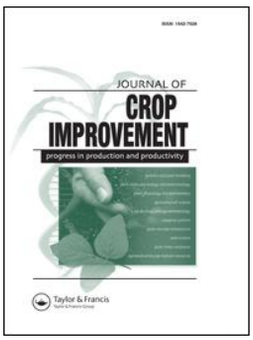

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Resistance to legume pod borer (*Maruca vitrata* Fabricius) in cowpea: genetic advances, challenges, and future prospects

Frejus Ariel Kpedetin Sodedji [a,b], Symphorien Agbahoungba[a], Simon-Pierre Assanvo Nguetta[b], Eric Etchikinto Agoyi [a], Mathieu Anatole Tele Ayenan [c], Samson Hospice Sossou[a], Cherif Mamadou[b], Achille Ephrem Assogbadjo[a], and Daouda Kone[b]

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ABSTRACT

Cowpea (*Vigna unguiculata* (L.) Walp) is a highly nutritious grain legume crop in the world. However, cowpea production is constrained by legume pod borer (*Maruca vitrata* Fabricius) (LPB), which feeds on various parts of cowpea plant, causing a complete crop failure. An analysis of the existing literature revealed LPB as a serious threat to cowpea production worldwide, with a more noticeable damage in Africa. Attempts to develop and use LPB-resistant cowpea varieties have not shown significant results because of challenges, such as interspecific crossing barriers, genetic variability among LPB strains, effects of genotype-by-environment interaction, limited knowledge of the genetic architecture of the trait, and the socio-political barriers to the adoption of transgenic cowpea varieties in some countries. Combining multi-environment trials with precise phenotyping would help optimize selection of best-performing cowpea genotypes to reduce LPB infestation. Many molecular tools (e.g., markers systems, genetics maps, high-throughput genotyping, and quantitative trait loci (QTL) analysis) are available to support breeding for LPB resistance in cowpea. In addition, mutation breeding, tissue culture, reverse genetics, clustered regularly interspaced short palindromic repeats (CRISPR) technologies can be used to increase genetic variability in cowpea for LPB resistance. The effective use of these technologies relies on an enabling legal and socio-economic-political environment for fast development and adoption of LPB-resistant cowpea varieties.

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Introduction

Feeding the ever-growing world population requires sustained food production and diversification of agricultural systems and diets (Dwivedi et al.

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2017). It is important to promote more balanced diets through an increased consumption of foods with enhanced nutritional profiles. Legumes are known for their ability to serve as a cheap source of proteins, essential amino acids, minerals, and vitamins (Gonçalves et al. 2016). Cowpea [*Vigna unguiculata* (L.) Walp; 2n = 2 x = 22] is a well-known nutritious grain legume crop in the world (Fatokun et al. 2002; Timko and Singh 2008). Cowpea plays a crucial role in food and nutrition security, and income generation for millions of households in Africa (Boukar et al. 2016, 2018). Cowpea is rich in nutrients, especially proteins (contains about 40% of crude protein) (Hussain and Basahy 1998). Cowpea also provides a range of essential micronutrients (e.g., zinc, iron) and vitamins (e.g., vitamin E, vitamin B) with health benefits (Pereira et al. 2014; Gonçalves et al. 2016). All parts of the plant are used, including grain, green pods and leaves (Hallensleben et al. 2009; Boukar et al. 2018).

Globally, cowpea is grown on about 12.5 million hectares of land, with a total production estimated at about 7 million metric tons (FAOSTAT 2017). Africa, the center of origin of cowpea (Singh et al. 1997), accounts for about 94% of the global cowpea production, with most of it coming from the western and central parts of the continent (FAOSTAT 2017; Boukar et al. 2018). In Africa, cowpea is mainly grown by smallholder farmers, who are faced with a number of production constraints that lead to extremely low yields. Cowpea yield can be as low as 25 Kg/ha in farmers' fields (Kamara et al. 2018), with an average yield of about 600 Kg/ha across the continent (FAOSTAT 2017). This is far below the potential yield of 1500–2500 Kg/ha reported for most improved cowpea varieties in Africa (Kamara et al. 2018).

The low productivity of cowpea is attributable to several biotic and abiotic stresses, with insect pests being the most important production constraint (Kormawa, Chianu, and Manyong 2002; Bett et al. 2017). Cowpea is susceptible to insect-pest infestations at all stages of its production and storage (Bawa, Ofori, and Osae 2017). The legume pod borer (LPB), also known as spotted pod borer (*Maruca vitrata* Fabricius; syn. *Maruca testulalis*), is one of the most damaging pests of cowpea (Reddy et al. 2017). It feeds on various parts of the plant, limiting cowpea production (Ba et al. 2009). LPB causes yield losses of up to 80% in infested fields, and a total crop failure may occur in the absence of proper control of the insect population (Bett et al. 2017; Boukar et al. 2018).

Review papers on the bionomics of LPB and management of its infestation in legume crops are available (Singh and Jackai 1988; Sharma 1998). During the two decades following the publication of these papers, numerous studies have been done, and a need exists to survey the key achievements and identify research avenues for LPB management.

In this paper, we focus on cowpea and provide an updated overview of the research on LPB, the extent of its damage across important cowpea-growing areas in Africa and the various management approaches. We also discuss the

achievements, challenges, and prospects of developing resistance to LPB in cowpea. The information generated should be useful for plant breeders and agronomists.

The legume pod borer, a cosmopolitan cowpea pest

LPB is a common pest of legume crops, infesting about 40 plant species, mainly from the Fabaceae family, including but not limited to *Vigna unguiculata* subsp. *unguiculata* (cowpea), *Vigna unguiculata* subsp. *sesquipedalis* (yard-long bean), *Vigna radiata* (mung bean), *Glycine max* (soybean), *Pueraria phaseoloids* (puero), *Phaseolus lunatus* (lima bean), and *Cajanus cajan* (pigeonpea) (Naveen et al. 2009; Margram et al. 2011). LPB probably originated from the Indo-Malaysian region and spread from northern Australia and East Asia to sub-Saharan Africa (Margram et al. 2011).

The adult LPB is a nocturnal moth, light brown with whitish markings on its forewings and it lives for up to a week (Singh and Allen 1979). It needs approximately 20–29 days to complete its life cycle, and optimum temperature for its growth and development ranges from 20°C to 28°C (Ganapathy 2010). Female moths lay about 200 flat, scaly eggs (Singh and Allen 1979; Ganapathy 2010). The eggs are milky white in color and oval in outline, dorsoventrally flattened and attached to the surface. The eggs hatch within 5 days, producing larvae that feed on tender parts of the stem, peduncles, flower buds, flowers and pods (Singh and Allen 1979; Naveen et al. 2009). There are five larval instars, which together last 8 to 14 days before the development of pupae in the soil, and grow into adult insects 5–7 days later (Singh and Allen 1979; Panickar 2004; Ganapathy 2010). The larval stage is the most damaging to cowpea plants because the young larvae feed on the flowers, reducing yield (Sharma, Saxena, and Bhagwat 1999). The late instars feed on green pods. The characteristic signs of larval feeding on cowpea are webbing of flowers, pods, and leaves and production of frass on pods (Singh and Allen 1979). The larvae, by boring into the cowpea pods, may also provide easy access to fungi, infecting cowpea seeds (Jackai and Daoust 1986; Dreyer, Baumgärtner, and Tamò 1994).

Extent of LPB damage in African cowpea cropping system

LPB is a ubiquitous insect herbivore, which causes important damage to cowpea throughout Africa (Figure 1), especially across the main cowpea-growing countries, such as Nigeria, Burkina-Faso, Niger, Mali, Sudan, and Kenya (Agunbiade et al. 2012). Each sowing date corresponds to a new generation of LPB (Capo-Chichi et al. 2009). Depending on the agro-ecological zone, three to four generations of LPB may occur annually on cowpea and the insect population survives the dry season on alternative host plants (Onstad et al. 2012). Insect migration favors the abundance and distribution of the pest. In the West African

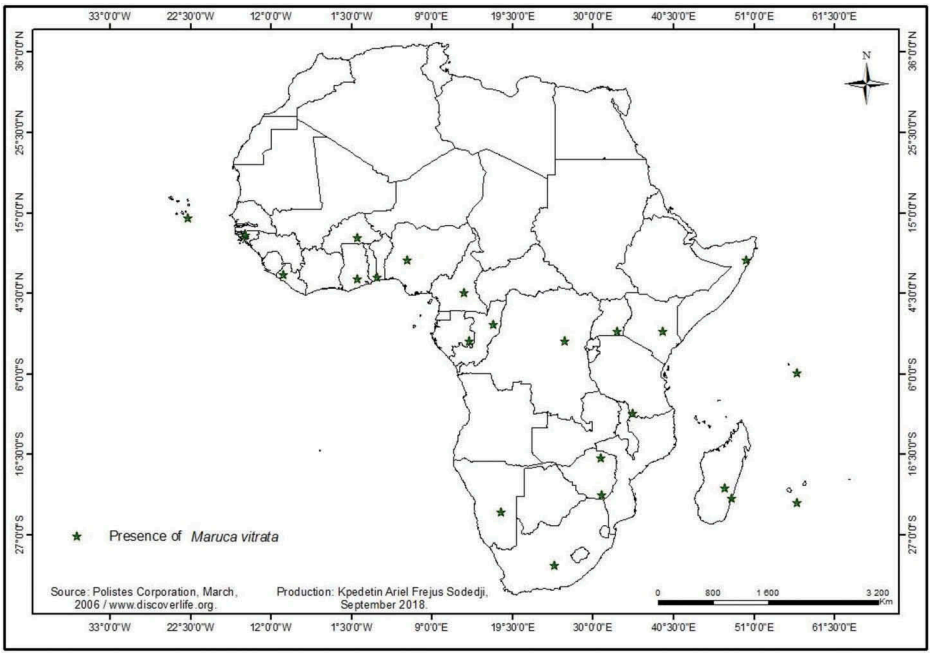

Figure 1. Distribution map of legume pod borer (*Maruca vitrata*) in Africa. This map was retrieved from www.dicoverlife.org and updated based on the information gathered from the literature on the distribution of *M. vitrata* in Africa. Georeferencing and digitization were done using ArGis software version 10:3 in WGS 84/UTM zone 31N.

region, it was reported that LPB population size and density increase from generation to generation, as the insects undergo a long-distance migration and find favorable feeding and reproductive conditions on a succession of different host plants (Agunbiade et al. 2012).

Huge yield losses attributable to LPB infestation are reported annually in cowpea production in Africa (Mohammed, Ishiyaku, and Sami 2013). The foraging behavior of this insect occurring throughout the growth cycle of the cowpea plant may explain the importance of its damage. LPB is an economically important pest of cowpea, as perceived by farmers in Benin republic (Adotenah et al. 2005). A yield loss of 72.1% attributable to LPB was reported in cowpea production in Nigeria (Ogunwolu 1990). Adekola and Oluleye (2008) recorded a yield loss of 75.1% on the susceptible cowpea genotype "IT84S2246 D". In Kenya, LPB caused a yield loss as high as 80% in cowpea production (Suh and Simbi 1983). The damage attributable to this pest may result in a complete crop failure in the presence of other stresses, such as aphids and pod-sucking insects (Sing 1987).

Management of LPB in cowpea

In cowpea farming system, there are various ways to control insect pests. These include chemical control, cultural controls, biological control and host plant resistance (Adipala et al. 2001). Chemical control is one of the most extensively used methods for legume pod borer (Agunbiade et al. 2014). A wide range of synthetic pesticides have been tested for controlling LPB infestation in cowpea fields (Table 1). Unlike the trend in developed countries, most developing countries still experience inefficient application of pesticides. This is mainly because of poor access to the right insecticides and equipment/knowledge required for the proper application of pesticides (Timko and Singh 2008). Besides, the use of pesticides poses significant risks to human health, the environment and the non-target organisms (Egho and Enujeke 2012; Singh and Singh 2015).

The use of biopesticides, such as neem (*Azadirachta indica* A. Juss.) seed extract, neem oil, and extract of *Piper guineense*, was reported as an environment-friendly alternative to the use of synthetic insecticides to control insect pests, including LPB in cowpea (Oparaeke, Dike, and Amatobi 2004). Biological control has also shown some success in integrated management of LPB damage in cowpea. The latter technique uses some entomopathogenic fungi and parasitoids, such as *Metarhizium anisopliae, Apanteles taragamae*, and *Beauveria bassiana* (Ganapathy 2010; Mehinto et al. 2014; Srinivasan et al. 2014). In addition, researchers have resorted to agronomic practices, such as intercropping (e.g., cowpea + sorghum; cowpea+ sesbania pea), adjustment of planting dates and increasing plant density to reduce damaging pressure from LPB in cowpea fields (Alghali 1993; Hassan 2009; Capo-Chichi et al. 2009; Muhammad, Malgwi, and Adamu 2017). Nevertheless, the development and use of resistant cowpea cultivars is regarded as the most cost-effective and sustainable option to control insect pests in cowpea (Ehlers

Table 1. Some chemical pesticides tested for the control of legume pod borer (LPB) in cowpea.

Chemical pesticides	References
Cypermethrin (10 EC)	Kawuki et al. (2005), Muhammad, Malgwi, and Adamu (2017)
Dimethoate EC	Adipala et al. (2001), Muhammad, Malgwi, and Adamu (2017)
Cyper diforce	Muhammad, Malgwi, and Adamu (2017)
Chlorpyrifos	Fernando et al. (2015), Mahalakshmi et al. (2016)
Teflubenzuron,	Fernando et al. (2015)
Chlorantraniliprole + lambda-cyhalothrin,	Fernando et al. (2015)
Indoxacarb 14.5% SC	Kanhere et al. (2012), Kattula et al. (2017)
Fipronil 5SC (0.015%)	Singh and Singh (2015)
Spinosad 45% SC	Kanhere et al. (2012), (Kattula et al. (2017)
Fludendiamide (480SC)	Singh and Singh (2015), Fernando et al. (2015)

and Hall 1997; Togola et al. 2017). Host-plant resistance helps to avoid the additional expenditures attributable to pesticide purchase.

Advances in breeding for resistance to LPB in cowpea

The development of new resistant plant cultivars involves key steps to explore or create genetic diversity for the trait of interest and selection of best-performing genotypes. This section examines the screening techniques, sources of for LPB resistance in cowpea and the underlying genetic mechanisms.

Screening for LPB resistance in cowpea

Breeding for pest and disease resistance often starts with germplasm screening to identify sources of resistance. It is important to develop reliable screening methods for resistance to insect pests in cowpea (Togola et al. 2017). These methods are host- or pest-specific; and require significant knowledge of the host-pest-environment interactions, which provides the basis for determining both the measurements and the plant parts to assess (Jackai 1982). For LPB resistance in cowpea, both artificial and field/natural screening techniques have been developed and used in various studies.

Field screening method for LPB resistance in cowpea

Jackai (1982) developed a field screening method for assessing LPB resistance in cowpea. This method relies on the natural infestation, wherein a susceptible cowpea cultivar is planted 2 weeks earlier than the test cultivars to serve as a source of insect pressure. Woolley and Evans (1979) had previously used a similar technique; however, the susceptible variety was planted 31 days before the planting of the test genotypes to increase pest pressure. In all cases, the ultimate goal was to guarantee enough pest pressure and identify true resistance. A good background information about the susceptible cultivar can help to adjust the planting dates for both test and susceptible genotypes. Because other pests, such as flower thrips and pod-sucking bugs, also feed on the same plant organs as LPB, it is recommended to apply a selective pesticide to limit possible interference by these pests during the screening process (Jackai 1982).

Assessment of insect resistance requires accurate measurement approaches (Jackai and Singh 1983). According to Jackai (1982), measurement of damage on flowers, pods, and seeds provides the most important assessment of LPB resistance in cowpea. Although highly informative, this technique may be complex and time-consuming to implement in large germplasm collections, as it requires

measurement of several parameters (Oghiakhe and Jackai 1992). Oghiakhe and Jackai (1992) suggested to use a fast method for initial screening of large collections of genotypes, which involves measurement of two damage parameters; incidence of damage on flowers and pod evaluation index.

The field-screening method has been extensively adopted, and most studies used the cultivar TVu 946 as a resistant check (Oghiakhe and Odulaja 1993; Oghiakhe, Jackai, and Makanjuola 1995). Although the field-screening method is quite efficient, it may bear some biases. For instance, in screening germplasm for LPB resistance, one has to ensure uniform pressure of the pest across experimental units. Ensuring this in open-field conditions can be challenging, as beyond the host plant, optimum environmental conditions (temperature, rainfall, relative humidity, and insolation) are required for effective pest development. Most of these environmental conditions are not under the control of the researcher in open-field conditions. Improvement of field-screening technique is important to avoid escape and identify lines that are truly resistant or susceptible to LPB.

Artificial screening method for LPB resistance in cowpea

Artificial infestation is used to overcome shortcomings in the field-screening method because of low or unknown level of infestation. This requires rearing the pest under a controlled environment. There has been significant progress in the development of quick protocols for mass rearing of LPB. Both cowpea diet and composite diet are used for the purpose. Jackai and Raulston (1988) proposed a cowpea flour diet (50 g of flour as the main ingredient) for the mass rearing of LPB. Wang et al. (2013) developed an artificial diet based on soybean flour and wheat germ, which could be used as an alternative for rearing the legume pod borer. More recently, Traoré et al. (2017) modified a commonly used diet to rear the stem borer (*Ostrinia nubilalis*) by supplementing cowpea flour for rapid multiplication of LPB.

After a sufficient number of insects have been obtained, one has to think of how to perform inoculation and how many insects to use and at what developmental stage of the cowpea plant. A number of inoculation methods are available to choose from, depending on the study conditions. Dabrowski, Bungu, and Ochieng (1983) explored the suitability of using young plants for rapid screening of cowpea genotypes for LPB resistance under artificial conditions and reported that the use of 10 eggs/plant at 5-7-shoot stage or flowering stage can help in segregating cowpea lines for resistance based on larval survival and level of damage on flower buds, flowers, and pods. This approach was used to determine the level of LPB resistance among 15 mutants cowpea genotypes (Adekola and Oluleye 2008). Jackai (1991) proposed two complementary bioassays to screen for LPB resistance in cowpea. The first assay consists of a dual-choice arena test (DCAT), where fresh pod segments of both test and control cowpea genotypes are exposed to LPB

larvae, feeding within a round plastic container, the so-called "arena." DCAT provides estimates of the feeding index (FI) and preference ratio (PR) for each test cultivar. FI serves as the basis for comparison between a given test genotype and a susceptible or resistant check, and PR for comparisons among cowpea varieties against the same check. DCAT helps to study antixenosis mechanism of resistance, whereas "intact pod test" (IPT) provides information about the insect response in a no-choice situation. The DCAT was used together with a no-choice laboratory feeding bioassay to identify sources of LPB resistance among *Vigna* species (*Vigna vexillata, Vigna oblongifolia*, and *Vigna unguiculata*) and to study the underlying mechanisms of resistance (Jackai and Padulosi 1996). In contrast to DCAT, a second bioassay, IPT, is performed on intact pods and only one cultivar is tested per assay. Each of these bioassays provides specific information, and if resources are available, combining them will help ascertain the true resistance status of the collection of cowpea genotypes.

The choice between natural and artificial infestations depends on the study objectives and the available facilities and skills. While the field method is highly informative and helps capture the natural variability, it is challenging to ascertain uniform pest pressure across experimental units and to separate the effects of confounding factors, such as damage from other insects and changes in weather conditions that may affect the insect feeding habit. The artificial-screening method is performed in a confined area, such as a screenhouse or an entomology lab, which helps to establish uniform pest pressure and to have control over environmental factors. It is also used to study antibiosis and antixenosis mechanisms of resistance (Jackai 1991; Derera, Pixley, and Giga 2001), which would be hard to measure using a natural-infestation method. However, this method may not give a real picture of what the performance of the genotypes would have been under open-field conditions.

The use of both methods can give complementary information. In fact, investigating the consistency of results under artificial and natural infestation may provide information for further refining the screening and guiding effective decision-making in a breeding program focused on LPB resistance in cowpea. For example, when starting with a large number of genotypes, it might be preferable to screen genotypes under controlled conditions to narrow down the number of genotypes before screening in open-field settings. This would help ascertain true resistance and save time and resources needed to screen a large cowpea germplasm collection under natural contrasting environments.

Sources of LPB resistance in cowpea

Successful development of insect pest-resistant cultivars begins with the identification of resistance sources (Timko and Singh 2008; Xiong et al. 2016).

Researchers have reported variation in LPB-resistance among cowpea accessions (Oghiakhe and Odulaja 1993; Oghiakhe, Jackai, and Makanjuola 1995).

Jackai and Padulosi (1996) screened a collection of 500 accessions from three wild *vigna* species, namely *V. unguiculata* subspecies *dekindhana, V. oblongifolia*, and *V. vexillata*. The authors found the most resistant accessions belonging to *V. vexillata*, followed by those from *V. oblongifolia*, and a few outstanding cultivars from *V. unguiculata*. Jackai and Oghiakhe (1989) reported low feeding by and developmental ability of LPB on pods of two wild cowpea accessions, TVNu 72 and TVNu 73. Continuous efforts to screen for LPB resistance among the cultivated cowpea (*Vigna unguiculata* (L.) Walp) have revealed some promising genotypes (Table 2). TVu 946 is one of the outstanding LPB-resistant cowpea cultivars reported by many authors (Jackai 1982; MacFoy, Dabrowski, and Okech 1983; Singh and Jackai 1988; Jackai 1991). This genotype was used as a resistant check in different studies and may be a possible donor in breeding programs focusing on LPB resistance. Jackai (1982) identified, in addition to TVu 946, five other cultivars as probable resistance donors, namely Kamboinse Local, TVu 1, VITA-5 (TVu 4557), TVx 3890-010F and VICAM-1/SP. Resistant status of TVu 946 and TVu 4557 was confirmed by Singh and Jackai (1988) in Nigeria.

As LPB feeds on various parts of cowpea plants, damage attributable to its occurrence can happen at any growth stage, leading to economic losses. MacFoy, Dabrowski, and Okech (1983) investigated resistance to both pre-flowering and flowering-stage infestation of LPB and identified TVu 946, Ife Brown and Vita 1 as resistant genotypes. Other studies revealed cowpea genotypes MRx2-84F, MRx49-84M, MRx109-84F as moderately resistant genotypes (Oghiakhe and Odulaja 1993; Oghiakhe, Jackai, and Makanjuola 1995). Among 50 local cowpea of Thrissur, three (Palakkad Local, Kottayam Local and Chengannur Local) were selected as resistant/tolerant. In India, genotype TVX-7 showed high resistance to LPB (Veeranna and Hussain 1997). More recently, Naveen et al. (2017) recorded low mean larval infestation per plant (3.1) on genotype C-152 in India. Mutation breeding has also been harnessed to deploy resistance against this pest in cowpea.

Here we identify some cowpea genotypes (Table 2) that have shown various resistance levels to LPB across varied environments. These gene pools are potential candidates to serve as parental lines in breeding programs (Adekola and Oluleye 2008).

Mechanisms of LPB resistance in cowpea

Defense against insect herbivores requires plants to develop morphological/physical and biochemical barriers (Lattanzio et al. 2000). It underlines some complex mechanisms (Togola et al. 2017). Three commonly known defense mechanisms exist in plants. These include strategies that repel the insects

Table 2. Sources of legume pod borer (LPB) resistance in cowpea.

Genotype(s)	Species	Resistance status/other traits	Origin	References
TVu 4557	*Vigna unguiculata*	Resistant to LPB with low damage on peduncles	IITA†, Nigeria	Jackai (1982), Singh and Jackaï (1988)
TVu 946	*Vigna unguiculata*	Resistant to LPB; semi-wild, pubescent	IITA†, Nigeria	Singh and Jackai (1988), Jackai (1991)
Vita-1, Ife brown	*Vigna unguiculata*	Resistant to LPB at pre-flowering and flowering stages	IITA†, Nigeria	MacFoy et al. (1983)
Kamboinse Local, TVu 1, TVx 3890-010F,VICAM-1/SP	*Vigna unguiculata*	Moderately resistant to LPB	IITA†, Nigeria	Jackai (1982), Jackai and Singh (1983)
MRx49-84M, MRx109-84M, MRx50-84M, MRx54-84M, MRx55-84M, MRx48-84M.	*Vigna unguiculata*	Moderately resistant to LPB; wide adaptability	IITA†, Nigeria	Oghiakhe and Odulaja (1993), Oghiakhe et al. (1995)
Palakkad Local, Kottayam Local,Chengannur	*Vigna unguiculata*	Moderately resistant to LPB; local cowpea cultivars with low percentage of flowers and pod damage	Thrissur, India	Anu (2004)
TVX-7	*Vigna unguiculata*	Moderately resistant to LPB; highly pubescent	Karnataka, India	Veeranna and Hussain (1997)
C-152	*Vigna unguiculata*	Resistant to LPB, with low mean larval population	Karnataka, India	Naveen et al. (2017)
V24; V25;V43; V87	*Vigna unguiculata*	Resistant to LPB; transgenic cowpea lines expressing Vip3Ba protein	Australia	Bett et al. (2017)
TVNu 72	*Vigna vexillata*	Resistant to LPB; wild cowpea, highly pubescent	IITA†, Nigeria	Oghiakhe et al. (1993),Jackai and Padulosi (1996),
TVNu 73	*Vigna vexillata*	Showed low preference for LPB oviposition	IITA†, Nigeria	Oghiakhe (1995)

†IITA = International Institute of Tropical Agriculture

(non-preference/*Antixenosis*), affect the biology of insect pest and alter its development (*Antibiosis*) or enable the plant to recover from the damage caused by the insects (*Tolerance*) (Rubaihayo 1996; Goggin, Lorence, and Topp 2015).

Both *antibiosis* and *antixenosis* have been observed in cowpea resistance to LPB (Jackai and Padulosi 1996). Oghiakhe, Jackai, and Makanjuola (1995) observed that, for oviposition, LPB females preferred some cultivars to others. MacFoy, Dabrowski, and Okech (1983) found cowpea cultivar TVu 946 to be less preferred by adult females for oviposition than Ife Brown and Vita 1. Most studies have pointed out trichomes to be physical barriers that slow down LPB infestation. For instance, Oghiakhe (1995) found the presence of trichomes in wild and cultivated cowpea to adversely affect LPB infestation. Jackai and Oghiakhe (1989) examined the relationship between pod-wall trichomes and LPB resistance in two wild cowpea genotypes (TVNu 72 and TVNu 73) and concluded that resistance based on trichomes was

a first line of defense against insects; phytochemicals were the second line of defense. High-density trichome cowpea cultivar TVX-7 showed high LPB resistance as compared to a low-density trichome and most susceptible cultivar (Veeranna and Hussain 1997). Trichome length and density were also associated with resistance to LPB in pigeonpea (Sunitha et al. 2008). These studies suggested that selecting or breeding for cowpea genotypes with long and dense trichomes on the pod wall would reduce the susceptibility of cowpea to LPB infestation.

Plants produce some chemicals that can either attract or repel insect herbivores (Lattanzio et al. 2000; Togola et al. 2017). Evidence of the influence of biochemical compounds in LPB resistance in cowpea has been provided. MacFoy, Dabrowski, and Okech (1983) demonstrated that there was a high accumulation of phenols and flavonoids in resistant cowpea cultivar TVu 946 as compared to the susceptible cultivars Ife Brown and Vita 1. When screening 45 cowpea cultivars in India, Veeranna (1998) found that tolerant genotypes had higher phenol and tannin contents as compared to the susceptible genotypes. Phenol content in fresh leaves was negatively correlated with low LPB damage in cowpea (Satpathi et al. 2017) and may be used as a criterion for selecting for LPB resistance in cowpea. Plant metabolites, such as sugars, proteins, fats, sterols, amino acids, and vitamins also influence host-plant susceptibility to insect pests (Sharma et al. 2007). For example, susceptible cowpea cultivars Ife Brown and Vita 1 accumulated higher amounts of sugars and amino-acids as compared to TVu 946. High concentrations of proteins and sugars in flowers and pods were also associated with susceptibility to LPB infestation in pigeonpea (Sunitha et al. 2008).

Identification of sources of LPB resistance in cowpea should use comprehensive methods that enable us to understand morphological, physiological traits and biochemical profiles underlying resistance in a working germplasm. These traits can be used as surrogate traits to select for LPB resistance in cowpea.

Challenges of breeding for LPB resistance in cowpea

The importance of breeding for LPB-resistant cultivars to sustain cowpea production across Africa cannot be overemphasized. However, there has not been much progress achieved so far because of challenges associated with selection for resistance to LPB in cowpea. The challenges range from interspecific crossing barriers to variability among LPB strains, genotype-by-environment influence, lack of research and problems associated with the adoption of transgenic varieties. These barriers are discussed below in greater detail.

Crossing barriers between cowpea gene pools

Crop wild relatives are known as reservoirs of rare allelic variants for characters that can be used to broaden the genetic base of agricultural food crops (Dwivedi et al. 2013). Interspecific cross-incompatibility often limits the transfer of those genes from wild relatives to cultivated species (Keneni et al. 2011). This holds true also for genes conferring LPB resistance in cowpea. Most studies have reported that sources of high LPB resistance exist among wild cowpea (*e.g., Vigna vexillata* and *Vigna oblongifoliu*), but its introgression into the cultivated germplasm is challenging because of crossing barriers between the gene pools (Jackai and Oghiakhe 1989; Jackai and Padulosi 1996; Togola et al. 2017). Two barriers to interspecific hybridization of *V. unguiculata* and *V. vexillata* have been reported: i) the reduction in fertilization attributable to a pollen-pistil incompatibility and ii) the abortion of fertilized ovules (Barone, Del Gindiee, and Ng 1992). Though cross-compatibility may be observed between some cultivated varieties and their wild relatives (Russom and Abdul 2010), in most cases successful crosses produce very few seeds, as some embryo and endosperm nuclei degenerate a few days after pollination (Barone, Del Gindiee, and Ng 1992; Lelou, Diatewa, and Van Damme 2011). There is need for further studies based on new emerging techniques to make use of the sources of resistance available in the wild cowpea germplasm.

Genetic variation in legume pod borer

Breeding for insect-pest resistance is a complex task because of the genetic variability in the pest populations (Keneni et al. 2011). Phylogeny analysis of a mitochondrial cytochrome c oxidase-I gene (cox1) fragment of LPB samples collected from Australia, Nigeria, Niger, and Puerto Rico revealed the presence of three *Maruca* sp. lineages (Margram et al. 2011). A later study on the genetic variation among LPB showed two putative subspecies of LPB in Asia and sub-Saharan Africa (Periasamy et al. 2015). This population substructure effect has significant implications for effective management of the pest and its damage on important grain legumes like cowpea, as one has to develop resistance for all three biotypes. A proper characterization of LPB biotypes present in the target areas and knowledge of the co-evolving insect-plant-environment interactions are needed for developing effective breeding strategies.

Influence of genotype-by-environment interaction (G × E)

Most of the traits of agricultural importance, such as yield, disease and pest resistance, nodulation and others, are influenced by environmental factors

(Asio, Osiru, and Adipala 2005; Ezeaku et al. 2014; Agoyi et al. 2017). Resistance/tolerance to LPB is a complex trait controlled by many genes and influenced by environmental factors (Sharma et al. 2007). Variation in cropping seasons/years influences the extent of LPB damage in cowpea (Ezeaku et al. 2014). Karungi et al. (2000) found that environment (location and season), time of planting and plant density influenced LPB infestation in cowpea. They observed a high level of LPB infestation in cowpea planted at the onset of rains as compared to that planted later in the season.

Furthermore, the fluctuation in environmental factors (temperature, relative humidity, rainfall, etc.) may influence the insect population, which is a determinant factor in the management of insect herbivores. It was reported that an increase in temperature from 14.4°C to 29.3°C had shortened the development cycle of LPB on cowpea (Adati et al. 2004), leading to rapid growth in the pest population across a short period of time; which is bound to increase yield losses. The distribution of rainfall is another important factor determining the fluctuations in pod borer populations. A significant relationship was observed between peaks in pod borer populations and peaks of the rainfall (Alghali 1993).

The variation in environmental factors influences not only the biology of LPB but also the response of the cowpea plant against the insect. Knowledge of these factors is needed to inform breeding strategies to use and define ideal environments where variety testing can take place to cover a wide range of the target production. Also, breeding activities toward LPB resistance in cowpea should be consistent in partitioning and/or determining the magnitude of genotypic and environmental effects influencing the overall performance of the test genotypes. This could serve as a basis for decision-making about candidate genotypes and effective breeding methods for increasing LPB resistance in cowpea.

Limited knowledge of the genetic architecture of LPB resistance in cowpea

Previous studies have shown that there is, to some extent, genetic variability for LPB resistance in cowpea. Success in introgressing resistance into farmers' preferred cultivars greatly relies upon the knowledge of heritability and gene action for the trait. Most insect resistance factors in cowpea often show low heritability under field conditions (Timko and Singh 2008). This is probably because of the high influence of environmental variables under field conditions, which affects the correlation between phenotype and genotype (Yan and Kang 2003; Shiri 2013).

The few studies on the genetics of LPB resistance in cowpea pointed at the high heritability of the trait. Woolley and Evans (1984) found that resistance

to LPB damage on flowers was highly heritable ($0.60 \leq h^2 \leq 0.80$) and polygenic, with alleles showing partial dominance. These authors also highlighted that LPB resistance in cowpea flowers and pods may be controlled by a different genetic system (Woolley and Evans 1979). A study by Anu (2004) confirmed the high magnitude of additive gene effects in the heritance of LPB resistance in cowpea. A high broad-sense heritability ($0.35 \leq H^2 \leq 0.76$) for the larval count at different stages was also reported for LPB resistance in chickpea (*Cicer arietinum* L.) (Jadhav and Gawande 2016).

Till date, there is no information about the number of genes, their position in the genome and their interaction in determining the reaction of cowpea against LPB infestation. There is a need for more in-depth research to dissect the genetic architecture of LPB resistance in cowpea, especially to identify specific regions of the genome and/or the actual number of genes that control the trait, and their effects.

Barriers to the adoption of transgenic LPB-resistant cowpea varieties

Transgenic approach has proved successful in developing resistance to many pests and diseases in cowpea. Advances in genetic engineering have expanded the sources of genes for plant improvement beyond the gene pool normally accessible via sexual or other tissue culture hybridization techniques (Rubiales et al. 2015). Genes conferring LPB resistance, such as *Bt* (*Bacillus thuringiensis*) genes and genes producing plant lectins and plant proteinaceous inhibitors of insect proteinases (serine, cysteine, aspartic, and metalloproteinase), can be incorporated into cowpea genome through genetic engineering to build resistance in the cultivated cowpea germplasm (Timko, Ehlers, and Roberts 2007). One of the recent and successful applications of such approach was the development of some transgenic cowpea lines expressing *B. thuringiensis* Vip3Ba protein, which showed resistance to LPB infestation (Bett et al. 2017). Although these are promising results, scaling up and adoption of the products developed to regions at high risk of LPB infestation, such as sub-Saharan Africa, are still challenging because of the political, social and environmental concerns and regulation barriers associated with the adoption of genetically modified crop (GMCs) varieties in this region.

There have been significant advances in setting up a comprehensive framework for genetic engineering work in countries like Uganda, Kenya, and Tanzania (Chambers 2013), but Africa, as a whole, is still lagging behind. For instance, in Benin, GMCs are banned both for consumption and research and people are still reluctant to adopt them because of their perceived negative impact on health and environment (Houdegbe, Tchokponhoue, and Sogbohossou 2018), despite recent reports that revealed high economic impact of non-adoption of the GMCs (Wesseler et al. 2017). The report

projected that the costs of a delay in adopting GMCs can be substantial. Even a single-year delay in the approval of LPB-resistant cowpea, for example, in Nigeria, which is the world's largest cowpea-producing country, could cost the country about 33 million USD to 46 million USD and between 100 and 3,000 lives (Wesseler et al. 2017). The situation may appear more dramatic at a regional level, considering, for instance, the number of countries in sub-Saharan Africa alone, whose populations depend heavily on cowpea for their daily protein intake. The benefits may outweigh the challenges in adopting GMCs. This calls for quick action from the African governments to develop a framework and policies for adopting or rejecting the technology based on the cost-benefit analysis. In the meantime, there is a need for more investments in conventional breeding to find alternatives for reducing the high yield losses in cowpea in the region.

The future of breeding LPB resistance in cowpea

Optimizing selection approaches

Breeding for LPB resistance in cowpea encompasses the identification of sources of resistance for use as parental lines. The success largely depends on accurate phenotyping and appropriate selection methods/strategies (Murdock et al. 2009). The diagram (Figure 2) represents a summary of the different techniques used in the selection of ideal genotypes.

Indirect selection for LPB resistance in cowpea

Assessing the resistance status of thousands of genotypes, on the basis of incidence and severity of LPB damage on pods, flowers, seeds and other organs, is a very tedious task. Since the objective is to identify resistant genotypes with optimum performance across a range of environments, applying multivariate selection criteria, together with selection indices, can give more significant results in selecting genotypes based on surrogate traits (Paiva et al. 2015). Best-performing genotypes for a primary trait, such as yield, can be identified on the basis of correlated response of this trait with LPB damage parameters (pod thickness, pod hairiness, percentage of pod damage, number of larvae per flower, and/or percentage of infested seeds) assessed across environments (Heumez et al. 2005). However, the effectiveness of this approach depends on the extent of the genetic correlation between the primary trait and correlated trait(s) (Kang 2002).

Another approach is to use selection index. Breeders, either consciously or unconsciously, assign weights to different traits when developing crop varieties (Kang 2002). Jackai (1982) developed a plant damage index for selecting LPB-resistant genotypes, which represents a combination of weighted measurements

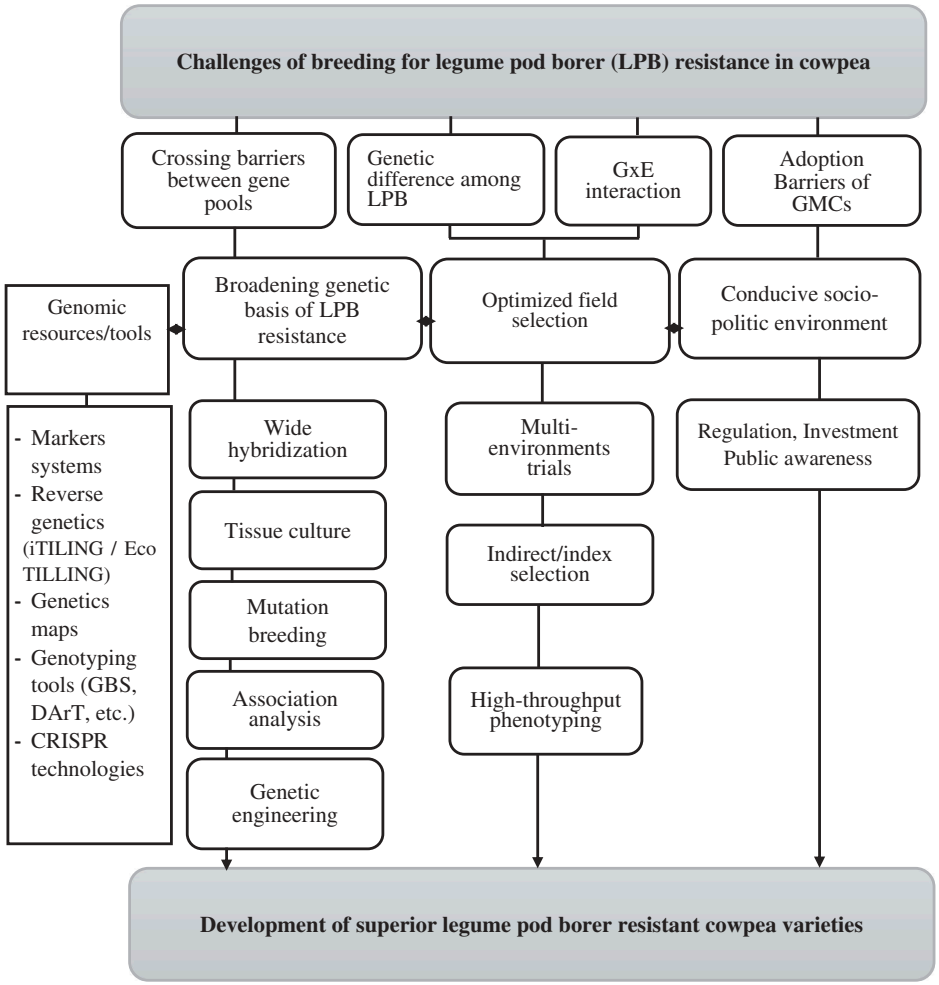

Figure 2. Summary diagram of the challenges and approaches/tools for breeding legume pod borer (LPB) resistance in cowpea.

of LPB damage on seed, flowers, and pods. The plant damage index can be optimized to include other factors influencing LPB resistance in cowpea (e.g. secondary metabolites, pod hairiness, pod thickness) for effective decision-making. This selection for multiple traits should increase the chances of success of a breeding program targeting LPB resistance in cowpea (Costa et al. 2008). Assigning a specific weight to traits of importance is somewhat complex and should be guided by the expected genetic gain for an individual trait.

Conducting multi-environmental trials to capture the genotype by environment interaction (G × E) effect

Like many other traits in cowpea, resistance to LPB infestation exhibits quantitative variation. Evaluation of breeding lines in contrasting environments helps

to quantify the effect of G × E on genotypic performance and select stable-performing or specifically adapted genotypes. Oghiakhe and Odulaja (1993) based a cluster analysis on LPB-damage parameters and yield performance from multi-environment trials to group cowpea genotypes into different LPB-resistance classes. The authors identified one cultivar (MRx6-84F) with wide adaptability in the presence or absence of LPB infestation. This approach can be adopted across specific cowpea-growing regions in selecting breeding materials. Statistical analyses, such as AMMI (Additive Main Effects and Multiplicative Interaction) and GGE (Genotype and Genotype by Environment Interaction) biplots can be deployed for easy and precise interpretation of data from multi-environment trials for LPB resistance (Yang et al. 2009). The use of GGE biplot could guide selection based on both performance and stability of the genotypes for LPB resistance, as it offers a highly comprehensible visualization of the multi-environment dataset (Blanche, Myers, and Kang 2007). On the other hand, with AMMI analysis, one can partition the overall variation observed in genotypic performance for LPB resistance across environments into genotype main effects, environment main effects, and G × E (Gauch 2006), and select superior genotypes under effective legume pod borer pressure.

Harnessing genomics resources for breeding LPB resistance in cowpea

Improving quantitatively inherited traits using conventional breeding is a very difficult and time-consuming task (Rubiales et al. 2015). Marker-assisted selection (MAS) was embraced to overcome limitations of this approach and to allow timely development of new crop varieties. MAS principle is based on markers linked to quantitative trait loci (QTL) (Bernardo 2008), which are regions within a genome containing genes associated with a particular quantitative trait (Collard et al. 2005). MAS helps to deal with complex and low-heritability traits. The complexity in the inheritance patterns of LPB resistance in cowpea and the challenges (natural fluctuations in pest pressure, precise setup and skillful mass rearing of insects) associated with the measurements of the trait in the field or greenhouse make LPB resistance a perfect target for MAS (Timko and Singh 2008).

Though the development of genomic resources for cowpea has been slower as compared with other crops (Boukar et al. 2016), association analysis has been applied in breeding resistance to some other important cowpea insect herbivores, such as foliar thrips and aphids (Huynh et al. 2015; Boukar et al. 2016; Qin et al. 2017). To our knowledge, there has not been so far any published work related to marker-trait association regarding LPB resistance in cowpea. There is a need to harness the diversity of cowpea genomic resources (Boukar et al. 2016, 2018) to explore the possibility of MAS for LPB resistance in cowpea. Next-generation sequencing (NGS) technologies have enabled the generation of high ultra-throughput sequencing tools for plant genotyping (He et al. 2014). Genotyping methods involving simple-sequence-repeat (SSR)-based genotyping

and sequence-based genotyping (Bajgain, Rouse, and Anderson 2016) can be used in association analysis for LPB resistance. Techniques, such as Diversity Arrays Technology (Kilian et al. 2012), Genotyping-by-Sequencing (GBS) (Elshire et al. 2011; He et al. 2014), IlluminaGoldenGate assay, KASPar, Affymetrix SNP array (Rubiales et al. 2015), are also available for genotyping and a range of molecular-marker systems have been developed for easy application of QTL analysis in cowpea. For instance, a total of 1071 unigene-derived SSR markers have been reported in cowpea (Gupta and Gopalakrishna 2010). About 1104 single-nucleotide polymorphisms (SNPs) marker in cowpea have also been converted in competitive allele-specific PCR (KASP) for cost-effective genotyping in cowpea (https://www.integratedbreeding.net) through the collaboration between the Generation Challenge Program/Integrated Breeding Platform and other partners. Furthermore, important efforts have been made to develop genetic maps for cowpea and/or related species (Ouédraogo et al. 2002; Muchero et al. 2009; Adetumbi et al. 2016), which could facilitate the identification of genes or QTL linked to LPB resistance in cowpea, and unravel inheritance patterns underlying this trait for its easy transfer into desirable cowpea genotypes. This indicates that there is a potential for unlocking the genetic architecture of LPB resistance in cowpea.

The effectiveness of the genomic resources described herein to detect a possible marker-trait association, leading to gene discovery and fast-tracking of progress in breeding for LPB resistance in cowpea, relies upon good phenotypic data (Rafalski 2010). Reliable phenotyping may require genotypic performance testing across environments and highly precise methods for data collection and management. In addition, data from different testing environments can provide insights into loci × environment effects (Zhao et al. 2005; Korte and Farlow 2013).

Advances in the development of platforms for high-throughput phenotyping of large plant populations in both field and greenhouse have been made (Goggin, Lorence, and Topp 2015; Araus et al. 2018). These techniques are based on automated image collection and analysis (Goggin, Lorence, and Topp 2015) and can be optimized for measuring LPB damage on cowpea plants to save time and increase the accuracy of the phenotypic data collected across environments.

Broadening the genetic base of cowpea for breeding LPB resistance in cowpea

Despite the evaluation of hundreds to thousands of cowpea accessions, it is still very challenging to identify plants with high levels of resistance to most important insect pests, including LPB (Timko and Singh 2008). Sources of LPB resistance have been reported in a distantly related species of cowpea, *V. vexillata* (Jackai and Padulosi 1996; Murdock et al. 2009), which can be

introgressed into cultivated cowpea. As it has been highlighted earlier, interspecific genetic barriers may limit this possibility, but approaches such as tissue culture, embryo rescue, and protoplast fusion can help overcome these barriers (Singh et al. 1997; Rubiales et al. 2015). The embryo-rescue technique was successfully used in hybridizing cultivated cowpea and the wild relatives, i.e., *V. vexillata* (Gomathinayagam et al. 1998) and *V. pubescens* (Fatokun and Singh 1987). These techniques were also deployed to cross the wild pigeonpea (*Cajanus platycarpus*) carrying resistance to pod borer with *Cajanus cajan* (Mallikarjuna et al. 2011). Though these approaches are promising, the progenies generated from the interspecific hybridization are often of small size and several backcrosses are required to recover the large seed size that is a key preferred trait in the cultivated cowpea (Boukar et al. 2016). Development and deployment of markers through foreground, background and recombinant selection can be useful in speeding up the recovery of desirable genotypes in the backcrossing process.

Mutation breeding could also be used to create a novel genetic variation for pod borer resistance in cowpea. Chemical mutagens (ethyl methane sulfonate) or physical mutagens (Gamma-ray irradiation) can be used to induce point mutations in the genome (Esfeld, Uauy, and Tadele 2013; Rubiales et al. 2015). Adekola and Oluleye (2008) reported significant variation among 15 gamma-ray-induced cowpea mutants for resistance to legume pod borer, with the best-performing cowpea mutant (Mutant 4) showing lower yield loss (46.1%) as compared to the susceptible wild type "IT84S2246 D" (75.1%). Non-transgenic and relatively low-cost reverse genetics methods, such as TILLING/EcoTILLING can also be deployed for easy application of the mutagenesis and high-throughput detection of LPB-resistant genetic variants (Vilanova et al. 2012; Boopathi 2013; Esfeld, Uauy, and Tadele 2013). These approaches could also be harnessed to broaden the genetic base of LPB resistance in cowpea.

Furthermore, genetic engineering has been effective in developing insect-resistant cowpea varieties (Ehlers and Hall 1997). This technology is already in use and some pod borer-resistant *Bt* cowpea lines have been developed and are either under confined field trials or adopted in some of the western Africa countries, including Nigeria and Burkina-Faso (Togola et al. 2017; Wesseler et al. 2017; Boukar et al. 2018). Since the genetic linkage map for *V. vexillata* is available (Ogundiwin et al. 2005), it would be of interest to make an effort in identifying and mapping LPB-resistance genes from this wild cowpea type, which has shown resistance to the insect, and transfer it into the cultivated cowpea. Gene editing systems like CRISPR/Cas9 (Clustered Regularly Interspaced Short Palindromic Repeats/Cas9 protein) technologies can be used for this purpose (Mudziwapasi et al. 2018).

Conducive socio-economic-political environment for fast development and adoption of LPB-resistant cowpea varieties

There is a need for governments, especially the African governments, to implement policies that support agricultural development (Tadele and Assefa 2012). The importance of private–public partnership for crop improvement cannot be overemphasized. There are ongoing collaborations among several research institutions to develop sustainable technologies against the legume pod borer infestation in cowpea. However, there is a need for more engagement from both local and regional government bodies to support breeding for LPB resistance in cowpea. As highlighted by Kang (2002), the potential benefits of genomic research will not be realized without investments. It would be of interest to develop and enact the regulatory framework for biotechnology in the countries, which are still lagging behind. There is also a need for these countries to invest in the acquisition of cutting-edge technologies and training of the workforce to implement the different breeding approaches (Figure 2).

Conclusion

The legume pod borer (LPB) causes serious yield losses in cowpea production, especially in Africa. Breeding for host-plant resistance represents the best alternative for the effective control of the infestation of this pest on cowpea. This review revealed that though a large amount of germplasm of cowpea has been screened for resistance to this pest, a very low level of resistance and very few sources of resistance were found among the cultivated cowpea. The sources of resistance existing in the wild cowpea cannot be easily transferred into the cultivated cowpea because of interspecific crossing barriers. In addition, the genetic differences among LPB races, effects of genotype-by-environment interaction, limited knowledge of the genetic architecture of LPB resistance and the socio-political barriers to the adoption of genetically modified crops are potential challenges faced by breeding programs targeting LPB resistance in cowpea. Optimized selection techniques to partition the G × E effect and application of indirect selection can help to overcome some of these challenges. We demonstrated that there are sufficient genomic resources that can be tapped for increasing breeding efficiency for LPB resistance in cowpea. Besides, the use of these tools, together with tissue culture, mutagenesis, and genetic engineering, can help in broadening the genetic base of cowpea and introgressing LPB resistance into cowpea. It is clear that the use of genomic tools and resources in practical plant breeding will increase the genetic gains in breeding for LPB resistance in cowpea. However, there is a need for an enabling socio-economic and political environment for the application of these technologies and quick adoption of the developed varieties.

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