

DOLICHOS BEAN (*Lablab purpureus* L. SWEET, VAR. LIGNOSUS) GENETICS AND BREEDING - PRESENT STATUS AND FUTURE PROSPECTS

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ABSTRACT

Dolichos bean is a multi-purpose cool-season legume crop. It is presently grown throughout the tropical regions in Asia, Africa and Australia. It is regarded as 'underutilized' crop as evidenced by limited area planted to the crop and efforts for genetic improvement. Nevertheless, it can contribute to food security, ecosystem stability and cultural diversity associated with local food habits. Enhancement of its economic value through development of stable and widely adapted high yielding varieties is expected offer competitive edge to dolichos bean to enable its popularity and wider cultivation. Production of dolichos bean is challenged by several factors which include fewer improved varieties and biotic stresses. The objective of this review is to discuss the status of germplasm and its characterization and evaluation, genetics of qualitative and quantitative traits, sources of, and breeding for resistance to insect pests, especially pod borers and diseases, particularly dolichos yellow mosaic virus and anthracnose and the use of DNA markers for detection of genetic variability and linkage map construction for identifying genomic regions controlling economically important traits and challenges ahead for enhancing the pace and efficiency of breeding dolichos bean for higher productivity.

Dolichos bean (*Lablab purpureus* L.) is a bushy semi-erect herb and belongs to family Fabaceae with $2n=22$ chromosomes (Goldblatt, 1981; She and Jiang, 2015). It is predominantly a self pollinated crop (Harland, 1920; Ayyangar and Nambiar 1935; Choudhury *et al.*, 1989; Shivashankar and Kulkarni, 1989; Kukade and Tidke, 2014). However, insect-mediated cross pollination up to 6-10 per cent is reported (Veeraswamy *et al.*, 1973). In India, it is commonly known as Field bean, Hyacinth bean, Country bean, Indian bean, Egyptian bean, Sem, Wal, Avare, Avarai, etc., (Ayyangar and Nambiar, 1935; Shivashankar and Kulkarni, 1989). In western countries, it is known as Bonavist bean, possibly due to its ornamental effect in full bloom (Ayyangar and Nambiar, 1935). It is one of the most ancient among the cultivated legume species-possibly more than 3000 years old (Ayyangar and Nambiar, 1935). It is presently grown throughout the tropical regions in Asia, Africa and America (Fuller, 2003). It is believed that dolichos bean has originated in India (Ayyangar and Nambiar, 1935; Nene, 2006), as it is documented by archaeobotanical finds in India from 2000 to 1700 BC at Hallur, the earliest Iron-Age site in Karnataka to 1200 to 300 BC at Veerapuram excavation site in Andhra Pradesh (Fuller, 2003). It is likely that dolichos bean was introduced into China, Western Asia and Egypt from India (Ayyangar and Nambiar, 1935).

Based on the shape and texture of the pods, and the angle of attachment of seeds to the suture of the

pods, two botanical types of dolichos bean are recognized (Ayyangar and Nambiar, 1935; Magoon *et al.*, 1974). These are (1) *Lablab purpureus* var. *typicus* and (2) *Lablab purpureus* var. *lignosus*. *Lablab purpureus* var. *typicus* produces pods that are flat, longer and more tapering with long axis of seeds parallel to the suture of the pod. It is predominantly grown for soft and fleshy whole pods for use as a vegetable. Due to its twinning habit it is trained on a pendal. *Lablab purpureus* var. *lignosus* is bushy type annual. It bears tough firm-walled parchmented pods which are relatively shorter and more abruptly truncated and long axis of the seeds is perpendicular to the suture of the pod. The pods of *Lablab purpureus* var. *lignosus* exude oily substances that emit characteristic fragrance, a highly preferred trait by farmers and consumers (Ayyangar and Nambiar, 1935; Shivashankar and Kulkarni, 1989). The pod fragrance is largely attributed to occurrence of two dominant fatty acids such as trans-2-dodecenoic and trans-2-tetradecenoic acids (Fernandes and Nagendrappa, 1979; Uday Kumar *et al.*, 2016). It is grown predominantly for fresh beans for use as a vegetable and to a limited extent for split dhal for use in various food preparations (Shivashankar and Kulkarni, 1989). Fresh pods with immature beans are the harvestable economic products in dolichos bean. Owing to its ability to form a thick vegetative cover on the ground, it is often called as 'carpet legume' (Magoon *et al.*, 1974).

Dolichos bean is highly popular in south Asia, where it is grown in rainfed ecosystems (Rahman *et al.*, 2002; Haque *et al.*, 2003). It is the third most important vegetable in central and south-western parts of Bangladesh with a total production area of 48,000 ha (Rashid *et al.*, 2007). It is grown commercially in Comilla, Naokhali, Shylhet, Dhaka, Kishoreganj, Tangail, Jassor and Dinajpur districts of Bangladesh (Jahan *et al.*, 2013). In India, dolichos bean var. Lignosus is primarily grown as a rainfed crop in Karnataka and adjoining districts of Tamil Nadu, Andhra Pradesh and Maharashtra both as an inter-crop and pure crop (Shivashankar and Kulkarni, 1989; Mahadevu and Byregowda, 2005). In pure crop stands, the productivity of dry seed yield is 1.2 t ha⁻¹ (raithamitra.co.in), while, it is 0.4 to 0.5 t ha⁻¹ in inter-cropping system (Shivashankar and Kulkarni, 1989). When it is grown for forage, it produces green fodder of 2.20 to 2.75 t ha⁻¹ under rainfed conditions (Magoon *et al.*, 1974). In Karnataka, dolichos bean is grown in an area of 0.65 lakh hectares with a production of 0.73 lakh t and contributes nearly 90 per cent of both area and production in India (raithamitra.co.in).

Despite its importance as a multi-purpose crop and ability to withstand drought better than cowpea (Nworgu and Ajayi, 2005; Ewansiha and Singh, 2006; Maass *et al.*, 2010), and adapt to acidic (Mugwira and Haque, 1993) and saline soils (Murphy and Colucci, 1999), dolichos bean truly qualifies as 'underutilized' crop as evidenced by limited area under the crop and efforts for genetic improvement. Nevertheless, it can contribute to food security and better nutrition, increased income to rural poor, ecosystem stability and cultural diversity associated with local food habits. Enhancement of its economic value through development of widely adapted high yielding cultivars is expected offer competitive edge to dolichos bean to enable its popularity and wider cultivation. This requires the availability of diverse genetic resources, their systematic evaluation, identification of useful sources of desired traits, unraveling the inheritance of economic product productivity *per se* traits and the traits that stabilize the economic product yield and the use of both conventional and genomic tools to combine desired traits.

In this article, an effort has been made to discuss the status of research on genetic resources-their collection, conservation, maintenance, characterization and evaluation, genetics of qualitative and quantitative

traits, breeding for productivity *per se* traits and plant defense traits and the use of genomic tools to complement conventional phenotype-based dolichos bean breeding.

1. Genetic resources

Genetic resources are the wealth / treasure of any country for continuous genetic improvement of economically important crops to cater the needs of present and future generations. The efforts to collect, conserve, characterize, evaluate and catalogue dolichos bean genetic resources are far from satisfactory given its multiple economic uses and ability to resist biotic and abiotic stresses. Shivashankar *et al.* (1971, 1977); Viswanath and Manjunath (1971); Viswanath *et al.*, (1972); Chikkadevaiah *et al.* (1981) at the University of Agricultural Sciences (UAS), Bengaluru, India have collected, evaluated and catalogued dolichos bean germplasm on a limited scale. Wang *et al.* (1991) collected 385 selections belonging to 14 legume species including *Lablab purpureus* in Hainan Island of China during 1987-89 and evaluated them for agronomic characters. Xu-Xiang-shang *et al.* (1996) collected 32 dolichos bean accessions from Qinling-Bashan mountain region, Sichuan of China. They investigated their area of distribution, cultivation, morphological characteristics and recommended four elite cultivars for commercial production. Pujari (2000) and Shanmugam (2000) have established dolichos bean germplasm consisting of 60 accessions, which included 22 improved varieties and 38 local landraces collected from different districts of Orissa, West Bengal and Andhra Pradesh states of India. While these are sporadic and limited attempts, systematic and relatively a more comprehensive efforts to collect, evaluate, catalogue, document and conserve dolichos bean genetic resources in several countries / regions / institutes are summarized in Table I.

Thus, largest collection of dolichos bean genetic resources (650 accessions) is held at the University of Agricultural Sciences (UAS), Bengaluru, India. These accessions were characterized and evaluated for vegetative, inflorescence, pod and seed traits. A set of 70 descriptors based on 16 vegetative, 14 inflorescence, 20 pod and 20 seed traits were developed considering the spectrum of variability for these traits following the guidelines of Bioversity International (Byregowda *et al.*, 2015). A few of these are based on easily field assayable and simply inherited (single / oligogenic) descriptors such as growth habit,

TABLE I
Summary of dolichos bean germplasm maintained in different countries / regions / institutes of the World

Countries / regions / Institute	Number of Accessions	Source
South America	134	BI (2008)
North America at United States Department of Agriculture (USDA)	52	GRIN (2009)
Europe	82	BI (2008); IPK (2009); VIR (2009)
Oceania including Australia at Commonwealth Scientific and Industrial Research Organization (CSIRO)	104	BI (2008)
China	410	BI (2008)
Philippines	209	Engle and Altoveros (2000)
Taiwan at Asian Vegetable Research and Development Center (AVRDC)	423	AVRDC (2009)
South-east Asia (countries other than Bangladesh and India)	82	BI (2008); NIAS (2009)
Bangladesh	551	Islam (2008)
India at National Bureau of Plant Genetic Resources (NBPGR), New Delhi	221	BI (2008)
South Asia	93	BI (2008)
Ethiopia including International Livestock Research Institute (ILRI)	223	BI (2008)
Kenya	403	BI (2008)
Sub-Saharan Africa including International Institute of Tropical Agriculture (IITA), Nigeria	67	BI (2008)
University of Agricultural Sciences (UAS), Bengaluru, India	650	Byregowda <i>et al.</i> (2015); Vaijyanthi <i>et al.</i> (2015a)

pod curvature, flower colour (Raut and Patil, 1985; Rao, 1987; Girish and Byregowda, 2009; Keerthi *et al.*, 2014a; Keerthi *et al.*, 2016) and seed traits (Ayyangar and Nambiar, 1936 a & b; Ayyangar and Nambiar, 1941; Patil and Chavan, 1961; D' cruz and Ponnaiya, 1968). These descriptors could be used as diagnostic markers of germplasm accessions for maintaining their identity and purity. They help minimize duplication and avoid mistakes in labeling the germplasm accessions and thereby enable their easy retrieval from the collection. They are also useful in conducting Distinctness (D), Uniformity (U) and Stability (S) test, a mandatory requirement for protecting varieties under Protection of Plant Varieties and Farmers' Rights (PPA & FR) Act of India and such other similar acts that are vogue in other countries (Byregowda *et al.*, 2015).

Considering that the genetic resources held at UAS, Bengaluru is unwieldy for precise characterization and evaluation and possibility of occurrence of duplicates due to repeated sampling of same accession and / or assigning different names / identity to the same accession, a core set consisting of 64 accessions was developed at UAS, Bengaluru (Vaijyanthi *et al.*, 2015 b and c) using PowerCore (v. 1.0) software, a program that applies advanced M-strategy with a heuristic search (Kim *et al.*, 2007). The core set retained more than 90 per cent of quantitative traits variability and polymorphism of qualitative traits in the base collection of 644 accessions. The core set is suggested for evaluation across target production environments and years to identify widely / specifically adapted and stable accessions to foster enhanced access and use of

dolichos bean germplasm in cultivar development. In similar efforts to reduce size and possible duplicates, Bruce and Maass (2001) in Ethiopia and Islam *et al.*, (2014) in Bangladesh also developed core sets of 47 and 36 accessions from the base collections of 251 and 484 accessions, respectively. The core sets are considered as first look sources of genetic resources for use in crop improvement programs. The availability of core sets is expected to result in enhanced utilization of genetic resources in crop breeding programmes which is the key to develop cultivars with broad genetic base which contribute to sustainable production of dolichos bean.

Based on two years (2012 and 2014) of evaluation of core set, promising traits-specific accessions (Table II) and those promising for multi-traits (Table III) have been identified at UAS, Bengaluru (Vaijyanthi *et al.*, 2016a). The accessions promising for multi-traits were evaluated in multi-locations representing eastern, southern and central dry zones of Karnataka during 2015 to identify those widely / specifically adaptable to the three agro-climatic zones. The accessions such as GL 250, FPB 35 and Kadalavare were found widely adaptable to the three agro-climatic zones of Karnataka with relatively high fresh pod yield (Vaijyanthi *et al.*, 2016 b). These accessions are

suggested for preferential use in breeding dolichos bean varieties widely adaptable to the three agro-climatic zones of Karnataka.

2. Genetics

A. Qualitative traits

Several researchers have reported the number and mode of action of genes controlling easily observable / assayable stem and growth habit traits (Table IV), leaf traits (Table V) inflorescence traits (Table VI), pod traits (Table VII) and seed traits (Table VIII) in dolichos bean. These traits are controlled by one to four genes.

Linkage between the genes controlling qualitative traits: Joint segregation analysis indicated independent segregation of genes controlling direction of inter-nodal hairs, pod width, orientation of dry pods on the branches and seed colour (Patil and Chavan, 1961). On the contrary, genes controlling pod width and seed shape and those controlling orientation of dry pods and nature of pod surface are closely linked without recovery of recombinants (Patil and Chavan, 1961). Patil and Chavan (1961) attributed non-recovery of recombinants to possible pleiotropic effect of a single gene in the inheritance of pod width, seed shape,

TABLE II
Promising trait-specific accessions in a core set of dolichos bean germplasm

Traits	Selection criteria	Range	Germplasm accessions
Days to 50 per cent flowering	Earliness	40-50	HA-11-3, GL 326, HA-12-9, GL 432, GL 661
Primary branches plant ⁻¹	High	5.5-7.5	GL 621, GL 199, GL 147, GL 228, GL 110, GL 12, GL 252, GL 205, GL 606, GL 527
Racemes plant ⁻¹	High	9-15	GL 326, GL 142, GL 205, GL 447, GL 12, GL 530, GL 606, GL 199, GL 110, GL 438, GL 412
Fresh pods plant ⁻¹	High	30-50	GL 447, FPB 35, GL 576, GL 418, KA, GL 142, GL 633, GL 527, GL 250, GL 66, GL 444
Fresh pod yield plant ⁻¹ (g)	High	150-250	GL 576, FPB 35, GL 527, GL 447, GL 142, GL 441, GL 66, GL 12, GL 418, GL 579
Fresh seed yield plant ⁻¹ (g)	High	90-120	FPB 35, GL 576, GL 527, GL 142, GL 447, GL 12
100 fresh seed weight (g)	High	60-85	GL 441, GL 6, GL 12, HA-12-9, GL 579, GL 142, GL 527, GL 68, GL 658, GL 66, GL 439, FPB 35

TABLE III

Promising accessions identified for multiple traits in a core set of dolichos bean germplasm

Identity of accessions	Geographical origin	Traits
GL576	Maharashtra	Fresh pods plant ⁻¹ , fresh pod yield plant ⁻¹ , fresh seed yield plant ⁻¹
GL110	Tamil Nadu	Primary branches plant ⁻¹ , racemes plant ⁻¹
GL527	Andhra Pradesh	Primary branches plant ⁻¹ , fresh pods plant ⁻¹ , fresh pod yield plant ⁻¹ , fresh seed yield plant ⁻¹
GL447	Unknown	Racemes plant ⁻¹ , fresh pods plant ⁻¹ , fresh pod yield plant ⁻¹ , fresh seed yield plant ⁻¹
GL142	Karnataka	Racemes plant ⁻¹ , fresh pods plant ⁻¹ , fresh pod yield plant ⁻¹ , fresh seed yield plant ⁻¹ , 100 fresh seed weight
GL441	Unknown	Fresh pod yield plant ⁻¹ , 100 fresh seed weight
FPB 35	Karnataka	Fresh pods plant ⁻¹ , fresh pod yield plant ⁻¹ , fresh seed yield plant ⁻¹ , 100 fresh seed weight.
GL66	Karnataka	Fresh pods plant ⁻¹ , fresh pod yield plant ⁻¹ , 100 fresh seed weight
GL12	Karnataka	Racemes plant ⁻¹ , fresh pod yield plant ⁻¹ , fresh seed yield plant ⁻¹ , 100 fresh seed weight.

orientation of dry pods and nature of pod surface. Raut and Patil (1985) reported a close linkage between genes controlling stem colour and flower colour and that between genes controlling flower colour and leaf margin with recombination of 3.01 and 2.13 per cent, respectively. The genes controlling photoperiod sensitivity and petiole colour are linked with recombination of 33.16 per cent and those controlling petiole colour and growth habit and photoperiod sensitivity and growth habit are also linked with recombination of 32.92 and 6.14 per cent, respectively (Rao, 1987). The genes controlling growth habit and photoperiod sensitivity are linked with recombination of 7.82 per cent (Rao, 1987). On the other hand, genes controlling photoperiod sensitivity and stem colour, growth habit and stem colour segregated independently (Rao, 1987). While, the genes controlling photoperiod sensitivity and growth habit, photoperiod sensitivity and raceme emergence from the foliage and growth habit and raceme emergence from the foliage are linked in coupling phases with recombination of 29, 24 and 21 per cent, respectively, those controlling flower colour and pod curvature are un-linked (Keerthi *et al.*, 2016). The qualitative traits controlled by single / oligogenes could be used to identify true F₁s, to rule out the possibility of selfing due to occurrence of pollination

before opening of the flowers (Harland, 1920; Ayyangar and Nambiar, 1935; Kukade and Tidke, 2014).

B. Quantitative traits

Jacob (1981) reported partial dominance with duplicate type of epistasis for green pod yield plant⁻¹ and predominance of additive gene action for seed yield plant⁻¹. Rao (1981) reported importance of all the three types of gene action (additive, dominance and epistasis) in different proportions in the inheritance of pod yield plant⁻¹, pods plant⁻¹, seed yield plant⁻¹, raceme length, pods raceme⁻¹ and plant height. Muralidharan (1980) reported complementary epistasis with preponderance of dominance genetic variance (σ^2_D) in the inheritance of seed yield, while, Reddy *et al.*, (1992) documented preponderance of additive genetic variance (σ^2_A) for number of pods plant⁻¹. Khondker and Newaz (1998) reported predominant role of σ^2_A in the inheritance of days to flower, pod width, seeds pod⁻¹ and 20-pods weight. On the other hand, traits such as number of inflorescences plant⁻¹, pods inflorescence⁻¹ and pod yield plant⁻¹ were mostly governed by σ^2_D .

Sakina and Newaz (2003) in dolichos bean reported preponderance of σ^2_A in the inheritance of

TABLE IV
Summary of genetics of growth habit and stem traits in dolichos bean

Trait and its different states	Number of genes and F ₂ ratio	Mode of action	Reference
Orientation of stem inter-nodal hairs Upwards / downwards	Single 3 downward: 1 upward	Downward > upward	Ayyangar and Nambiar (1935)
Orientation of stem inter-nodal hairs Upwards/downwards	Single 3 downward: 1 upward	Downward > upward	Patil and Chavan (1961)
Stem pigmentation on nodes and internodes	Three 27 pigmented: 37 non-pigmented	Pigmented > non-pigmented complementary epistasis	Manjunath <i>et al.</i> (1973)
Growth habit Spreading / compact	Single 3 Spreading : 1 compact	Spreading > compact	Rao (1987)
Growth habit Erect / Prostrate	Three (1 basic and two complementary genes) 57 Erect: 7 Prostrate	Erect > Prostrate	Girish and Byregowda (2009)
Growth habit Determinate / indeterminate	Two / Three 9 Indeterminate: 7 determinate (two complementary genes) 57 Indeterminate: 7 determinate (1 basic and two complementary genes)	Indeterminate > determinate Complementary epistasis	Keerthi <i>et al.</i> (2014a) Keerthi <i>et al.</i> (2016)
Stem colour Purple / green	Single 3 Purple: 1 green	Purple > green	Raut and Patil (1985)
Stem colour Purple / green	Three (1 basic and two complementary genes) 57 Purple: 7 green	Purple > green Complementary epistasis	Rao (1987)

all the characters considered for the study. They also documented the presence of complete dominance in controlling flowering time and partial dominance for raceme plant⁻¹ and number of flowers raceme⁻¹. Alam and Newaz (2005) reported the importance of both σ^2_A and σ^2_D in the expression of flower and pod traits. Raihan and Newaz (2008) also documented the

importance of both σ^2_A and σ^2_D with a preponderance of σ^2_A in the expression of all the traits except number of inflorescences plant⁻¹. Desai *et al.*, (2013) also reported preponderance of σ^2_A for all the traits considered for the study except days to 50 per cent flowering and number of pods cluster⁻¹. Das *et al.* (2014) reported the importance of σ^2_A in the inheritance

TABLE V
Summary of genetics of leaf traits in dolichos bean

Trait and its different states	Number of genes and F ₂ ratio	Mode of action	Reference
Leaf margin colour Purple / green	Single 3 Purple: 1 green	Purple > green	Raut and Patil (1985)
Leaf vein colour Purple / green	Two 9 Purple: 7 green	Purple > green Complementary epistasis	Raut and Patil (1985)
Petiole colour Purple / green	Two 9 Purple: 7 green	Purple > green Complementary epistasis	Rao (1987)
Leaf colour Dark green / green	Three complementary genes 54 Dark green: 10 green	Dark green > green Complementary epistasis	Girish and Byregowda (2009)
Leaf texture Rough / smooth	Two 9 Rough: 7 smooth	Rough > smooth Complementary epistasis	Girish and Byregowda (2009)

TABLE VI
Summary of genetics of inflorescence traits in dolichos bean

Trait and its different states	Number of genes and F ₂ ratio	Mode of action	Reference
Photoperiod sensitivity to flowering Sensitive / insensitive	Single 3 sensitive: 1 insensitive	Sensitivity > insensitivity	Rao (1987)
Photoperiod sensitivity to flowering Sensitive / insensitive	Single 3 sensitive: 1 insensitive	Sensitivity > insensitivity	Prashanti (2005)
Photoperiod sensitivity to flowering Sensitive / insensitive	Single 3 sensitive: 1 insensitive	Sensitivity > insensitivity	Keerthi <i>et al.</i> (2014a) Keerthi <i>et al.</i> (2016)
Flower colour Purple / white	Single 3 purple: 1 white	Purple > white	Raut and Patil (1985)
Flower colour Purple / white	Single 3 purple: 1 white	Purple > white	Keerthi <i>et al.</i> (2016)
Raceme emergence from foliage Emerge out of the foliage / remain within the foliage	Two 13 emerge out of the foliage : 3 remain within the foliage	Emergence > remaining within the foliage Inhibitory epistasis	Keerthi <i>et al.</i> (2016)

TABLE VII
Summary of reported genetics of pod traits in dolichos bean

Trait and its different states	Number of genes and F ₂ ratio	Mode of action	Reference
Orientation of dry pods to branches Erect / drooping	Single 3 erect: 1 drooping	Erect > drooping	Ayyangar and Nambiar (1935)
Width of pods Medium / narrow narrow	Single 3 medium: 1 narrow	Medium width > narrow width	Ayyangar and Nambiar (1935)
Pod width Broad / narrow	Single 3 Broad : 1 narrow	Broad > narrow	Patil and Chavan (1961)
Nature of surface of narrow pods Septate / non-septate	Single 3 septate: 1 non-septate	Septate > non-septate	Ayyangar and Nambiar (1935)
Pod position after drying Erect / drooping	Two 15 Erect : 1 drooping	Erect > drooping Duplicate dominant	Patil and Chavan (1961)
Nature of pod surface Smooth / shriveled	Two 15 Smooth : 1 shriveled	Smooth > shriveled Duplicate dominant	Patil and Chavan (1961)
Pod colour Green / light green	Single 3 green: 1 light green	Green > light green	D' cruz and Ponnaiya (1968)
Pod shape Flat / bloated	Single 3 flat: 1 bloated	Flat > bloated	D' cruz and Ponnaiya (1968)
Pod curvature Straight / curved	Four Two complementary, one inhibitory and one anti-inhibitory 117 straight: 139 curved	Curved > straight Two complementary, one inhibitory and one anti-inhibitory	Girish and Byregowda (2009)
Pod curvature Straight / curved	Two 9 straight : 7 curved	Straight > curved complementary, epistasis	Keerthi <i>et al.</i> (2016)
Pod fragrance High / low	Two 13 high : 3 low	High > low Inhibitory epistasis	Girish and Byregowda (2009)

TABLE VIII
Summary of reported genetics of seed traits in dolichos bean

Trait and its different states	Number of genes and F ₂ ratio	Mode of action	Reference
Seed coat colour Khaki / Chocolate / black / brown	Single / Two 9Khaki:3 Chocolate:	Khaki > chocolate > black > buff Supplementary epistasis	Ayyangar and Nambiar (1936 a & b) Ayyangar and Nambiar (1941)
Seed shape Round / flat	Single 3 Flat: 1 Round	3 Flat > 1 Round	Patil and Chavan (1961)
Seed colour Red / white	Single 3 Red: 1 white	Red > 1 white	Patil and Chavan (1961)
Seed coat colour Chocolate / brown	Single 3 chocolate: 1 brown	Chocolate > brown	D' Cruz and Ponnaiya (1968)

of number of inflorescences plant⁻¹ and number of nodes inflorescence⁻¹. On the contrary, length of inflorescence, number of pods inflorescence⁻¹, pod length and number of seeds pod⁻¹ were influenced by σ^2_D , while the characters such as days to 50 per cent flowering, number of pods plant⁻¹, pod weight and pod yield plant⁻¹ were controlled by both σ^2_A and σ^2_D . Keerthi *et al.*, (2015) reported the predominance of σ^2_A in the inheritance of racemes plant⁻¹ and predominance of σ^2_D in the inheritance of pod weight plant⁻¹. Only σ^2_A was important in the inheritance of days to flowering and seed weight plant⁻¹. Further, Keerthi *et al.*, (2015) documented not only important role of epistasis but also significant bias in the estimates of both σ^2_A and δ^2_D for most of the traits investigated. It is therefore not advisable to ignore epistasis in studies designed to estimate σ^2_A and σ^2_D controlling quantitative traits. Identification and non-inclusion of the genotypes that contribute significantly to epistasis could be a better strategy to obtain unbiased estimates σ^2_A and σ^2_D . Selection based on unbiased estimates σ^2_A and σ^2_D is expected to be reliable and effective. Alternatively, one or two cycles of bi-parental matings in the F₂ generation is expected to dissipate epistasis and selection will be effective (Chandrakant *et al.*, 2005). Further, considering that direct selection for pod yield is less effective due to its complex inheritance, field-assayable and highly heritable traits such as primary branches plant⁻¹, racemes plant⁻¹, raceme length and pods racemes⁻¹ have been suggested for use as surrogates of selection for pod yield in dolichos

bean (Chandrakant *et al.*, 2015; Showkath Babu *et al.*, 2016).

3. Breeding

A. Productivity *per se* traits

Dolichos bean has evolved as highly photoperiod sensitive crop requiring long-nights (short-days) for switching over from vegetative to reproductive phase (Ayyangar and Nambiar 1935; Schaaffhausen, 1963; Vishwanath *et al.*, 1971; Kim *et al.*, 1992; Kim and Okubo 1995; Shivashankar and Kulkarni, 1989). Photoperiod is one of the two important environmental factors that influence adaptation of dolichos bean through its effect on days to flowering. Photoperiod influences the duration of vegetative phase *v s.* reproductive phase, partitioning of photosynthates and hence crop yield. Most of the varieties grown by farmers are landraces which are highly photoperiod sensitive (PS) and display indeterminate growth habit. Indeterminacy is advantageous for subsistence production of dolichos bean as it enables harvesting of pods in several pickings ensuring continuous availability of pods for longer time. However, market-led economy has necessitated the production of dolichos bean throughout the year and development of cultivars with synchronous pod bearing ability to enable single harvest which is possible only from photoperiod insensitive cultivars (PIS) with a determinate growth habit (Keerthi *et al.*, 2014 b; Keerthi *et al.*, 2016). Hence, major emphasis /

objective of dolichos bean breeding has been to develop PIS determinate cultivars. When using PIS cultivars, farmers can control date of flowering and hence, maturity simply by either varying the sowing date or choosing cultivars with different heat–unit requirements. However, selection for photoperiod insensitivity most often result in reduced vegetative phase, fewer branches, racemes and pods and hence, reduced economic product yield. Although, yields of such PIS varieties could be maximized by high density planting (Vishwanth *et al.*, 1971; Shivashankar and Kulkarni, 1989), developing PIS varieties with a minimum of 45 days from seedling emergence to early blooming would enable vegetative growth adequate enough to produce acceptable economic product yield even under normal density of planting as is practiced for PS cultivars (Keerthi *et al.*, 2016). Being highly self-pollinated crop with non-availability of pollination control system, pure-line is the only cultivar option for commercial production of dolichos bean (Keerthi *et al.*, 2015).

Currently, in India, the most active dolichos bean var. Lignosus breeding programmes are being carried out at UAS, Bengaluru (Mahadevu and Byregowda, 2005; Girish and Byregowda, 2009). In Bangladesh, dolichos bean breeding is being carried out in Mymensingh (Alam and Neewaz, 2005; Nahar and Newaz, 2005; Arifin *et al.*, 2005). These programmes are aimed at developing improved photoperiod insensitive determinate pure-line varieties for round-the-year production of dolichos bean for food use. On the other hand, in India at Indian Grass Land and Fodder Research Institute (IGFRI) (Magoon *et al.*, 1974) and in Australia (Whitbread and Pengelly 2004), dolichos bean breeding programmes are focused towards developing pure-line varieties for fodder use. In Australia, the strategy is to combine the traits of wide-spread forage variety, Rongai with those of African wild perennial germplasm accessions (Whitbread and Pengelly, (2004). Some of the varieties developed for food and fodder use in India, China, Australia and USA are summarized in Tables IX and X.

TABLE IX

Summary of dolichos bean grain purpose varieties developed for commercial production

Varieties	Pedigree	Location	Source
Grain purpose Hebbal Avare (HA) 1	Photo period sensitive local land race × photoperiod insensitive red typicus	University of Agricultural Sciences (UAS), Bengaluru, India	Vishwanath <i>et al.</i> (1971)
HA 3	HA 1 × US 67-31 (an introduction from USDA)	UAS, Bengaluru, India	Shivashankar <i>et al.</i> (1975)
HA 4	HA 3 × Magadi local (photoperiod insensitive)	UAS, Bengaluru, India	Hiremath <i>et al.</i> (1979); Mahadevu and Byregowda (2005)
Selections 1 & 2	Not reported	Indian Institute of Horticulture Research (IIHR), Bengaluru, India	Anon. (1988)
Koala	Selection from accession introduced from France to Australia as Q 6680	Australia	Holland and Mullen (1995)
IPSA Seam -1 & IPSA Seam -2	Not reported	Bangabandhu Sheikh Mujibur Rahman Agricultural University (BSMRAU), Gazipur, Bangladesh	Rokhsana <i>et al.</i> (2006)
Xiangbiandou 1	Not reported	China	Peng <i>et al.</i> (2001)
RioVerde	Not reported	USA	Smith <i>et al.</i> (2008)

TABLE X

Summary of dolichos bean forage varieties developed for commercial production

Varieties	Pedigree	Location	Source
IGFRI-1-S - 2214 and IGFRI-1-S-2218	Not reported	IGFRI, India	Magoon <i>et al.</i> (1974)
Rongai	Pure-line selection from germplasm accession, CPI 17883 introduced from Kenya	Australia	Wilson and Murtagh (1962)
Endurance	Rongai × African wild perennial germplasm accession, CPI 24973	Australia	Liu (1998)
Highworth	Pure-line selection from germplasm accession, CPI 30212 introduced from south India to Australia	Australia	Liu (1998)

Traditionally farmers in southern Karnataka, India are using long duration highly photoperiod sensitive landrace varieties for dolichos bean production. Due to their high photoperiod sensitivity, production and hence, availability of dolichos bean is restricted only to the seasons characterized by short days. However, with the availability of photoperiod insensitive HA 3 and HA 4 varieties, dolichos bean is being produced round-the year and hence, dolichos bean is available throughout the year. The pods of HA 4 fetch premium price in the market as they emit characteristic fragrance, a trait highly preferred by consumers. Similarly, IPSA Seam -1 and IPSA Seam - 2 could be grown during both hot / dry and humid / cooler seasons ensuring the availability of dolichos bean round-the-year in Bangladesh (Rokhsana *et al.*, 2006). Contrary to South Asia, the production of dolichos bean is limited to gardens in eastern Africa (Nagilo *et al.*, 2003). However, Ewansiha *et al.*, (2007) have identified dolichos bean germplasm accessions with acceptable grain and forage yields for use in cereal-legume-livestock systems in the moist savannah zone of West Africa (Maass *et al.*, 2010).

B. Biotic stresses

Insect pests

Of the several biotic stresses, anthracnose (caused by *Colletotrichum lindemuthianum*) and dolichos yellow mosaic virus (DVMV) diseases and pod borers (*Heliothis armigera* and *Adisura atkinsoni*) and bruchids (*Callasobruchus theobrome*) are major production constraints in dolichos bean. Among pod borers, *Adisura atkinsoni* are dominant ones (Chakravarthy, 1983). While pod borers cause damage in the field, bruchid cause

damage both in field and storage. Losses to these pod borers and bruchids could be up to 100 per cent. Breeding for resistance to these insect pests is currently limited to screening and identification of resistance sources in germplasm and breeding lines. Chakravarthy and Lingappa (1986) identified two stable sources of resistance to larval boring and to pod borers in field and laboratory conditions based on screening of 111 dolichos accessions. The two sources of resistance to pod borers exhibited significant degree of antibiosis as demonstrated by reduced larval survival, larval and pupal weights, prolonged larval duration and altered sex ratio (Chakravarthy and Lingappa, 1988). Combined effect pod colour, pubescence and fragrance appeared to be associated with resistance response. However, none of pod colour, pubescence and fragrance *per se* imparted resistance to pod borers. The accessions highly resistant to pod borers were highly susceptible to aphid infestation (Chakravarthy and Lingappa, 1988).

Jagadeesh Babu *et al.* (2008) identified germplasm accessions such as GL 1, GL 24, GL 61, GL 69, GL 82, GL 89, GL 196, GL 121, GL 135, GL 412, and GL 413 with < 10 per cent insect damage as resistant to pod borers (*Heliothis armigera* and *Adisura atkinsoni*) and bruchids (*Collosobruchus chinensis*) based on two years (2004 and 2005) of field sowing of 133 germplasm accessions. Based on laboratory screening of 28 selected germplasm accessions under no choice conditions, Rajendra Prasad *et al.* (2013) identified resistant accessions, GL 77, GL 233 and GL 63 with least seed damages of 13.4 per cent, 14.69 per cent and 18.34 per cent, respectively (Rajendra Prasad *et al.*, 2013).

During 2007 and 2008 at UAS, Bengaluru, another set of 132 germplasm accessions were screened for responses to infestation by *Helicoverpa armigera* and *Adisura atkinsoni* and bruchids. Pod damage due to *Helicoverpa* ranged from 1.8 (GL 187) to 36.8 per cent (GL 9), while *Adisura* infestation varied from 0.5 (GL 55) to 7.9 per cent (GL 14) and *Bruchids* infestation ranged from 0.6 (GL 187) to 40 per cent (GL 37). The average infestation of germplasm accessions by *Helicoverpa* was 18 per cent followed by bruchids with 12.1 per cent and by *Adisura* with 3.1 per cent (Table XI). The infestation by *Helicoverpa* was < 10 per cent in 13 accessions, while, that by bruchids was < 10 per cent in 42 accessions and by *Adisura* was < 10 per cent in 132 accessions (Table XII). GL 187 was identified as resistant to *Helicoverpa armigera*, *Adisura atkinsoni* and *Bruchids* infestation. Another study at UAS, Bengaluru, indicated the role of both antixenosis and antibiosis mechanisms of resistance to damage by *Helicoverpa* in the germplasm accessions GL 233, GL 426, GL 357 and GL 187 which were found moderately tolerant (Rajendra Prasad *et al.*, 2015).

TABLE XI

Per cent pod infestation of Helicoverpa, Adisura and Bruchids in Dolichos bean

Total	Range (%)	Helicoverpa	Adisura	Bruchids
145	Lowest	18.0	0.5	0.6
	Highest	36.8	7.9	40.0
	Average	18.0	3.1	12.1

TABLE XII

Number of germplasm lines with different level of infestation

Infestation range (%)	Helicoverpa	Adisura	Bruchids
0-10	13	132	42
11-20	70	-	83
21-30	46	-	07
31-50	03	-	-
>50	-	-	-
Total	132	132	132

Diseases

Dolichos yellow mosaic virus (DYMV) is caused by Gemini virus and transmitted by whitefly (Capoor and Verma, 1950). The disease is characterized by yellow to bright yellow patches and vein clearing on leaves (Maruthi *et al.*, 2006). Initially a few yellow patches are seen on the leaf lamina, but, later on the entire leaf becomes yellow (Raj *et al.*, 1989). The disease causes up to 80 per cent crop loss (Muniyappa *et al.*, 2003). As is true with insect pests, breeding dolichos bean for DYMV resistance is confined to identification of resistance sources. Singh *et al.* (2012) identified VRSEM 894, VRSEM 887 and VRSEM 860 as resistance to DYMV among 300 germplasm accessions based on initial field screening under natural infection followed by screening of 34 symptomless accessions using sap inoculation in field condition (Rai *et al.*, 2015). Rajesha *et al.*, (2010) screened 195 genotypes of dolichos bean against anthracnose disease caused by *Colletotrichum lindemuthianum* under field conditions. They identified nine genotypes, such as GLB 3, GLB 4, GLB 8, GLB 9, GLB 11, GLB 19, GLB 60, GLB 166 and GLB 167 that were immune; 48 genotypes resistant and 83 genotypes moderately resistant to the disease. Deshmukh *et al.*, (2012) screened 44 genotypes which included varieties and germplasm accessions of dolichos bean for responses to anthracnose infection under conditions and identified three varieties and two germplasm accessions resistant to the disease.

C. Abiotic stresses

Dolichos bean has better inherent capacity to withstand moisture stress than the comparable legumes such as cowpea, horse gram, etc. (Nworgu and Ajayi, 2005; Ewansiha and Singh, 2006; Maass *et al.* 2010) and adapt to acidic (Mugwira and Haque, 1993) and saline soils (Murphy and Colucci, 1999). With its deep root system, dolichos bean is not only drought tolerant (Kay, 1979; Cameron, 1988; Hendricksen and Minson, 1985), but, also has the ability to harvest soil minerals which otherwise not available for annual crops (Schaaffhausen, 1963 a & b). In the event of imminent extremities of abiotic stresses driven by climate change (IPCC, 2007), dolichos bean would be a better alternative to popular legumes. Thus, breeding and enhancing the economic value of dolichos bean would provide competitive edge to dolichos bean producers and enable preparing for unfriendly agriculture production climate. In this backdrop, dolichos bean is

regarded as one of the future crops for sustainable agricultural production. The reported research on breeding dolichos bean for resistance to abiotic stresses is limited.

4. Use of genomic tools

Use of genomic tools such as DNA markers in dolichos bean breeding is still in infancy as they are not available. Nevertheless, sequence independent marker systems such as RAPD and AFLP have been used to detect and characterize genetic variation among germplasm accessions and breeding lines. Reported literature on the use of DNA markers in analysis of genetic variability is summarized in Table XIII. Most of the studies on genetic diversity analysis are based on RAPD and AFLP. However, the information obtained from these markers is not reliable due to their poor reproducibility. Hence, sequence dependent simple sequence repeat (SSR) and single nucleotide polymorphism (SNP) are highly preferred by researchers owing to their simple inheritance and amenability for automation and high reproducibility. The use of cross species / genera SSR markers in

crops where they are not available is considered as the most cost effective strategy as *de novo* development of SSR markers is both expensive and time consuming. Taking cue from several successful examples of cross transferability of SSR markers, Yao *et al.*, (2012) demonstrated that all tested EST-SSR markers from soybean were cross transferable to dolichos bean although only 16 per cent of them could differentiate the genotypes. At UAS, Bengaluru, transferability of SSR markers from cowpea, soybean, *Medicago truncatula*, greengram and chickpea to dolichos bean was examined and the results (Shivakumar and Ramesh, 2015; Uday Kumar *et al.*, 2016) are summarized in Tables XIV and XV. Transferable SSR markers help enrich marker resources for various applications in dolichos bean genetics and breeding research such as (1) characterize and assess genetic variability in working germplasm and /or breeding lines, (2) fingerprint to identify duplicate germplasm accessions, (3) fingerprint varieties for protecting IPR and (4) Select genetically diverse genotype for effecting crosses to generate variability to identify genotypes with best combination of traits.

TABLE XIII

Summary of DNA marker-based genetic diversity analysis in dolichos bean

Genetic material used	Marker used	References
CSIRO: 40 accessions	RAPD	Liu (1996)
Mapping population from cross of two CSIRO accessions	RFLP, RAPD	Konduri <i>et al.</i> (2000 a & b)
Bangladesh / Japan germplasm + 60 CSIRO accessions	RAPD	Sultana <i>et al.</i> (2000)
Mapping population for comparative mapping with mungbean (<i>Vigna radiata</i>)	RFLP	Humphry <i>et al.</i> (2002)
USDA > 30 germplasm accessions	SSR	Wang <i>et al.</i> (2004)
103 CSIRO accessions	AFLP	Maass <i>et al.</i> (2005)
11 varieties from Hunan province of China	RAPD	Tian <i>et al.</i> (2005)
12 landraces from southern India	RAPD	Gnanesh <i>et al.</i> (2006)
Mostly core collection (28 accessions) + Tanzanian landraces	AFLP	Tefera (2006)
62 landraces collected from southern India and core collection accessions	AFLP, SSR	Venkatesha <i>et al.</i> (2007)
USDA: 47 accessions	SSR	Wang <i>et al.</i> (2007)
40 accessions from India	AFLP	Patil <i>et al.</i> (2009)
10 insect tolerant and susceptible landraces from India	RAPD	Sujithra <i>et al.</i> (2009)
Mapping population from cross of two Chinese accessions	RAPD	Yuan <i>et al.</i> (2009)
50 Kenya accessions	AFLP	Kinmani <i>et al.</i> (2012)
30 Indian accessions	RAPD	Rai <i>et al.</i> (2010)

TABLE XIV
Per cent transferability of cross legume crop species / genera genomic / EST-SSR markers to dolichos bean

Crop	Total number of markers used	Number of markers amplified	% Transferability	Conditional probability that a given cross species / genera SSR markers transferable to dolichos bean is from a particular crop
Cowpea	150	50	33.33	0.40
Soybean	90	48	53.33	0.38
<i>Medicago truncatula</i>	12	10	83.33	0.08
Greengram	14	11	78.57	0.09
Chickpea	09	07	77.77	0.06
Total	275	126	45.81	

Shivakumar and Ramesh (2015)

TABLE XV
Crop and repeat motifs based distribution of amplified cross legume species / genera SSR markers in dolichos bean

Crop	Number of markers used	Number of markers amplified	Per cent amplification	Length of repeat motifs			
				di -	Tri -	Tetra -	Complex -
Soybean	65	29	44.61	26	-	-	03
<i>Medicago truncatula</i>	12	02	16.66	-	01	01	-
Green gram	14	08	57.14	04	01	02	01
Chickpea	10	04	16.66	01	01	-	02
Total	100	43	43.00	31	03	03	06

Uday Kumar *et al.* (2016)

Besides analysis of genetic diversity, DNA markers have also been used to develop linkage map, a prelude to identify DNA markers linked to genomic regions controlling target traits. The linked markers after validation could be used for marker assisted selection of target traits to enhance the pace and efficiency of breeding dolichos bean. The first ever linkage map consisting of 127 RFLP and RAPD markers using 119 F₂ mapping population derived from Rongai × CPI 24973 cross was developed by Konduri *et al.* (2000 a & b). The map comprised of 17 linkage groups with a total length of 1610 cM and an average of 7 cM between markers. The

comparison of dolichos bean linkage map with that of mungbean revealed a high level of co-linearity between the two genomes (Humphry *et al.*, 2002).

5. Future prospects

The expected increased incidence of existing and emergence of new biotic and abiotic stresses driven by imminent climate change (IPCC 2007) warrants accelerated breeding for these production constraints. This necessitates screening of released varieties and

advanced breeding lines to identify those resistant to these production constraints for use in commercial production as a short-term strategy. Germplasm accessions' screening, identification and their use in

breeding for resistance to these production constraints would be a long-term strategy to address increased incidence of existing and anticipated production constraints.

There is need for deployment of genomic tools such as DNA markers especially SSR and SNP markers to enhance the pace and precision of breeding dolichos bean for all economically important traits. Large number of SSR and SNP markers should be identified and validated given the small genome size and less expensive whole genome sequencing. The SSR and SNP markers should be routinely used for discovery of quantitative traits loci controlling economically important traits followed by genomic selection to complement phenotype-based selection to enhance the pace and efficiency of dolichos bean breeding. Genome sequencing help identify novel and useful genes through genome analysis with comparable and extensively researched legumes such as soybean and *Medicago* spp., and introgression into elite agronomic background. This review would benefit all those who are interested in dolichos bean breeding.

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