variable reactions were observed on 12 soybean lines inoculated with five different isolates from five different locations in Uganda. Three of the lines produced TAN-type lesions in the five different locations, while four of the resistant lines produced RB-type lesions (Maphosa *et al.*, 2013). This short-term durability of resistance genes reflects virulence variability among *P. pachyrhizi* populations and the development of new physiological races in field populations. Presumably, the variable populations of rust in a given area allow for new populations to become dominant that are not targeted by the resistance mechanisms effective against previously dominant forms. More research is needed to understand the virulence profile of soybean rust populations in other countries in Africa.

Soybean rust control strategies and current research

The knowledge on pathogen variability of *P. pachyrhizi* in a given region is essential because it helps to guide deployment, screening and/or introduction of novel resistance genes against the currently prevailing pathotype groups. Furthermore, it will help in monitoring the dynamics and changes that occur in the population of existing pathotypes through the entry of new pathotypes from other regions. Thus, pathogen variability studies provide a means of monitoring the present state of the interaction with respect to pathogen virulence and plant resistance for a given pathogen and host population (Ramstedt *et al.*, 2002).

Virulence characterization of the soybean rust populations in eastern and southern Africa is geared towards understanding the variability and dynamic plasticity of the rust population and aims to guide targeted breeding for resistance. Moderately resistant soybean cultivars, namely Maksoy 1N, Maksoy 2N, Maksoy 3N and Namsoy 4M, all developed in 2005 in Uganda, have been used in the management of soybean rust (Oloka *et al.*, 2005). These cultivars contain partial resistance to soybean rust; however, some of the cultivars (Maksoy 1N, Maksoy 2N and Namsoy 4M) have recently been reported to succumb to this disease (Maphosa *et al.*, 2013). This suggests the existence of variable virulence patterns among rust populations in Uganda and therefore a regular screening of germplasm is necessary to monitor virulence changes of the pathogen. Tolerant soybean varieties have been developed in Zimbabwe based on the stability of their yields, or a tolerance approach that was followed by selecting genotypes with high yield potential even when infected by soybean rust (Tichagwa, 2004). Screening for yield stability to soybean rust involves determining yields from paired plots, with and without fungicides. High-yielding genotypes with relatively low yield loss under conditions of severe rust infestation are considered to be tolerant. Varieties identified through this method have been released and are currently being used in eastern and southern Africa to reduce yield losses due to soybean rust epidemics.

Evolution of new virulence spectra through migration, mutation, recombination of existing pathogenicity and virulence genes and their subsequent selection on susceptible plants has been more frequent in rust as compared to necrotrophic pathogens (Singh *et al.*, 2011). Therefore, successful breeding and deployment of resistance genes against soybean rust, in combination with knowledge on the virulence spectrum of rust populations and the reaction of soybean lines to field isolates from different regions, is paramount. Because the major resistance genes are considered to be race-specific, soybean breeding lines and cultivars cannot be used without prior knowledge of the differences in virulence and race composition of a given rust population. Germplasm from the United States Department of Agriculture (USDA) is currently being tested in Malawi to identify novel resistant germplasm that can be used in national breeding programmes. Through the extensive breeding programme at the International Institute of Tropical Agriculture (IITA), soybean rust-resistant lines have been tested and released across Africa (Hartman *et al.*, 2011a). Two

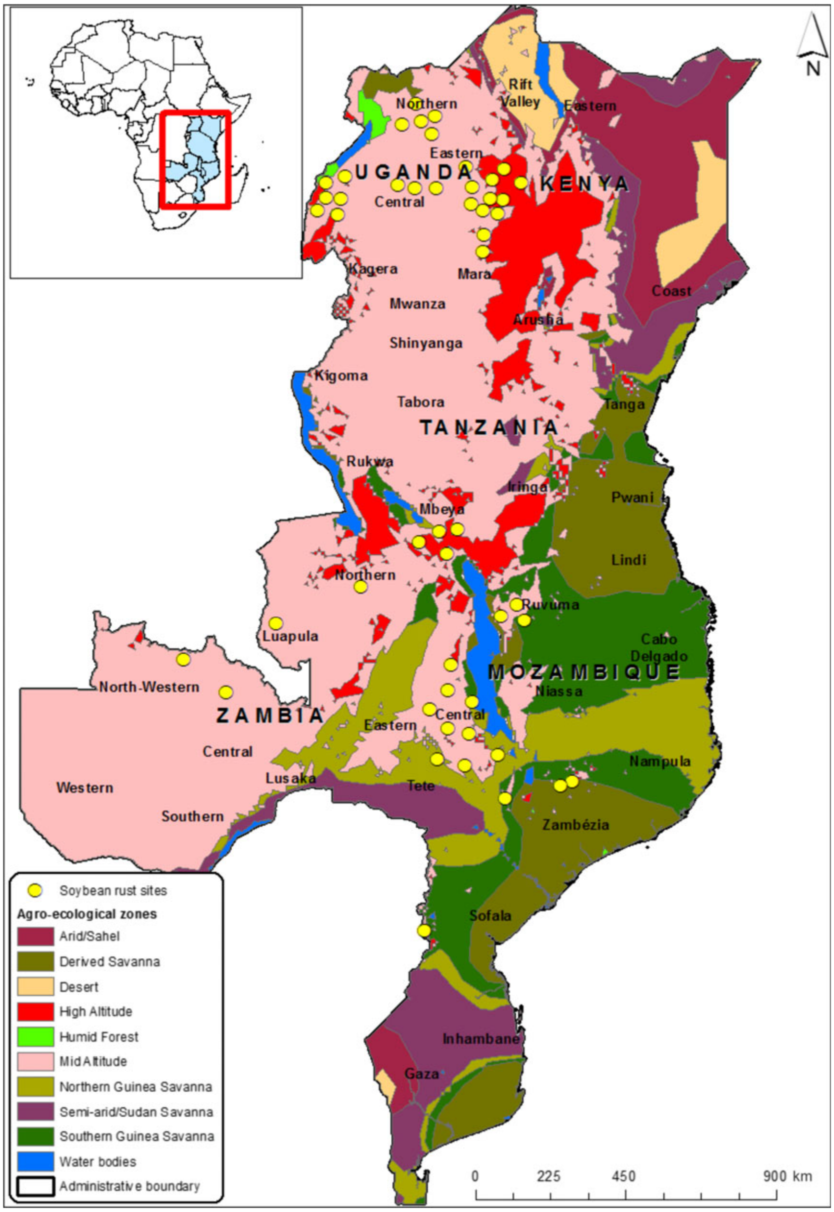


Figure 3 Soybean rust distribution over different agro-ecological zones in eastern and southern Africa.

resistant varieties, TG × 1988-5F and TG × 1989-19F (NCRISOY-1 and -2, respectively), were recently released in Nigeria (IITA, 2015).

A rapid spread of soybean rust in farmers' fields was observed in field surveys conducted during the 2011–2014 growing seasons in soybean producing areas in Kenya, Uganda, Tanzania and Malawi. Rust is spread across different agro-ecological zones (Fig. 3) and causes symptoms on up to 80% of the leaf area. Leaf samples with and without symptoms collected from these countries were subjected to quantitative PCR (qPCR) using *P. pachyrhizi*-specific primers to confirm the disease (Frederick *et al.*, 2002). *In vivo* cultures were established in detached leaf assays (Twizeyimana *et al.*, 2007) of soybean rust differential sets to determine the virulence and distribution of the pathotypes present in this region.

To understand the population biology of pathogenic fungi, the amount and distribution of genetic variation among and within the population is important; however, little is known of *P. pachyrhizi* populations in eastern and southern Africa. Genes encoding effector proteins secreted by pathogens during infection can be used as molecular markers to understand the biology of rust pathogen interactions and further identification of new resistance genes (Saunders *et al.*, 2012). Molecular markers are used for the assessment of genetic diversity, phylogenetic relationships and characterization of pathotypes (Keiper *et al.*, 2003). Anderson *et al.* (2008) developed highly polymorphic microsatellite markers for the characterization of different strains of *P. pachyrhizi*. Eighty-four distinct genotypes were revealed among 116 isolates collected from three different agro-ecological zones in Nigeria, suggesting a high genetic variability of the pathogen (Twizeyimana *et al*., 2011). These microsatellite markers are currently being used to establish the genetic diversity of *P. pachyrhizi* populations in eastern and southern Africa in order to guide the deployment of resistant cultivars in breeding programmes.

Monitoring and surveillance of *P. pachyrhizi*

Phakopsora pachyrhizi development and dispersal is heavily influenced by environmental conditions, plant age and host species. Tracking of soybean rust races and monitoring the disease status globally is absolutely a priority. Monitoring factors, such as the prevailing wind patterns and climatic factors that favour its survival, sporulation and distribution in soybean producing areas, can help in controlling the disease. Monitoring of soybean rust is necessary to alert growers of significant dispersal before symptom development. For chemical control of soybean rust, it is critical for the grower to decide on whether and when to apply a fungicide. Early application of a fungicide when the pathogen has not yet established leads to waste, while when a fungicide is applied too late, yield losses are likely to occur due to disease development. Sentinel plots have been successfully used in the USA in a national network system aimed at monitoring the appearance of soybean rust (Geisler *et al*., 2007; Young *et al*., 2011). The sentinel plots are used to detect soybean rust already present at low densities and are established in multiple locations in the soybean growing regions. Typically, they are planted earlier than commercial soybeans to provide an early warning system for commercial soybean fields. The plots use a variety of soybean maturity groups to extend monitoring throughout the growing season. Soybean rust monitoring begins with collecting and observing leaves from sentinel plots at regular intervals throughout the season. Spore traps and rain collectors are used in the sentinel plots to capture spores that are present in the air and that may lead to the development of disease (Dufault *et al*., 2010; Vittal *et al*., 2013).

Fluorescent antisera specific for detection of *P. pachyrhizi* urediniospores are regularly used to detect airborne spores collected from the traps (Baysal-Gurel *et al*., 2008). Samples collected from the spores are also detected using qPCR to confirm the disease and to quantify the relative amounts throughout the season. These methods have already been used successfully in the USA to generate accounts on the real-time status of soybean rust spores in the atmosphere and alert growers about the risk of soybean rust establishment on their soybean fields in a particular season. These monitoring efforts in the USA have saved the soybean industry millions of dollars in fungicide costs, as a result of the availability of accurate disease forecasting based on pathogen surveillance and environmental data. Other monitoring information tools, such as RUSTMAPPER application, have also been successfully used in monitoring wheat stem rust globally. This is a Google Earth-based application that provides up to date information on the current status and the potential spread of wheat stem rust (Hodson *et al*., 2012). Such applications can be developed for monitoring soybean rust across the globe, showing the current survey sites and the wind patterns that can influence spore dispersal. Sentinel plots and spore trap monitoring methods will be tested on a small scale in eastern and southern Africa to evaluate their workability. These methods will be optimized for adaptation to the conditions in the region to contribute to controlling soybean rust.

Concluding remarks and further perspectives

The substantial contribution of soybean to human nutrition, its use in animal feeds and its potential source of cash income for small farmers from selling the crop, are some of the factors contributing to the adoption of the crop among smallholder producers in eastern and southern Africa. Soybean production will continue to increase in eastern and southern Africa, driven by an increased production per acre and an expansion of the production area, especially through increased intercropping and crop rotation. The threat of soybean rust to the soybean industry in eastern and southern Africa is serious and the variability of the virulence spectrum of the pathogen around the globe confirms the challenges it poses to crop protectors as they search for effective management tools. Although a variety of fungicides effective against soybean rust are available, the use of such fungicides is limited due to the high costs of the product and its application, as well as environmental concerns. Due to this restricted fungicide use, an early monitoring system for detection of rust threats for steering fungicide might only be relevant for large-scale producers in eastern and southern Africa. Host plant resistance provides a cheaper, environmentally friendly, and much more sustainable approach for managing soybean rust among smallholder agriculture that characterizes the agricultural landscape of eastern and southern Africa. Identification of dominant pathotypes will therefore guide breeding for resistance to specific *P. pachyrhizi* populations. Furthermore, determining genetic diversity of *P. pachyrhizi* populations will provide vital information for breeders to develop resistant germplasm. Identifying, screening and deploying high yielding disease-resistant varieties in the soybean growing regions of eastern and southern Africa will help in reducing the yield losses due to soybean rust. A continuous monitoring of the *P. pachyrhizi* population using sentinel plots and spore traps, in combination with a consistent screening of *P. pachyrhizi* isolates, will be essential to understand the pathogenic differentiation of the rust population in eastern and southern Africa. The use of single gene resistance may not be sustainable, whereas pyramiding of soybean rust resistance genes in a single soybean cultivar may provide more durable resistance against the highly variable rust populations in the field (Lemos *et al*., 2011; Maphosa *et al*., 2012). The loci of the six resistance genes (*Rpp1–Rpp6*) have been mapped with molecular markers and can thus be tagged and pyramided by making use of the linked molecular markers. For instance, a genotype with three resistance genes (*Rpp2*, *Rpp4* and *Rpp5*) has significantly higher resistance than genotypes with single resistance genes (Yamanaka *et al.*, 2010). These lines can be used in breeding programmes to deploy stable resistance. In addition to gene pyramiding, selection for novel sources of resistance to *P. pachyrhizi* is desirable. Mid-term interventions would include breeding for tolerance and/or partial resistance. These methods can be incorporated into regional breeding programmes to develop slow rusting cultivars. Use of molecular techniques, such as marker-assisted selection of resistance genes and genetic transformation, will ease prebreeding efforts in the long run.

Due to the enormous potential of the soybean crop to improve the diet of people and its significant contribution to better incomes and livelihoods in eastern and southern Africa, efforts to protect the crop from abiotic and biotic constraints, among which soybean rust poses a serious threat, are required to ensure sustainable soybean production.

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