



Breeding potential of lablab [*Lablab purpureus* (L.) Sweet]: a review on characterization and bruchid studies towards improved production and utilization in Africa

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Received: 12 February 2021 / Accepted: 14 September 2021
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Abstract Lablab (*Lablab purpureus*) [*Lablab purpureus* (L.) Sweet] is termed a lost, underutilized and neglected crop in Africa. Despite the multipurpose use, production, consumption and research are still limited. Wide genetic diversity of lablab germplasm exists in Africa. Diversity studies provide significant information for subsequent research programs and improvement. The advent of genotyping and sequencing technologies has enabled the identification of unique and agronomically important traits. Application of next-generation sequencing on lablab as a pioneer orphan crop is currently underway. This has enabled description of the whole genome, generation of reference genome and resequencing that provide information on variation within the entire genome. Information from these technological advances helps in identifying potential traits for biotic and abiotic stress for further breeding programs. Storage pests specifically bruchids (*Callosobruchus* spp.), are

considered a major obstacle in lablab production. Screening of available genotypes for bruchid resistance and studies on the physical and biochemical factors that confer resistance in lablab is required. Applying advanced technologies provides precise and reliable identification of the novel markers responsible for bruchid resistance allowing for introgression of important genes to breeding programs. This review provides a detailed analysis on the characterization of lablab and the information on bruchid resistance vital for breeding farmer-preferred varieties that possess agronomically beneficial traits. Concerted efforts and research on this neglected crop will enhance its production, utilization and consumption.

Keywords *Lablab purpureus* · Characterization · Bruchids · Biochemical · Mode of resistance · Breeding

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Introduction

Lablab [*Lablab purpureus* (L.) Sweet] has been termed as a 'lost, underutilized and neglected orphan crop' (Maass et al. 2010) owing to limited research programs and development concerns. Lablab contributes to tackling food insecurity, nutrient deficiencies, diversification of diets, generation of income, health benefits, soil conservation and climate-smart

crop (Joshi et al. 2020). Production patterns of lablab have been on a decline due to genetic, agronomic, eroded cultural factors, reduced research focus, economic, market, less awareness of the nutritional value, lack of improved varieties, poor management practices and improvement, as well as the variation in the climate patterns (Bhatt et al. 2019). Competition from the improved legumes whose yield and production patterns are well known has brought about this shift by the producers and the end-user. The waning existence of lablab contributes to a narrow genetic base and decline in important traits considered vital for crop existence and adaptability to various environmental conditions.

Lablab is a multipurpose crop. Several plant parts can be consumed as food i.e. seeds, immature grains, green pods, leaves, biscuits (Davari et al. 2018; Habib et al. 2017; Kilonzi et al. 2017; Rana et al. 2021), animal feed (Murphy et al. 1999), to improve soil fertility (Gebreyowhens 2017; Qamar et al. 2014; Sitienei et al. 2017) and in the form of green manure (Okumu et al. 2018). The latest research findings report the effectiveness of lablab bean extracts being able to impede infections of viral diseases such as influenza and SARS-CoV-2 which has been described as a world pandemic (Liu et al. 2020). This demonstrates the necessity of improving its production and utilization.

Lablab production has been hampered by biotic factors resulting in low production and consumption. Insect pests such as legume pod borer (*Helicoverpa armigera* Hubner and *Maruca vitrata* Fabricius) (Boit et al. 2018; Liao et al. 2000; Popoola et al. 2019; Srinivasan 2014), pod boring caterpillars, stem borer (Satyagopal et al. 2014), stink bugs (*Coptosoma cribraria* Fabricius) (Chawe et al. 2019; Forsythe 2019; Grotelüschen 2014; Mondal et al. 2017; Njarui et al. 2004), parasitic plant such as *Anoplocnemis curvipes* Fabricius (Watson et al. 2018), *Podagrica unifirma* (Jac.), *Ootheca mutabilis* (Sahlb), *Nemato-cerus acerbus* (Faust) aphids (*Aphis sp.*) (Chawe et al. 2019; Srinivasan 2014) pose a major threat during lablab production. During storage, the most important storage pest in Lablab is bruchids (*Callosobruchus sp.*) as reported by (Chawe et al. 2019), resulting in a total loss of up to 90% of the stored legume grain (Ebinu et al. 2016). Due to a lack of research on the best control method for bruchids attack on lablab, farmer adoption of lablab production has decreased.

Studies on bruchid resistance are necessary to understand the mode of resistance and to be able to breed varieties with the desired traits for farmers.

Current research on lablab has primarily focused on animal feed (Ewansiha et al. 2017) and soil conservation (Whitbread et al. 2011) resulting in genetic erosion and a reduced gene pool in Africa, despite the crop's importance for food and nutritional security (Minde et al. 2020). During the 1930s, studies on land use management in Tanzania's northern region reported the cultivation and production of lablab. However, the acreage under production was reduced to a negligible size by 2000 (Ngailo et al. 2001). Lablab bean germplasm is widely distributed throughout the country, and there is a need to study and document the existence and variation of these germplasms. Germplasm collection, evaluation, characterization, conservation and management are critical steps in lablab crop improvement.

Characterization generates important knowledge on genetic diversity and relationships between populations in a given germplasm resource required for breeding programs. Characterization can be classified based on phenotypic traits (morphological), variation of isoenzymes (biochemical) and deoxyribonucleic acid (DNA) variation (molecular). Morphological and biochemical characterization is limited by the environment and the plant growth and development (Kordrostami et al. 2015). Molecular characterization relies on DNA found abundantly in the genome is more robust and reliable, and is not influenced by the environment or plant growth. Studies on morphological and molecular characterization of lablab have been done to distinguish the relationship and compare evolution paths of genetic resources. However, limited research on biochemical characterization has been documented.

Information on phenotypic and genotypic characters is used to develop a core collection which represents the entire collection with maximum genetic variation and least repetitiveness of the population (Brown 1989b). Germplasm identification and genetic diversity studies are core in crop improvement towards developing improved varieties with farmers' preferred traits such as high yielding, nutritious, marketable value, and ability to withstand abiotic and biotic stresses. Lablab production is constrained by pests and diseases, bruchids (*Callosobruchus* spp.). Understanding the existing knowledge on bruchid

resistance management, mechanism and gene action is thus critical for providing a roadmap for plant breeders and geneticists involved in crop improvement.

The previous review on lablab described its status as an underutilized crop (Maass et al. 2010; Naeem et al. 2020) genetic resource status (Ramesh et al. 2016), nutritional importance (Minde et al. 2020), pharmacology and medicinal aspects (Al-Snafi 2017), as a forage (Murphy et al. 1999), production constraints (Khan et al. 2020) and omic sciences in lablab (Rai et al. 2018). However, little information on characterization and bruchid resistance has been reported in regards to lablab. This review discusses the status, morphological and molecular characterization, core development; management, mechanism and the gene action of lablab genetic resources. The information generated will pave the way for future research focus, especially concerning farmers' preferred traits.

Nutritional importance of Lablab

Lablab has important nutritional components required for normal growth and development. It is an inexpensive source of protein and micronutrients as compared to other legumes, attesting to the need for research on it to improve food and nutritional security. These micronutrients include fiber, phosphorus, niacin and thiamin which form an important part of the diets of resource-poor households in the rural setting. These highlighted components emphasize lablab as a potential functional crop to help in combating malnutrition and micronutrient deficiency diseases. Table 1 compares the nutritional value of lablab to that of other related legumes such as Cowpea (*Vigna unguiculata* (L.) Walp.), Bambara groundnut (*Vigna subterranea* (L.) Verdc.), Common bean (*Phaseolus vulgaris* L.), Soybean (*Glycine max* (L.) Merr.), Chickpea (*Cicer arietinum* L.) and Lentil (*Lens culinaris* Medik.).

Germplasm resource conservation of lablab

Ex situ lablab genetic resources are maintained in various locations across the African, Asian, American, Oceanic and European continents (Table 2). Germplasm conservation of lablab plays a critical role in identifying the existing and unknown crop diversity as

well as maintaining the genetic basis to enhance the development of improved varieties. The advances in phenotypic and genotypic studies allow effective and efficient exploration of the germplasm collections present in gene banks. Research focuses on understanding the conservation status is important for future breeding programs.

Characterization of lablab germplasm

Determining the genetic variation of a particular species is paramount for its improvement. Knowledge of the genetic constitution of given germplasm provides a critical groundwork for further breeding programs (Xu et al. 2017). Several genetic diversity studies on lablab crops have been undertaken. These genetic studies range from the classical methods to the current advanced high throughput genotyping methods that are precise, accurate and generate a large amount of information regarding the crop of interest (Yang et al. 2020).

Lablab breeding has incorporated the application of morphological, biochemical and cytogenetic markers with significant contribution in describing important genes as well as determining the genome size and variability (Farooq et al. 2002). Despite this critical contribution, these markers offer narrow genetic information and thus there is a need for advanced methods that exhibit more complex and precise variability of the genes linked to the most important agronomic traits for lablab breeding (Nadeem et al. 2018). The discovery of DNA markers enabled the prediction of individual and population genetic information by detecting the polymorphism existing among the alleles of a given gene (Nadeem et al. 2018).

Germplasm collection, characterization and evaluation are paramount for any given breeding program. Germplasm characterization helps to identify preferred traits of interest by the breeders and farmers (Mwenda 2019). Genetic variation can be distinguished based on morpho-physical, biochemical and DNA-based markers to describe the extent of evolutionary divergence and similarities. The research status in terms of characterization in lablab is discussed below. Most of the research is focused on morphological and DNA-based characterization.

Table 1 A summary of the comparison of the nutritional composition of lablab with other legumes *Source:* Adopted and modified from (Ganesan et al. 2017; Tolera 2006; Wallace et al. 2016)

Component	Lablab	Cowpea	Bambara groundnut	Common bean	Soybeans	Chickpea	Lentils
Carbohydrates (g)	62	61	61	60	8.36	27.42	20.13
Fiber (g)	8.6	5.4	4.8	4.4	6	7.6	7.9
Fat (g)	1	1.4	6.2	1.5	8.97	2.59	0.38
Protein (g)	22.8	22.5	18.8	21.7	18.21	164	9.02
Calcium (mg)	90	104	62	120	102	49	19
Iron (mg)	9	N/A	12.2	8.2	5.14	2.89	3.33
Phosphorus (mg)	328	416	276	323	245	168	180
Ascorbic acid (mg)	trace	2	trace	1	1.7	1.3	1.5
β-carotene (mg)	N/A	70	10	10	9	27	8
Niacin (mg)	2.3	4	1.8	2.4	0.399	0.526	1.06
Riboflavin (mg)	0.1	0.9	0.1	0.2	0.285	0.063	0.073
Thiamin (mg)	0.5	0.1	0.5	0.4	0.155	0.116	0.169

Table 2 Lablab genetic resources in different gene banks *Source:* Kirkhouse Trust (2019); Maass et al. (2010); Ojiewo et al (2010); Ramesh and Byre Gowda (2016)

Continent	Country and Institutions involved	Acc. No	References
Asia*	South-east Asia (Other than Bangladesh & India)	82	(BI 2008)
	South Asia	93	(BI 2008)
	Philippines	209	(Engle 2000)
	National Bureau of Plant Genetic Resources (NBPGR), India	221	(BI 2008)
	China	410	(BI 2008)
	World Vegetable Research and Development Centre (AVRDC), Taiwan	447	(AVRDC 2009)
	Bangladesh	551	(Islam 2008)
Africa*	University of Agricultural Sciences (UAS)- Bengaluru, India*	650	(BI 2008)
	Sub-Saharan Africa including International Institute of Tropical Agriculture (IITA), Nigeria	67	(BI 2008)
	World Vegetable Centre, Eastern and Southern Africa, Arusha-Tanzania	73	(Ojiewo et al. 2010)
	Ethiopia including International Livestock Research Institute (ILRI)	403	(BI 2008)
	Kenya	403	(BI 2008)
Oceania	Nelson Mandela African Institutions of Science & Technology (NM-AIST), Tanzania*	450	(Kirkhouse Trust 2019)
	Commonwealth Scientific and Industrial Research Organization (CSIRO), Australia	104	BI (2008)
America	United States, Department of Agriculture (USDA)	52	(BI 2008)
	Europe	82	(BI 2008)
Europe	South America	134	(GRIN 2009)
	Total	4251	

(Acc. No = Accession Number)

*The largest world collections of lablab germplasm are reported in Asia at UAS Bengaluru, India while in Africa is held at NM-AIST, Tanzania. This demonstrates that Africa has fewer lablab collections than Asia

Morphological characterization

Morphological characterization is based on visual observations of growth habits and structure of plants across a variety of edaphic factors. The variation of major qualitative and quantitative characteristics is entirely responsible for crop improvement in lablab. Byregowda et al. (2015) developed a lablab descriptor with 29 qualitative characters and 41 quantitative characters on a study of 650 accessions depicting the presence of a wide range of phenotypic characters. These morphological variations depend on the vegetative, inflorescence, fruit and seed characters of the lablab. Descriptors help to maintain the genetic purity and identity of a given crop, allow ease of varietal identification and reduce duplication. Lablab exhibits a wide morphological difference in most of its parameters, such as leaf color, leaf vein color, stem pigmentation, flower, pod and seed color and growth habit. Some of the photos of the different seed and flower morphology are as shown below in Fig. 1.

Genetic diversity analysis contributes significant information for breeding and crop improvement. The initial diversity studies involved the application of

Mahalanobis D statistics to determine the variation of 48 Indian bean genotypes (Chaitanya et al. 2013). In this study, the maximum divergence was exhibited in protein content, inflorescence number per flower, pod length and pod number per plant respectively. Similar results were observed on sixty-one (61) genotypes in Bangladesh (Shibli et al. 2021). This generated critical information on hybridization for developing elite recombinants.

Characterization of a germplasm resource as per morphological characters provides knowledge and information to researchers and breeders on the potential to tap and utilize in improving their genetic value. Lablab has high plasticity and is grown across different agro-ecological zones. This has enabled the presence of wide variation of the morphological and agronomic characters and enhance adaptability to the environment. Understanding the existing genetic diversity allows the development of new and improved varieties with farmers' preferred traits. Lablab has been characterized by several agro-morphological factors, as illustrated in Table 3 below.

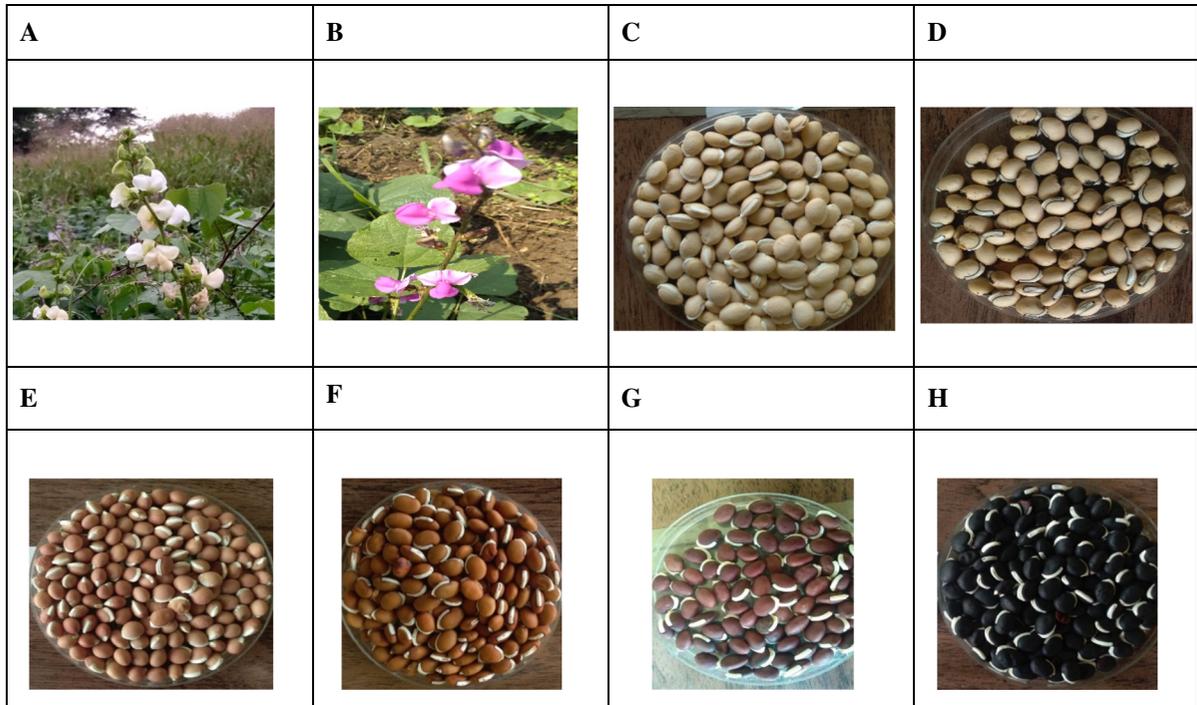


Fig. 1 Diversity in flower and seed morphology of lablab (a) White flowers color (b) Purple flowers (c) White seed color (d) White seed with black hilum edges (e) Cream seed color (f) Brown seed color (g) Red seed color (h) Black seeds

Table 3 Morphological characterization of lablab traits in different countries

Traits	No. of Accessions	Country	Reference
5 quantitative and 9 qualitative characters	12	India	(Chattopadhyay et al. 2010)
21 quantitative traits as per (Byregowda et al. 2015)	41	Tanzania	(Chawe et al. 2019)
Leaf vein pigmentation, growth habit, branching habit, stem color, flower color, pod color and characters, such as size, shape, weight and seed number per pod	63	India	(Naghera et al. 2016)
17 quantitative and qualitative characters (Byregowda et al. 2015)	37	India	(Patil et al. 2015)
Seed (length, width, weight, and thickness) leaf (length, and width), pod (length and width)	15	Indonesia	(Purwanti et al. 2019)
Leaf size, vine color, flower color, pod (color, shape and type) and seed color	23	Nepal	(Ram et al. 2016)
Stem color, leaf size, flower color, pod color, pod size, seed size, seed weight	14	India	(Singh & Abhilash 2019)
21 qualitative traits and 20 quantitative traits	650	India	(Vaijayanthi et al. 2015)

Table 4 Biochemical characterization of lablab in different countries

Biochemical character	Country	Accessions	Reference
Digestibility, proximate and energy composition	Nigeria	1	(Abeke et al. 2012)
Fatty acid and sugars	United States of America	17	(Bhardwaj et al., 2019)
Water, ash, lipid, protein, and amylose contents	Indonesia	12	(Purwanti et al. 2019)
Proteins and essential fatty acids	Bangladesh	1	(Hossain et al. 2016)
Proximate composition, seed protein fractions, vitamins, amino acid profile, mineral profiles, antinutritional factors and fatty acid profiles	Bangladesh	2	(Kalpanadevi et al. 2013)
Dry matter, protein, fat and ash, phytates, tannins and trypsin inhibition	Kenya	3	(Kilonzi et al. 2017)
Sensory characteristics and volatile compounds	Kenya	24	(Kimani et al. 2019)
Nutritional and antioxidant properties	India	21	(Rai et al. 2014)
Chemical, physicochemical and starch components	South Africa	1	(Naiker et al. 2020)
Phytochemical constituents, proximate composition, anti-nutritional factors and mineral composition	Nigeria	1	(Sulaiman et al. 2018)
Nutritive and anti-nutrient contents	South Africa	1	(Washaya et al. 2018)

Biochemical characterization

Description of the biochemical factors present in lablab species is fundamental. However, limited biochemical characterization has been done (Table 4). Estimation of biochemical components is essential to establish a breeding strategy for the compounds desired by the end-user. Lablab is associated with anti-nutritional factors that hinder its consumption. Characterization guides towards breeding of varieties with consumer-preferred components that will allow their adoption, consumption and utilization. There is a need to characterize biochemical compounds present in lablab to document existing variation among different germplasms.

Molecular characterization of lablab

Molecular characterization provides comprehensive information on genetic information of agricultural traits as well as diversity within and between accessions that is fundamental for marker-assisted and genomic breeding programs. The discovery of molecular markers paved the way for the description of species at the DNA level. Considerable number of molecular markers have been applied to determine the genetic diversity, relationships and describe population structure in lablab as shown in Table 5. Most of the studies reveal a narrow genetic variation among studied genotypes. For an effective and efficient breeding system, a wide genetic variation of genotypes is preferred to allow the development of new varieties.

In addition to the above-mentioned DNA markers, genomic and Next Generation Sequencing (Rapholo et al. 2020) approaches have proved pivotal in hastening variety development, release and crop improvement of lablab. Lablab is among the 101 crops selected for the high throughput-sequencing program under the African Orphan Crops Consortium (AOCC) for crop improvement (Hendre et al. 2019). The whole-genome characterization allows Single Nucleotide Polymorphism (SNPs) studies essential for crop genomics and identifying the trait of interest in the genome. This is vital for crop improvement, variety development and breeding for biotic and abiotic stresses.

Core collection of lablab

Core collection refers to a limited set of accessions selected to represent the maximum genetic diversity within a given set of germplasm pools with a minimum level of redundancy (Brown 1989b; van Hintum et al. 2000). It is recommended not to exceed 10% of the initial collection as well as being not more than 2000 entries (Brown 1989a, 1989b). Core collection plays an important role in varietal development. Effective and efficient plant breeding requires the use of a representative sample that possesses the desired traits. Breeding of crops for biotic and abiotic stresses is a critical venture, especially with the twin challenges of an ever-spiraling population and the impacts of climate change. Phenotyping for important traits in a whole collection of germplasms is an expensive and labor-intensive venture. To minimize this cost, core collection evaluation allows for the description of desired agronomic alleles in germplasms and also the study of existing genetic variation (Rivera et al. 2018).

Limited information on core collection in lablab has been documented. Pengelly et al. (2001) studied agro-morphological attributes of (122) Australia and (127) Ethiopian dolichos lablab accessions and grouped them into two: subsp. *purpureus* and subsp. *uncinatus* with the most significant variation occurring in the Ethiopian accessions. This study contributes to the assumption of Eastern Africa being the center of origin of lablab. Similarly, a core collection of 64 representative accessions was developed based on 21 qualitative and 20 quantitative traits from 644 accessions in India. During the study, a comparison of standard stratified clustering and the Heuristic approach was performed to determine the efficiency of developing a representative sample and reported the Heuristic approach to be more appropriate (Vaijayanthi et al. 2015).

The above-highlighted core collections of lablab are currently being researched and documented in regards to its crop improvement. Despite the existence of large germplasm collections, there is a lack of developed core collections in Africa. There is a need to research existing lablab accessions in Africa and to document the core collections which can serve as the foundation for lablab breeding, crop improvement, production and consumption.

Table 5 A summary of the results of the studies genetic diversity of lablab, molecular markers used, country of the study, genetic material used, key findings and references

Molecular marker	Genetic material	Country	Key findings	References
AFLP	50 accessions	Kenya	Narrow genetic base and extensive germplasm exchange of lablab amongst farmers	(Esther et al. 2012)
AFLP	103 accessions (Wild and cultivated)	Australia	Domestication pathway and distribution of lablab from Africa to Asia	(Maass et al. 2005)
AFLP	40 accessions	India	High genetic diversity of the lablab accessions	(Patil et al. 2009b)
AFLP	33 accessions	Germany	Lablab accessions from East Africa showed distinct agro-morphological characters	(Tolera et al. 2008)
AFLP	78 accessions	India	Narrow genetic diversity of Indian accessions as compared to African accessions	(Venkatesha et al. 2007)
DArT	65 accessions	Uganda	Narrow genetic diversity of Uganda, CIAT and ILRI accessions	(Sserumaga et al. 2021)
EST-SSR	19 accessions	China	SSR as a vital molecular tool for breeding of lablab	(Huang et al. 2021)
EST-SSR	2 accessions	China	Application of SSR in genetic diversity studies	(Yao et al. 2012)
EST-SSR	459 accessions	China	Narrow genetic diversity of Chinese lablab accessions	(Zhang et al. 2013)
ISSR	6 genotypes	Sudan	ISSR allows discrimination of lablab genotypes	(Abdallah et al. 2015)
RAPD	15 genotypes	India	Wide genetic variation among studied genotypes	(Gnanesh et al. 2005)
RAPD	11 accessions	Bangladesh	RAPD clearly distinguishes genetic diversity	(Sanaullah et al. 2012)
RAPD	10 accessions	India	RAPD can differentiate closely related species	(Singh Kudesia et al. 2019)
RAPD, ISSR and SSR	20 accessions	India	SSR most preferred for genetic diversity	(Dholakia et al. 2019)
RAPD, ISSR and SSR	39 accessions	India	Close relatedness among Indian genotypes	(Saravanan et al. 2013)
RFLP, RAPDs	119 F2 individuals	Australia	Linkage map construction	(Konduri et al. 2000)
SSR	299 accessions	Thailand	Low genetic diversity of Thailand lablab accessions	(Amkul et al. 2021)
SSR	96 accessions	Kenya	Narrow genetic diversity of Kenyan lablab accessions	(Kamotho et al. 2016)
SSR	16 accessions	India	Genetic diversity exists in the tested genotypes	(Keerthi et al. 2018)
SSR	143 accessions	India	Evaluation of cross-species SSR markers for genetic diversity of lablab	(Rai et al. 2016)
SSR	91 accessions	United Kingdom	Lablab originated from East Africa	(Robotham et al. 2017)
SSR	13 genotypes	Kenya	Narrow variability among the genotypes evaluated	(Shivachi et al. 2012)
SSR	2 genotypes	India	SSR markers can efficiently show polymorphism within lablab species	(Shivakumar et al. 2015)
SSR	48 accessions	India	Narrow genetic diversity of the studied populations	(Wang et al. 2007)

Bruchid studies in lablab

Bruchids (*Callosobruchus spp*) belong to the order Coleoptera, family Bruchidae and genus *Callosobruchus* and consist of over 1300 species with 20 of them reported to adversely affect legume crops in the developing countries (Credland 1994). The main species that attack legumes during storage include *C. chinensis* Fabricius, *C. maculatus* Fabricius, *C. theobromae*, *C. analis* Linnaeus, *C. phaseolin*, *Acanthoscelides obtectus* and *Zabrotes subfasciatus* (Credland 1994). The bruchids feed on leguminous crops in and off the field and are the most destructive pests in storage (Southgate 1979). The dried leguminous seeds contain carbohydrates, proteins, and lipids easily consumed by bruchids. The adult lays eggs on the pod or seed surface, which hatch into larvae and burrow through the pods into the seed, feeding on the nutrient-rich cotyledon. The larvae grow utilizing the food substances and also damage the embryo in the seed and the adult bruchids emerge out by creating holes on the seed surface (Atanda et al. 2012; Tripathy 2016). Therefore, the physical and physiological seed quality is affected (Chipungahelo et al. 2007; Ebinu et al. 2016; Lawrence et al. 2017), through primary infestation and secondary infestation by contamination with their excreta and mold growth (War et al. 2017) and thus decreases the market value (Mishili et al. 2011).

Similar to other legumes, Lablab is also attacked by bruchids. A study of *C. maculatus* on 22 lablab accessions reported four accessions (12,022, 12,028, 12,003 and 12,167) with a low number of adults emerging and prolonged development period which is associated with relative resistance (Legume Society 2016). In an experiment involving 16 lablab genotypes, GI 187 had the lowest egg number, lowest damaged seeds, least adult emergence, prolonged growth period and the lowest growth index, an indication of the presence of resistance to *C. theobromae* (Naveena et al. 2011). Additionally, only 3 genotypes (GL 63, GL 77 and GL 233) in a seed lot of 28 genotypes showed reduced attack by *C. theobromae* exhibited by the low number of eggs, lowest adult emergence, least damaged seeds and lowest seed infestation which is correlated with resistance. Screening of 133 germplasm accessions against *C. chinensis* revealed 11 genotypes (GL 1, GL24, GL 61, GL 69, GL 82, GL 89, GL 121, GL 135, GL 196, GL412 and

GL 413) with < 10% damage which points to the presence of resistance of the genotype (Jagadeesh et al. 2008). It is clear from the preceding studies that lablab bruchid resistance studies have been limited to screening and identification of resistant varieties only. Screening allows the identification of resistant genotypes to be used in developing varieties. There is a knowledge gap on the host plant resistance mechanism and inheritance of genetic resistance. Further studies are paramount to provide information for breeding programs.

Bruchid management

Bruchid control methods include chemicals, cultural, botanical and biocontrol. Chemical use includes pirimiphos methyl (Odeyemi et al. 2006), organophosphate (Sharma et al. 2016; Subekti et al. 2019) carbamates (Ebadollahi et al. 2012) and Organochlorines (Bogamuwa et al. 2002). Chemical control has been associated with environmental pollution and food safety concerns (Tripathy 2016), increasing the cost of production and hence minimizing the profitability of the farmers (Srinivasan 2014) and developing resistance by the pest. Cultural control methods such as appropriate time of planting and harvesting, harvesting frequency, weeding of the bruchid host plant in the field, crop hygiene (Kesho 2019; Van Huis 1991) and application of ash, sand, kaolin and clay on the seed surface (Alice et al. 2013; Srinivasan 2014) have contributed towards managing bruchids. However, cultural methods require prolonged planning procedures coupled with large quantities of the above substances to be applied to the seed.

Application of pesticidal plant products such as leaves of *Tephrosia vogelii* Hook (Fabaceae), *Alstonia boonei* De Wild (Apocynaceae), Pawpaw (*Asimina triloba* (L.) Dunal) and *Hyptis suaveolens* (L.) Poit (Lamiaceae), (Ehimemen and Salisu 2020), *Tithonia diversifolia* (Hemsl.) A. Gray extracts, *Jatropha curcas* L. seed, *Cyperus rotundus* L. (Kolawole et al. 2014) Anona (*Annona muricata* Vell.) seed powder and citrus (*Citrus reticulata* Blanco) peels (Ibrahim et al. 2018) have been reported to control bruchids in cowpea. Leaf extracts of fresh leaves of *Tithonia diversifolia* (Hemsl.) A. Gray, *Tephrosia vogelii* Hook, *Lantana camara* L. and *Vernonia amygdalina* Delile in common bean and peas (Mkindi 2016) have proved effective in controlling bruchids.

Vegetable oils such as olive (*Olea europaea* L.) and mustard (*Brassica* spp. and *Sinapsis* spp.) are all alternative botanicals that have been studied on legumes and showed a positive result in controlling bruchid infestation (Srinivasan 2014). Botanicals degrade easily, are slow in action, does not affect non-target organisms and interfere with seed germination (Yusuf et al. 2011). Biological control strategies include entomopathogenic fungi *Metarhizium anisopliae* (Metchnikoff) Sorokin and *Beauveria bassiana* (Bals.-Criv.) Vuill. (Iqbal et al. 2018; Ozdemir et al. 2020). Parasitoids such as *Anisopteromalus* (Hance 2007), *Prostephanus truncates* Horn (Helbig 1998) *Dinarmus basalis* Rondani (Boateng et al. 2008) revealed efficient bruchid management. Some of these biocontrol organisms become an environmental hazard due to their persistence and some develop to be invasive to the environment, posing a threat to the natural inhabitants of the ecosystem.

Limited information on the control methods of bruchids in lablab exists. Application of vegetable oil, powdered detergent, bamboo charcoal, bleach solution, galangal powder and carbaryl in controlling bruchid pest in lablab showed positive results by limiting pest population (Lawrence et al. 2017). However, the application of these treatments reduced seed vigor and germination rate with the oil application killing the seeds (Lawrence et al. 2017). Studies on the application of oil and seed kernel extract of neem ascertain its efficiency in controlling bruchids in lablab (Naveena et al. 2010) but determining the correct concentration and proportions to be applied for control as well as the safety limits of its use. The gap existing in control methods of lablab illustrates the necessity to understand the mechanism of resistance and the gene action which is integral in breeding resistant varieties.

Host plant resistance to bruchids

Host plant resistance describes the interaction of the pests and the host plant and is usually cumulative and constant. The development of resistant varieties is simple, cost-effective, environmentally friendly and can be applied concurrently with other strategies such as chemical and bio-control. Varietal resistance to pest attack is the most appropriate method since it is efficient, affects target organisms only, sustainable

and reduces the cost of production. Studies on host plant resistance to bruchids have been undertaken in soybean (Msiska 2019), common bean (Maro 2017; Tigist et al. 2018), cowpea (Weldekidan 2019), mung bean (L.) R. Wilczek (Somta et al. 2006) and pigeon pea (*Cajanus cajan* L.) Millsp.) (Mishra et al. 2019). Host plant resistance is categorized into antixenosis (physical/morphological) and antibiosis (biochemical).

Antixenosis

Antixenosis describes a physical or morphological resistance mechanism possessed by plant/seed to prevent insect colonization that relies on plants for food substances, shelter and oviposition sites. Antixenosis resistance mainly occurs at the initial phase where insects damage the susceptible seed as compared to the resistant seed material thus the number of insects will vary. Morphological characters of seed (surface/texture, color, size, shape, hardness), pod (shape and texture) (Divya et al. 2013; Saruchi et al. 2014; Somta et al. 2007) act as a direct defense strategy against pests growth and development. Oviposition density directly correlates to the population establishment of the pest in the host species.

Seed surfaces significantly influence seed protection. The majority of *Callosobruchus* species oviposit their eggs on the seed/pod surface, where they hatch into young larvae that penetrate the pod wall into the seed. A hard pod, capsule, or seed and seed coat prevent the newly hatched larva from penetrating the seed (Mei et al. 2009). Small pods or seeds, do not support larva growth to full size due to little food reserves (Somta et al. 2007). Concerning color, black seeds are less preferred by female bruchids for egg oviposition (Somta et al. 2007). Similarly, large and dull seeds are preferred to small and shiny seeds in mung beans during oviposition (Tripathy 2016). Soft and thin seed coated varieties were preferred by *C. maculatus* in cowpea as compared to hard seeded counterparts (Tripathy 2016).

In lablab, studies revealed that female bruchids preferred to oviposit on the surface of bright colored and smooth-surfaced seeds (Prasad et al. 2013b). Similar results of influence on seed parameters like shape, color, thickness and diameter correlate with oviposition by *C. theobromae* (Naveena et al. 2012; Pawara et al. 2019). Reduced oviposition through

antixenosis is directly related to low fecundity rate (Kar et al. 2016) and migration of the larva (Seram et al. 2016) or increased juvenile mortality rate of the pest. Morphological characteristics such as seed color, size, texture, hardness and shape could be an indication of the presence of bruchid resistance in lablab but cannot be the only mechanism of resistance.

Testing for antixenosis resistance involves both choice and no-choice situations and is quantified based on oviposition, growth, survival (Stout 2014) and the number of insects infesting the test cultivars (Kogan et al. 1978). Analysis of the antixenosis mechanism describes the behavior of the pest on the seed lot with varying genetic resistance (Kenehi et al. 2011). The scanty information on the morphological basis of resistance in lablab pinpoints the need to do further research and evaluation to obtain the characters associated with resistance.

Antibiosis

Antibiosis refers to the mechanism where plant biochemical compounds/secondary metabolites and anti-nutritional factors hinder insect infestation by influencing its biological activity and establishment (Mishra et al. 2019; Smith 2005). Studies report that plants exude secondary metabolites as a defensive mechanism against insect pests attack (War et al. 2012). Secondary metabolites refer to compounds obtained by biosynthesis of primary compounds such as sugars, lipids, amino acids and simple organic acids (Kenehi et al. 2011). They are synthesized into secondary metabolites such as lignins, tannins, phytates, alkaloids, quinines, phenolic acids, saponins and flavonoids found in plant structures such as seed coat and integuments and secrete antinutritional factors such as arcelins, trypsin inhibitors, enzyme inhibitors, lectins, vicilin, cyanogenic glycosides, phytic acid and phaseolin which acts as repellents and feeding inhibitors (Panda et al. 1995). This mechanism leads to reduced larval growth, increased larval mortality, and decreased pupal weights, prolonged larval and pupal development periods, low pupation, low fecundity rates and decreased egg viability (Sharma et al. 2017; War et al. 2013).

Antibiosis mechanisms are evaluated using no-choice tests in which pests or insects are enclosed with the plant or plant materials with restricted movement. The main aspects under study involve the collection of

data on the number of dead insects, level of damage to the seed, insect biology, development, fecundity, and survival (Mendesil 2014). Several chemical components within the seed develop synergistic or additive effects on the insects' pests, such as bruchids. The biochemical factors in lablab involve studies on trypsin inhibitors, arcelin, α -amylase inhibitors, tannins, peroxidase and vicilin.

Trypsin inhibitors aid in predicting resistance/vulnerability to bruchid attack in leguminous crops. Low trypsin inhibitors in a variety of Indian pea or grass pea (*Lathyrus sativus* L.) exhibited reduced bruchid resistance. There is thus a correlation between trypsin inhibitor amounts and *C. maculatus* attack (Southgate 1979). In Lablab, the correlation is inverse where genotypes with increased chymotrypsin inhibitors and trypsin levels revealed resistance to *C. maculatus* with the brown seeds showing high levels as compared to black seeds (Ignacimuthu et al. 2000). Trypsin inhibitors bind proteolytic enzymes providing a natural defense mechanism against bruchid attack.

Peroxidase (POD) and polyphenol oxidase (PPO) enzymes play a significant role in plant resistance to insect pest attack (He et al. 2011). These enzymes generate reactive oxygen species that transfer defense-related signals, initiating the hypersensitive reaction and strengthening the cell walls by enhancing lignin formation and cross-linking, thus protecting against attack (De Jager et al. 1996). Evaluation of 12 rice bean genotypes exhibited variation in response to peroxidase activity, suggesting resistance of rice beans against bruchid attack (Pavithravani et al. 2013). Peroxidase catalyzes the oxidation of toxic metabolic compounds which cannot be consumed by the insect pest. In this regard, the pest will not attack the genotype.

In lablab, genotypes with resistance to *C. theobromae* had high peroxidase activity as compared to the susceptible ones (Babu et al. 2011). High peroxidase activity is associated with increased tolerance/resistance of a crop to bruchid attack. Three varieties, GL 187, GL 63, GL 127 and GL 195 revealed high peroxidase and were classified as resistant varieties whereas GL 36, GL 46, GL 102, HA4, HA3 were susceptible due to low levels. Quantification of peroxidase activity in lablab could thus be used as one of the methods of identifying resistant varieties for pre-breeding programs.

Enzyme inhibitors such as α -amylase inhibitors are found in abundance in seeds and other plant parts of most legumes and are reported to interfere with the metabolism of carbohydrates and protein by inactivating the digestive enzymes present in the bruchid gut cells, impairing the digestion and absorption of food substances. Studies reveal the presence of α -amylase inhibitors in lablab seed extracts (Janarthanan et al. 1999). Characterization and purification of the α -amylase inhibitor from a brown-seeded undomesticated variety of lablab expressed a great amount of resistance to the *C. maculatus* attack while still in the field and during storage (Janarthanan et al. 1999). Evaluation of germplasm resources with potentially high levels of α -amylase inhibitor is paramount to breed resistant varieties.

Arcelin is the main seed protein found in indigenous accessions of legumes and exhibits elevated levels of resistance to *Callosobruchus* spp. (Osborni et al. 1988). Arcelin interferes with the digestion of food by the pest, leading to the death of larvae as a result of starvation. In addition, insects feeding on legumes with high arcelin compounds had lower weight as compared to those from arcelin free, indicating the reduced consumption of beans with arcelin (Duarte et al. 2018). Purified seed extracts of lablab proteins contain different forms of arcelins and related plant defensive proteins (Janarthanan et al. 2008). Several propositions have been given on the insecticidal activity of arcelin-1, with others arguing that the chemical disrupts the epithelial cells in the gut. Others hypothesize the toxicity caused by arcelin results from the interaction of the protein with specific glycosylation present in the gut of the bruchid or by secretion of poorly digestible protein that is harmful to the insect (Janarthanan et al. 2008). Knowledge of this antimetabolic effect is important in developing resistant crops.

Tannins refer to polyphenolics with heavy molecular weights ranging from 500 to 4000 Da and their hydroxyl groups denature proteins, thus precipitating from the solution. They are usually contained between the aleurone layer and outer integument of the seed tissues (Lattanzio et al. 2005). Tannins reduce attacks due to their bitter taste affecting palatability and intake by the insects. It inactivates the enzymes along with the digestive tract and forms complexes with their proteins, hence affecting the consumption. Correlation of tannin levels and *C. maculatus* resistance on *Vigna*

species (Marconi et al. 1997) and against *C. chinensis* in soybean (Msiska et al. 2019) has been studied. Bruchid-resistant varieties exhibited high tannin levels with low adult bruchid emergence, prolonged development period, least seed weight loss, and delay in growth index (Msiska et al. 2019). However, contrasting results in cowpea genotypes were reported where the resistant genotypes expressed low concentrations of free and condensed tannins while the susceptible ones had the highest levels (Weldekidan 2019). These conflicting results could be species-specific as well as the variability in the genotype production environment and thus there is a need to determine each species individually. Lablab contains a wide range of tannins as their chemical constituent (Harsur et al. 2011). There is a need to investigate the potential effect with bruchid resistance. Limited information exists in regards to tannins present in lablab on control of bruchids.

Vicilins or storage globulins refer to specific-chain proteins lacking disulfide bonds that form trimers of subunits with differing molecular masses ranging from (45–53 kD). They usually contain a vast number of genes with the sequences of vicilin subunits from the leguminous family exhibiting a increased degree of sequence similarity pointing to the same evolutionary path (Sales et al. 2000). The bruchid-resistant genotypes possess vicilin that binds to the chitin matrix along the gut membranes of *C. maculatus* (Sales et al. 2000) and resists proteolysis. Lablab seeds have been studied to contain high levels of vicilin compounds associated with the transfer of insect resistance to the species (Ignacimuthu et al. 2000). Brown seeded varieties possess higher vicilin levels and were categorized as resistant as compared to the dark seeds which had low vicilin levels (Ignacimuthu et al. 2000; Lim 2012; Tripathy 2016). This suggests that increased vicilin in lablab confers bruchid resistance and that more research on a broader range of genetic resources is needed.

Despite the increased emphasis on lablab research, few efforts have been made to study bruchid resistance, particularly in East Africa (Legume Society 2016), where it is thought to be the starting point of domestication forming. Knowledge regarding the presence of resistant genotypes will be pivotal for breeding programs. Determination of sources of bruchid resistance in lablab should incorporate approaches, which provide knowledge in regards to

physical, morphological, and biochemical compounds responsible for resistance.

Lablab gene action and bruchid resistance

Studies on the genetics of bruchid resistance and its inheritance are paramount in developing a breeding. Developing resistant lines is regarded as the most appropriate and effective way of controlling bruchids in major crops. Identification of bruchid resistance through screening of gene pools both from local as well as exotic/foreign has been considered to build the base for breeding programs (Tripathy 2016). According to research, the inheritance patterns of resistance are complex because the seed components originated from different sources and hence possess different ploidy levels. The seed coat is obtained from maternal tissues and is diploid while embryo and endosperm tissues are triploid (Tripathy 2016). Information on the existing resistance of lablab to bruchid attack provides a ground for undertaking the breeding towards this trait.

Development of resistant crop varieties relies on the presence of potential genes and their inheritance (Rubiales et al. 2015). Bruchid resistance can be monogenic (single major gene) polygenic (several minor genes) (Togola et al. 2017). Polygenes control several pests and pyramiding them into new varieties is complex. The genetic basis of leguminous crop resistance to storage insects varies from monogenic to oligogenic for pests like *C. maculatus* and *C. chinensis* in mungbean (Redden et al. 1983). Normally, additive and dominant genes are responsible for bruchid resistance during the storage of most leguminous species (Somta et al. 2008). Recent studies on major leguminous crops have reported the mechanisms of gene actions on the inheritance of resistance. Msiska et al. (2018) observed the existence of additive and non-additive gene factors that influence soybean resistance to *C. chinensis*. The research also described the maternal effects of the parental genotypes that are core during hybridization. Furthermore, elite progenies from crosses with negative General Combining Abilities (GCA) require further screening and advancing for the release of resistant varieties.

Weldekidan (2019) using a diallel mating scheme revealed the presence of genetic variation of tested cowpea cultivars in relation to their resistance to *C. chinensis*. GCA and Specific Combining Abilities

(Msiska) analysis showed significance among studied cultivars for number of eggs oviposited, level of insect emergence and the median development period implying that additive and non-additive gene influence the transfer of resistance to cowpea bruchids (Weldekidan 2019). Similar results in other legumes common bean genetic inheritance to *Acanthoscelides obtectus* Say (Kananji 2007), common bean genotypes for genetic inheritance to *C. maculatus* (Mwila 2014) have been reported.

Farmers reported the development and release of bruchid-resistant varieties as the most preferred trait concerning lablab production (Chawe et al. 2019). There is still a lack of research on the mechanism of lablab resistance to bruchid attack, and more research is required. In Tanzania, it is necessary to identify the bruchid-resistant sources in germplasm, the biochemical compounds associated with resistance and conduct genetic resistance studies on lablab germplasm.

Conclusion

Lablab is an agro-morphological diverse crop with multiple uses and adaptability to different agro-climatic conditions. Despite the manifold uses, the research, production, consumption and funding opportunities remain low. Assessment and exploration of genetic diversity present in a given germplasm collection are fundamental for any breeding program. The use of molecular markers and high throughput sequencing techniques have enhanced crop improvements and breeding programs. Increased crop improvement efforts in Africa to develop farmer-preferred cultivars that are high-yielding, early maturing, nutritious for food and feed, drought-tolerant, and bruchid tolerant/pest tolerant are required for successful adoption of lablab by farmers. Research towards focussing on prioritized traits such as yield, maturity; field pest (aphids and pod borers) and storage pest (bruchids) needs to be initiated. Defensive mechanisms possessed by lablab and the mode of inheritance need to be identified to enable the development of bruchid-resistant lines.

Author contributions statement FKL conceptualized the idea of this review and drafted. PBV reviewed and revised the manuscript critically. PAN read, edited and approved the

manuscript. The manuscript was read and refined by all authors and finalized by FKL.

Data availability statement Not applicable.

Declarations

Conflict of interest The authors declare no conflicts of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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