REVIEW



Rice bean: a lesser known pulse with well-recognized potential

Arunava Pattanayak¹ · Somnath Roy² · Salej Sood³ · Banshanlang langrai⁴ · Amrita Banerjee² · Sanjay Gupta⁵ · Dinesh C. Joshi¹

Received: 31 August 2018 / Accepted: 20 May 2019 / Published online: 27 May 2019 © Springer-Verlag GmbH Germany, part of Springer Nature 2019

Abstract

Main conclusion Required genetic resources for the improvement of agronomic, nutritional and economic value of rice bean are available in the world collection. International cooperative effort is required to utilize and conserve them.

Abstract Rice bean [Vigna umbellata (Thunb.) Ohwi and Ohashi], a lesser known pulse among the Asiatic Vigna, has long been considered as a food security crop of small and marginal farmers of Southeast Asia. Considered as a nutritionally rich food and fodder, it is also a source of genes for biotic and abiotic stress tolerance including drought, soil acidity and storage pest. Although it spread from its centre of domestication in the Indo-China region to other parts around the world, it never became an important crop anywhere probably because of agronomic disadvantages. Crop improvement for determinate nature, good yield, less variable seed colour, pleasant organoleptic properties and lower antinutrients is required. Scanning of scientific literature indicates that genetic resources with desirable agronomic and nutritional traits exist within the current collection but are spread across countries. Genomic studies in the species indicate that except for insect resistance and aluminium toxicity tolerance, not much attention has been paid to decipher and utilize other stress tolerance and nutritional quality traits. Collaborative efforts towards improving farming, food, trade value and off-farm conservation of rice bean would not only help marginal farmers but will also help to preserve the yet to be explored genomic resources available in this sturdy pulse.

Keywords Rice bean · Orphan crop · Nutrition · Genomic resources · Economic value

Arunava Pattanayak, Somnath Roy and Salej Sood contributed equally and are joint first authors.

- Arunava Pattanayak apat.icarneh@gmail.com; pattanayak.a@icar.gov.in http://www.vpkas.icar.gov.in
- ¹ ICAR-Vivekananda Parvatiya Krishi Anusandhan Sansthan, Mall Road, Almora, Uttarakhand 263601, India
- ² Central Rainfed Upland Rice Research Station, ICAR-National Rice Research Institute, Hazaribagh, Jharkhand 825301, India
- ³ ICAR-Central Potato Research Institute, Shimla, Himachal Pradesh 171001, India
- ICAR Research Complex for North Eastern Hill Region, Umiam, Meghalaya 793103, India
- ICAR-Indian Institute of Soybean Research, Khandwa Road, Indore, Madhya Pradesh 452001, India

Introduction

In the marginal farming environment, agricultural sustainability depends on many less-known crops cultivated mainly as intercrops with staple cereals such as rice, maize and wheat. These crops persist because of their adaptation to special niches in low-input production systems, specific taste and social importance, supply of essential nutrients and soil quality improvements. In many production systems, they also satisfy the need of a multi-tier agriculture. Several terms such as underutilized crops, minor crops, neglected spices, orphan crops and potential crops have been used to group them. In general, traditional knowledge is associated with their use while scientific knowledge is still emerging (Gruére et al. 2006).

Although there is no specific convention for the different terms used for these crops, generally the term 'minor' indicates that these species have less commercial value compared to major agricultural commodities of the same or related group.



The term 'underutilized' refers to species, which were either grown extensively in the past or have a potential in the future but, for agronomic, genetic and economic reasons are currently grown in a limited area (Gruére et al. 2006). These species are also termed as 'orphan' crops as they did not receive due attention for research and development, and as such there is scanty scientific knowledge about them (Eyzaguirre et al. 1999). Rice bean, a legume with multiple uses, is a typical example of all the above.

Rice bean [Vigna umbellata (Thunb.) Ohwi and Ohashi (2n-2x=22)] also known as red bean, oriental bean and climbing mountain bean is a warm-season annual vine legume with yellow flowers and small edible beans. Grown mainly for its beans, it is equally important as vegetable (green pod), fodder and folk medicine. Its area under cultivation is very low compared to other pulses such as black gram, mung bean, lentil and chickpea. The dried beans are rich source of protein. Being rich in lysine, they make an excellent addition to cereal diet. In several parts of the northeast India, the beans are also fermented to improve the nutritional value.

There are calls for paradigm shift in agriculture to explore the underutilized crops as potential future crops. Rice bean is one among them, which has many useful traits such as disease resistance, drought tolerance, aluminium toxicity tolerance and being nutrient dense can address micronutrient deficiencies in affected areas. This pulse has been little studied probably because of its use within isolated communities and consequent low economic value. Most of the research conducted in the past focused on its high level of resistance to grain storage pest bruchid beetles (Calloso bruchus spp.) (Tomooka et al. 2000; Kashiwaba et al. 2003) although resistance to yellow mosaic virus, Cercospora and bacterial leaf spot (Arora et al. 1980) and mung bean yellow mosaic virus (Pandiyan et al. 2008) has been reported in this crop. In the recent years, some reports on genetic diversity (Tian et al. 2013; Iangrai et al. 2017; Pattanayak et al. 2018), genomics (Somta et al. 2006; Isemura et al. 2010) and nutritional quality (Katoch 2013; Bepary et al. 2017) have been published.

Despite the recognition that rice bean has a current private value (more important for specific area or community but insignificant commercial use) for people living in the vulnerable agricultural systems, and it is a source of many valuable agronomic and nutritional traits, the potential value of the crop is underestimated. International effort to flag the issue of rice bean is limited. Here, an effort has been made to summarize the work done in the area of research and cooperation to establish the potentials of this crop.



The review is based on the existing literature on rice bean, field work, exploration and evaluation of rice bean germplasm. An extensive exploration, collection and evaluation programme of rice bean was carried out under the 'National Agricultural Technology Project' (NATP) of Indian Council of Agricultural Research (ICAR) starting from 1998. Collections made in this project were evaluated by various groups in India, including our group. Similar work was taken up under an international project 'Food security through rice bean research in India and Nepal' (FOSRIN) about a decade later. Results published from both the programmes form the base of this review. In addition, work carried out in other parts of the world, especially on taxonomy, interspecific hybridization and genomics have been reviewed. Information available at rice bean portal (www.ricebeanportal.com), NARO gene bank website (www.gene.affrc.go.jp), World Vegetable Centre (http://seed.worldveg.org) and general search results in various search engines were also used.

A large chunk of the literature on rice bean addresses issues related to biological, nutritional, genomic and agronomic issues. However, several authors have also tried to project the case of rice bean as a crop of immense value (for example, Andersen 2012). All these literatures were consulted to give an overview of what has been done and what can be done to establish the true value of this underutilized pulse.

Origin, distribution, taxonomy and morphology

Origin

Rice bean [(Vigna umbellata syn. Phaseolus calcarata (Roxb.) Kur2; Azuki umbellata (Thunb.) Owhi] is considered to be of South and Southwest Asian origin (Bisht and Singh 2013). It was probably domesticated in the Indo-China region (Doi et al. 2002). Wild forms of the species (V. umbellata var. gracilis) with which it exists as a complex are found in the Himalayas and Central China to Malaysia (Seehalak et al. 2006). It is believed that rice bean was domesticated from these wild forms. These wild forms occur in natural or disturbed habitats and are intermediate with twining plant types, freely branching, photoperiod sensitive with small seeds. Many intermediate land races are cultivated in northeast India (Iangrai et al. 2017). Inter- and intraspecific genetic diversity and inter-species relationships of Vigna species from Thailand and neighbouring region have been assessed using AFLP analysis (Seehalak et al. 2006). This study suggested that *V. umbellata* and *V. mungo* evolved



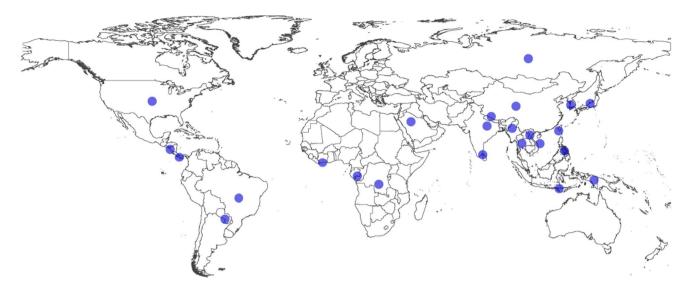


Fig. 1 Map showing world distribution of rice bean

from wild relatives in a single domestication event. The cultivated type and wild and weedy relatives of *V. umbellata* are poorly differentiated as compared to *V. mungo*. The study also suggested Thailand and neighbouring Shan state in Myanmar as the probable centres of domestication for *V. umbellata*.

Distribution

Rice bean is a traditional crop of South, Southeast and East Asia (Seehalak et al. 2006; Tomooka et al. 2002a). *V. umbellata* var. *gracilis* from which rice bean is believed to have originated is conspecific with the cultivated *V. umbellata* and widespread in distribution in South and Southeast Asia (Bisht et al. 2005; Seehalak et al. 2006; Tomooka et al. 1991, 2002a). It is mainly grown in Bhutan, India, Myanmar, Northern Thailand, Southern China, Laos, Vietnam, Indonesia and East Timor (Tian et al. 2013; Iangrai et al. 2017; Pattanayak et al. 2018). The crop was introduced as a garden and cover crop in Fiji, Sri Lanka, Ghana, Jamaica, Mexico and Haiti. It is also cultivated to a limited extent in West Indies, Americas (USA, Honduras, Brazil—Fig. 1), Australia and tropical Africa (Burkill 1953; Rajerison 2006; Khadka and Acharya 2009).

In China, rice bean collection has been reported from 12 provinces (Wang et al. 2015). As a crop, rice bean is suited to areas with annual rainfall ranging from 1000 to 1500 mm but it is fairly tolerant to drought. In Japan, rice bean was earlier grown in the southwestern part (Noda 1951) but its cultivation has almost disappeared now. It grows better in areas where temperature ranges from 18 to 30 °C. Although rice bean can tolerate 10–40 °C, it is highly susceptible to frost. There is no specific record of its trade. In India,

Myanmar, Nepal and Thailand, rice bean is sold in the local markets in an unorganized trade. In 1991, Japan imported approximately 15.5 metric tonnes of rice bean from Myanmar and Thailand as a substitute of azukibean.

Although rice bean possesses an ability to thrive in diverse climatic conditions, its cultivation is limited to areas with moderate to high rainfall and temperature (the crop does not tolerate frost). Furthermore, it appears that being a highly photosensitive but indeterminate crop, it lost ground to other pulses such as black and green gram, lentil, field pea, pigeon pea and chickpea from the economic yield point of view. The crop duration creates a problem for planting of subsequent crops. Ironically, the tastier varieties are late (Andersen 2012). Also, the crop so far is not amenable to a mechanized cultivation system. Its harvest index is low (25.8–27.3) (Sarma et al. 1995) compared to other economically important pulses such as soybean, field pea and lentil (36.6–44.6) (Jayasundara 2015). Because of seed coat type, rice bean cannot be split into two halves easily, and remains relatively intact even after boiling. It is possible that these factors caused its little use as a pulse for daily consumption leading to limited spread.

Taxonomy

A number of workers attempted to elucidate phylogenetic relationship within the subgenera *Ceratotropis* using isozymes (Jaaska and Jaaska 1990, Vaillancourt and Weeden 1993), RAPD (Fatokun et al. 1993a), RFLP (Fatokun et al. 1993b), AFLP (Tomooka et al. 2002b; Seehalak et al. 2006), etc. In addition, antigenic peptide (Kajiwara and Tomooka 1998), rDNA ITS and atpB–rbcl intergenic spacer (Doi et al. 2002), ISSR (Vir et al. 2010) and plastid DNA sequences



(Javadi et al. 2011) were used to decipher phylogenetic relationship in the subgenus. Genetic relatedness of 44 *Vigna* accessions belonging to four subgenera was assessed using RFLP analysis (Fatokun et al. 1993b). The distinctness of the Asiatic grams in subgenus *Ceratotropis* was elucidated by this study. Vir et al. (2010) used 24 ISSR markers to elucidate species relationships in 46 accessions representing 20 *Vigna* species. *V. umbellata* grouped closely with *V. stipulacea, V. tenuicaulis* and *V. minima*.

Phylogenetic analysis based on DNA sequences from the ITS and atpB-rbcL regions showed a close relationship between V. umbellata, both cultivated and wild forms, with species of section Angulares such as V. hirtella, V. exilis, V. tenuicaulis, V. napalensis, V. minima, V. nakashimae and V. ruikiuensis (Doi et al. 2002). These findings were supported by a recent study using seventy-one Vigna accessions, consisting of 28 species and three subgenera (Ceratotropis, Plectrotropis, and Vigna) conserved at the National Institute of Agrobiological Sciences, Japan (Takahashi et al. 2016). Sequence data from four intergenic spacer regions of chloroplast DNA of 18 species of the subgenera Ceratopteris were analysed using Bayesian and parsimony methods (Javadi et al. 2011). Two major geographical clades, the East Asia-SE Asian clade and the Indian subcontinent clade, were identified within 18 species. This study further classified major clades into eco-geographical groups: temperate and subtropical (the East Asia-SE Asian clade) and tropical (the Indian subcontinent clade). V. umbellata clustered under V. hirtella-V. exilis-V. umbellata subgroup within the subtropical group which also included the *V. nakashimae–V.* riukinensis-V. minima subgroup. The genetic relationship of different species within Ceratotropic subgenus is given in Fig. 2, as adapted from three different studies (Doi et al. 2002; Javadi et al. 2011; Takahashi et al. 2016).

Morphology

Rice bean is an annual with semi-erect, erect or twining habit, stems up to 3 m long, usually covered with fine deciduous, deflexed hairs. Root system is extensive with a tap root that can go up to 1.5 m deep. Stems are branched. Leaves are alternate, trifoliate, stipules lanceolate 1.2–1.5 cm long, petiole 5–10 cm long, stipels linear to lanceolate about 0.5 cm long, leaflets broadly ovate to ovate-lanceolate, $5-13 \times 1.5-7$ cm, entire or 2-3 lobed, the lateral leaflets unequal sided, membranous, almost glabrous (Sarma et al. 1995). The flowers are borne on 5-10cm axillary racemes, 5–20 in number but usually in pairs, peduncle up to 20 cm long. They are bisexual, papilionaceous, calyx campanulate and five toothed, approx. 4 mm in length. Corolla is bright yellow, wings large and enclose the curved beak keel. Stamens are ten in number (two groups of nine and one); ovary is superior, one celled with broad

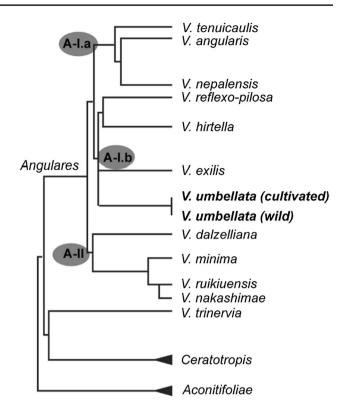


Fig. 2 Genetic relationship among different species of Ceratotropis

and curved style. Five to sixteen seeded pods (5–15 cm) are linear (5–15 cm), deflexed, glabrous, green when young and blackish brown at maturity. Seeds are oblong, highly variable in size (4–37 g 100 seed weight) (Fig. 3) and coloured (Fig. 4a), have smooth surface (Sarma et al. 1991), excentric hilum, which is elongated and hidden by a cream-coloured rim (Fig. 4b). Seedlings have hypogeal germination.

Nutritional composition

Rice bean is primarily consumed as a *dal* (*boiled soup*/ *sauce*) in the South Asian countries with rice or other staple cereals. Its use as a pure *dal* (not mixed with any other pulse) is uncommon. A number of other recipes are also found such as boiled or roasted whole grain, addition to chickpea flour to make deep-fried snacks, addition to wheat flour and as fermented whole grains. Consumption of green pod, although seen in some areas, is uncommon due to the presence of undesired hairs on the pod. Indirect contribution of rice bean to human nutrition comes through fodder for livestock.

In terms of nutritional value, rice bean is comparable to other low-fat grain pulses. The content of protein as reported in different studies varies (Table 1) and is towards the lower end in pulses. The in vitro protein digestibility is higher than mung bean and cowpea (86.1–88.5% of the albumin



Fig. 3 Variability in seed morphology in a set of accessions from northeast India





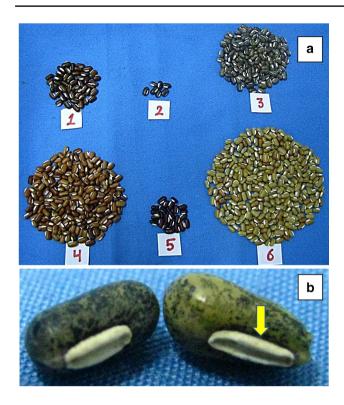
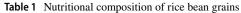


Fig. 4 Colour variation in rice bean seed. **a** Colour variations within a single accession of rice bean. **b** Cream-coloured rim hiding the hilum (arrow)

fraction, 82–85% of the raw seed meal, Rodriguez and Mendoza 1991). Katoch (2013) reported protein digestibility to range from 51.23 to 55.57%. On the other hand, the amino acid composition, especially methionine and tryptophan is appreciably high (Chandel et al. 1978). Mohan and Janardhanan (1994) reported that methionine content of rice bean grain was higher than black gram and green gram while contents of lysine, tyrosine and valine were comparable. Katoch (2013) compared amino acid composition of 16 genotypes of Indian rice bean and his findings were also similar. Although Mohan and Janardhanan (1994) did not estimate tryptophan, Mal (1994) reported tryptophan content ranging from 0.79 to 1.10% and Katoch (2013) reported tryptophan content ranging from 1.23 to 2.00%.

Relatively little is known about the vitamin composition of rice bean. de Carvalho and Vieria (1996) reported that rice bean is rich in niacin, riboflavin and thiamine. Kaur and Kapoor (1992) also reported high niacin (30 mg/100 g) content in rice bean grains. Andersen (2007) reported high vitamin B complex in an accession of rice bean *Pahelo marsyang* from Nepal. Katoch (2013) analysed 16 genotypes of rice bean and reported 15.33–28.23 mg (per 100 g) ascorbic acid and 3.48–4.26 mg (per 100 g) niacin. Kaur and Kapoor (1992), Mohan and Janardhanan (1994), Katoch (2013) and Bepary et al. (2017) studied mineral content in rice bean grain. From these studies, it can be concluded that rice bean



Component	Content
Crude protein (%)	14.00–26.10
Amino acids (mg/100 g)	
Arginine	4.32–7.12
Alanine	3.26-6.60
Aspartic acid	10.39-13.50
Glutamic acid	12.36-17.00
Glycine	2.96-4.26
Lysine	5.38-8.75
Methionine	0.90-2.88
Proline	2.54-8.36
Tryptophan	1.23-2.00
Tyrosine	2.12-3.31
Valine	4.40-5.89
Minerals (mg/100 g)	
Sodium	6.00-347.40
Potassium	610.40–2875.00
Calcium	111.5–598.23
Magnesium	73.0–356.12
Zinc	2.45-10.44
Iron	3.72-9.25
Manganese	2.04-5.0
Copper	0.68-4.97
Phosphorous	124.0-567.69
Fatty acid (%)	
Palmitic acid	5.60-16.88
Stearic acid	2.10-5.87
Linoleic acid	7.50–18.98
Oleic acid	15.62-68.00
Linolenic acid	39.89-44.38

Source: Chandel et al. 1978; Duke 1981, FAO 1982; Gopinathan et al. 1987; Malhotra et al. 1988; Rodriguez and Mendoza 1991; Kaur and Kapoor 1992; Mohan and Janardhanan 1994; Saikia et al. 1999, Upadhayay 2010; Katoch 2013, Bajaj 2014; Bepary et al. 2017

is rich in sodium (Na), potassium (K), calcium (Ca) and phosphorous (P). Zinc (Zn) content is low while iron (Fe) content is moderate to low (Table 1).

Rice bean is considered as a low-fat food. The range of saturated and unsaturated fats varied considerably in the reported studies (Kaur and Kapoor 1992; Saikia et al. 1999; Katoch 2013; Bepary et al. 2017). Crude fat content varied from 0.46 to 2.3%. Range of saturated fats varied from 27.4 to 55.0% while that of unsaturated fats (mono and poly unsaturated) varied from 36 to 73.2%.

Flatulence-producing oligosaccharides are common disadvantages of pulses. In rice bean also, flatulence-producing disaccharides raffinose (1.48 to 2.39%), stachyose (0.94 to 3.29%) and verbascose (0.85 to 1.23%) are found (Kaur and Kawatra 2000; Katoch 2013). However, their contents are significantly lower than soybean, lima bean and sword



Table 2 Rice bean germplasm holding at some key centres worldwide

Country	Centre	Number of accessions*
India	ICAR—National Bureau of plant genetic resources	2071**
China	Institute of Crop Genetic Resources	1363
Japan	National Agriculture and Food Research Organization	399
Taiwan	World Vegetable Centre	351
Nepal	Nepal Agricultural Research Council	300***
Philippines	National Plant Genetic Resource Laboratory, UPLB, Laguna	161
Indonesia	Centre of Biology, Indonesian Institute of Science Research and Development, Bogor	100
USA	ARS-GRIN	147*

^{*}Source: Bisht and Singh (2013); **source: ICAR-NBPGR database accessed on 8. 5. 2019; ***source: Gautam et al. (2007)

bean. Phytic acid, which affects availability and absorption of mineral nutrients in the human body, is one of the major antinutrients in pulses. In rice bean, low phytic acid content ranging from 0.20 to 2.27% has been reported (Saharan et al. 2002; Bepary et al. 2017). The range is lower than soybean, black gram and green gram (Bepary et al. 2017). The effect of two processing treatments—soaking and pressure cooking on the level of nutrients and antinutrients in rice bean was investigated in four rice bean varieties, viz., RBL-1, RBL-6, RBL-35 and RBL-50 (Bajaj 2014). Significant percent of reduction was observed in content of phytic acid, trypsin inhibitor activity, polyphenols and saponins after soaking and pressure cooking, respectively. Soaking and pressure cooking, however, did not affect the protein, ash, fat and fibre content of rice bean varieties significantly.

Germplasm collection and evaluation

A number of national and international centres maintain collections of rice bean accessions. The ex situ collection of V. umbellata at the World Vegetable Centre (AVRDC), Taiwan consists of 351 accessions from 24 different countries, with major contributions from India, Nepal, Philippines, Brazil and Congo (http://seed.worldveg.org/search/ passport; accessed on 09.04.2019). Out of these, characterization data for seedling, vegetative, inflorescence, pod and seed traits are available for about 289 accessions. The Plant Genetic Resources Unit of Nepal Agricultural Research Council (NARC) maintains about 300 rice bean accessions collected from 29 districts of the country. In India, the National Bureau of Plant Genetic Resources (NBPGR) conserves a total of 2071 accessions in the National Gene bank out of which 1993 are indigenous collections (ICs) and 96 are exotic collections (ECs) (based on the record on the PGR Portal; http://www.nbpgr.ernet.in:8080/PGRPo rtal/(S(tz1a0qzpschmntqzx1qdvwf4))/default.aspx accessed on 08.05.2019). Most of the indigenous collections were collected from NE India (656 accessions), followed by NW (240), Eastern (187), Southern (40), and Central (7) parts. The passport data of rice bean accessions conserved in different ex situ gene banks are incomplete. An examination of the biological status of those conserved in NBPGR, India, indicated that about half of the gene bank accessions are landraces or primitive cultivars. Only 23 accessions are improved or notified cultivars, indicating a lack of systematic breeding for rice bean improvement. A list of institutions with their germplasm holding is collated in Table 2.

The geographical distribution pattern of rice bean indicates great adaptive polymorphism of the crop in diverse environments, with its distribution ranging from humid tropical to sub-temperate climates. A comparative account of agronomic traits reported in the literature is given in Table 3. From the table, it appears that the genotype with the shortest duration (< 66 days) is available in the East Asian (Japan and Korea) cultivated types (Tian et al. 2013). Genotypes with a very high number of pods/plant and very high yield/plant are present in the collection from Nepal. Genotypes with a higher number of branches/plants, higher pod length and seeds/pod are available in the Indian collection.

Although the germplasm collection across gene banks appears to be satisfactory, availability of characterization data appears to be the main bottleneck for its effective utilization in breeding. Systematic characterization and germplasm exchange will help to realize the potential of this crop.

Genetic and genomic resources

Molecular diversity

Genomic studies of rice bean have lagged behind that of other legume crops, such as soybean, common bean, mung bean, and azuki bean due to the lack of polymorphic DNA markers. To date, there are only few reports on the intraspecies molecular diversity in *V. umbellata* analysed



Table 3 A comparative account of agronomic traits of rice bean

Trait	Singh et al. (2006) India*	Joshi et al. (2007) Nepal*	Tian et al. (2013) Asia*	Pattanayak et al. (2018) NE India*	Overall range
Days to 50% flowering	62–123	55–112	31–134	82–107	31–134
Days to 80% maturity	95-180	118-151	< 66–Not reported	127-177	<66-177
Plant height (cm)	62.4-372.5	119–268	_	41.75-254.2	41.75-268
No. of branches/plant	3.0-13.0	_	0–5	3.2-20.0	0-20.0
No. of clusters/plant	3.0-28.0	_	_	_	_
Pods/cluster	2.0-7.0	_	_	_	_
Pods/plant	38.0-296.0	58-516	_	_	38-516
Pod length (cm)	7.60-12.80	5.9-11.6	_	7.78-12.15	5.9-12.8
Seeds/pod	7.0-12.0	2.4-9.5	_	6.2-9.4	2.4-12.0
100 seed wt (g)	4.7–21.4	4.3-23.4	3.7–37.2	6.64-29.86	3.7-37.2
Yield/plant (g)	2.7-73.0	26.1–274.4	_	7.90-63.09	2.7-274.4

^{*}Collection area

using RAPD, AFLP, ISSR and SSR markers (Bajracharya et al. 2008; Muthusamy et al. 2008; Thakur et al. 2017; Tian et al. 2013; Iangrai et al. 2017). Ten rice bean landraces from NE India were genotyped with 74 RAPD and 37 ISSR primers (Muthusamy et al. 2008). Inclusion of only a few landraces from a small geographic region resulted in the detection of a low genetic diversity among the accessions. Genetic diversity in 13 rice bean varieties and their 11 narrow leaf crosses was studied using RAPD markers (Shafiqul et al. 2017). However, this study mainly focused on identifying RAPD markers suitable for determining relationships between parental lines and their nearhomozygous progenies. Genetic diversity in a set of 112 rice bean germplasm collected from a wide geographical area of India and Nepal was analysed using 35 polymorphic markers sampled from azuki bean (Bajracharya et al. 2008). High level of genetic diversity was explained by the SSR markers. The genotypes were characterized for diversity indices, and the work suggested that azuki bean SSR markers could be used for assessing genetic diversity in rice bean. Three clusters were found within 112 rice bean accessions: cluster I corresponded to most of the Nepalese genotypes; cluster II consisted of the Indian genotypes; cluster III corresponded to the most diverse Nepalese genotypes and landraces from the high hills of Far West Nepal. These accessions were close to the check samples of azuki bean and Gurans, which is similar to azuki bean (Bajracharya et al. 2008).

The first comprehensive SSR analysis on a total of 472 diverse rice bean accessions (388 cultivated and 84 wild) from 16 Asian countries was reported by Tian et al. (2013). This study used 13 azuki bean SSR markers (Wang et al. 2004). The gene diversity in cultivated populations was about 83% of the wild populations. Cultivars from Vietnam, Myanmar, Nepal, and India were the most genetically

diverse. East Asian accessions, sampled from Japan, North and South Korea, China and Thailand, formed a distinct cluster. Indonesian-cultivated rice bean accessions had the most similar genetic structure to wild accessions, and thus showed high genetic divergence from other cultivated populations. In Nepalese-cultivated accessions, many accessions from western regions were quite distinct from others and formed a specific group (also reported in Bajracharya et al. 2008). These Nepalese accessions were considered as a unique gene source for rice bean breeding.

All the above studies used markers which were either random or from a species related to rice bean. Chen et al. (2016) identified a total of 3011 potential genic SSR markers from rice bean using next-generation sequencing. Initially, 300 selected SSRs were validated but the amplifiable markers showed low polymorphism. Based on 23 polymorphic SSRs, three clusters were identified within 32 Chinese rice bean germplasm (Chen et al. 2016). Wang et al. (2016) also developed and characterized a set of microsatellite markers from a SSR-enriched genomic library of rice bean. Iangrai et al. (2017) developed a set of 28 SSR markers and analysed genetic diversity in northeast Indian rice bean accessions. They reported high PIC value for SSR markers, which detected a high genetic diversity among 65 accessions.

Comparative genomic studies

Comparative studies are the basis of evolutionary and syntenic relationships between individuals. The framework for comparative studies was laid out long back by taxonomists and cytologists. Kihara (1924) and Sears (1941) while studying the plant chromosomes explained that similar group of genes are present in different species on the chromosomes. Comparative genomics allows the application of data from one species to investigate the details of particular traits or



Table 4 Mapped QTLs of important traits in rice bean

Mapping population	Туре	Trait	Markers used	Linkage groups resolved	Phenotypic variation explained by the QTL	References
V. umbellata/V. nakashimae	F ₂ (interspecific)	Resistance to azuki bean weevil (Callosobruchus chinensis) and cowpea weevil (C. maculatus)	RFLP and SSR	11	53%	Somta et al. (2006)
JP217439 (cultivar)/ JP210639 (wild form)	Back cross (BC ₁ F ₁)— intra-specific	Domestication-related leaf, pod, seed, plant architecture traits	SSR and AFLP	11	Major QTLs (explaining > 10% of phenotype varia- tion) distributed as clusters on LGs 2, 4 and 7	Isemura et al. (2010)

function of the traits in other species (Heslop-Harrison 2000). The studies on SSR cross-transferability across Vigna species have been found useful (Gupta et al. 2013; Bansal et al. 2012) and have been applied for genetic studies in rice bean (Isemura et al. 2010; Somta et al. 2006; Tian et al. 2013; Zhong et al. 2012; Wang et al. 2015). SSRs identified from EST sequences of cowpea were highly polymorphic and showed 88% transferability in other Vigna species, including rice bean (Gupta and Gopalakrishna 2010). Similarly, 50 cowpea and 95 azuki bean SSRs showed 34 and 64% cross-transferability in different Vigna species (Bansal et al. 2012). Many mung bean SSRs (1205) showed high transferability rate of 50.0, 73.3, and 81.6% with 4.1, 1.7, and 1.5% polymorphic SSRs in cowpea, adzuki bean and rice bean, respectively. The mung bean genomic SSRs were highly transferable in azuki bean and rice bean than in cowpea (Zhong et al. 2012). However, Wang et al. (2015) observed low transferability of mung bean SSRs in rice bean.

The transferability of microsatellites across species depends on the extent of genome sequence conservation. In rice bean, SSRs from azuki bean and mung bean are more transferable than cowpea. This could be because cowpea belongs to the subgenus Vigna, while azuki bean and other species such as mung bean and rice bean belong to the subgenus Ceratotropis of the genus Vigna. Thus, phylogenetically, rice bean is closer to azuki bean and mung bean than cowpea. Microsatellite transferability across species increases their utility and potentially decreases the cost of marker development. The soybean genome sequence provides an opportunity to effectively utilize gene synteny between soybean and Vigna spp. Extensive investigation into distribution and extent of paralogous genomic segments within soybean genome sequence is essential to utilize soybean sequence information in Vigna.

Linkage maps and domestication traits using comparative genomics

A first-generation linkage map was developed with 86 F_2 plant derived from an interspecific cross between azuki bean and rice bean using RFLP and RAPD markers (Kaga et al. 2000). This study reported 14 linkage groups (LGs) each containing four markers, and several loci in different LGs showed segregation distortion due to predominance of rice bean alleles. Another interspecific F_2 mapping population comprising of 74 plants was reported between V. umbellata and wild species V. nakashimae (Table 4) (Somta et al. 2006). This study used both RFLP and SSR markers for constructing the linkage map. A total of 175 DNA marker loci were mapped onto 11 LGs spanning a total length of 652 cM. Segregation distortion was observed for several markers throughout the LGs. Comparative analysis of the linkage map with that of azuki bean revealed 121 common markers on the two maps of which 114 (94.2%) were located on the same linkage groups in both maps.

The first intra-specific genetic linkage map of V. umbellata was reported by Isemura et al. (2010) in a population derived from cultivated and wild rice bean using crossspecies SSR and AFLP markers (Table 4). The authors screened a total of 528 SSR markers reported in azuki bean (Wang et al. 2004), cowpea (Li et al. 2001) and common bean (Yu et al. 2000; Gaitan-Solis et al. 2002; Blair et al. 2003; Guerra-Sanz 2004), out of which only 218 markers were found to be polymorphic between rice bean cultivars and wild forms. Altogether, 326 markers consisting of 223 SSR and 103 AFLP loci converged into 11 LGs, corresponding to n = 11 of rice bean. A high level of co-linearity in marker-order between the rice bean and azuki bean linkage map (high genomic synteny) had been observed (Figs. 5 and 6) (Isemura et al. 2010). Several large-effect QTLs for rice bean domestication-related traits such as leaf, pod and



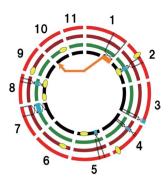


Fig. 5 Comparative linkage map of rice bean with three major Asian *Vigna* species. Numbers along the circumferential map indicate the name of the linkage group. (Fig source: https://www.gene.affrc.go.jp/pdf/misc/international-WS_14_33.pdf). Red: azuki bean (*V. angula-ris*); brown: rice bean (*V. umbellata*); green: mung bean (*V. radiata*); blue: inversion; orange: translocations; yellow: significant differences on genetic distance

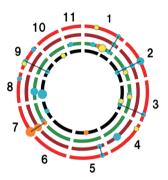


Fig. 6 Distribution of major QTLs for seed size, pod shattering and seed dormancy on a comparative map for rice bean with other *Vigna* spp. (Fig source: https://www.gene.affrc.go.jp/pdf/misc/ international-WS_14_33.pdf). *Lines*—red: azuki bean (*V. angularis*); brown: rice bean (*V. umbellata*); green: mung bean (*V. radiata*); black: black gram (*V. mungo*). *Circles*—blue: seed size; orange: seed shattering; yellow: seed dormancy. Phenotypic variation explained by the QTL_05-20%; 20-40%; ->40%

seed characteristics and plant architecture were identified on LG2, LG4 and LG7. QTLs explaining up to 17.6% of phenotypic variation for seed and pod size were found on LG2. Important QTLs for seed, pod and leaf sizes were found on LG4 between SSR markers CEDG103 and CEDG175. This region on LG4 also found to harbour other QTLs for number of branches per plant and seeds per pod. On LG7, QTLs for pod dehiscence, stem length, seed size and epicotyl length were detected. Alleles from cultivated types seemed to increase seed and pod sizes, stem thickness and days to maturity, whereas the wild allele for pale seed hilum was dominant over white hilum of the seeds of cultivated types. This study reported segregation distortion of some markers on LG11. Similar observations were also made in two other studies with interspecific crosses between rice bean x

azuki bean (Kaga et al. 2000) and rice bean x *V. nakashimae* (Somta et al. 2006).

Sources for novel genes for resistance and adaptability

Most research conducted on rice bean has focused on its high level of resistance to the major storage pest bruchid beetles (Callosobruchus spp.) (Tomooka et al. 2000; Kashiwaba et al. 2003; Somta et al. 2006). QTL analysis in an interspecific mapping population derived from rice bean and V. nakashimae led to the mapping of bruchid resistance (Somta et al. 2006). Four putative bruchid-resistant QTLs were detected with 18–60% effects on the phenotype. One putative QTL for resistance to each of these bruchid species was located on different LGs. Other putative QTLs associated with resistance to both C. chinensis and C. maculatus were localized on the linkage group 1. Likewise, QTLs for various domestication-related traits in rice bean were identified using intra-specific mapping population, as discussed earlier (Isemura et al. 2010). Resistance to mung bean yellow mosaic virus in rice bean was analysed in an interspecific F_2 mapping population from a cross between mung bean (VRM (Gg) 1) and rice bean (TNAU RED) (Sudha et al. 2013a, b). It was found that resistance is conferred by a single recessive gene. They also developed a SCAR marker that specifically amplified a 400-bp fragment in the resistant parent, TNAU RED, and not in six other species or in the resistant or the susceptible bulks of the mapping population (Sudha et al. 2013b).

Rice bean also shows tolerance to soil acidity. Mechanism for aluminium tolerance in rice bean has been attributed to the release of citric acid on exposure of roots to aluminium (Yang et al. 2006; Fan et al. 2014). Two genes for aluminium-activated citrate transporter (VuMATE1 and VuMATE2) have been cloned from rice bean (Yang et al. 2006; Liu et al. 2018) and these are found to belong to multidrug and toxic compound extrusion family (MATE). Two types of patterns for organic acid efflux have been identified in aluminium-tolerant species. In Type II response, the organic acid efflux is quick while in Type II response, it is delayed. Rice bean *VuMATEs* belong to the Type II. These two MATE genes work in a coordinated manner. Al-induced citrate secretion from the root apex occurs in two phases with VuMATE2 expressing first.

Crop improvement

Conventional breeding

The prolific growth and abundant pods in rice bean suggest that it has a high yield potential as a vegetable, grain, and



Table 5 Rice bean varieties released in India for grain and fodder

Variety	Year of release	Developed by	Yield (q/ha)	Salient feature	Recommendation zone
Grain type					
RBL-1	1987	PAU, Ludhiana	15.0	Normal duration* with high yield	Punjab and northern plains
PRR-1	1995	GBPUAT, Ranichauri	16.0	Normal duration with high yield	Uttarakhand Hills
PRR-2	1997	GBPUAT, Ranichauri	15.0	Normal duration with high yield	Northwest Hills
RBL-6	2000	PAU, Ludhiana	15.0	Early type	Northern plains
RBL-50	2003	PAU, Ludhiana	15.5	Normal duration, high yield	Northern plains
RBL-35	2003	PAU, Ludhiana	15.0	Normal duration with green colour grain	Northern plains
BRS-1	2003	ICAR-NBPGR, Bhowali	17.0	Normal duration, black seed	Northwest Hills
Him Shakti (VRB-3)	2013	ICAR-VPKAS, Almora and ICAR-NBPGR, Shimla	17.1	Normal duration, light green seed	Northeast and Northwest Hill
Fodder type					
Konkan rice bean 1	1997	BSKKV, Dapoli	220.0	High fodder yield	Konkan region
Bidhan rice bean 1	2000	BCKV, West Bengal	350.0	High fodder yield, insect resistant	East and Northeast zone
Bidhan rice bean 2	2005	BCKV, West Bengal	300.0	High fodder yield, insect resistant	East and Northeast zone
Suravi	2013	KAU, Thrissur	220.0	High fodder yield	Kerala
Bidhan rice bean 3	2015	BCKV, West Bengal	350.0	High fodder yield, insect resistant	East and Northeast zone

^{*}Normal duration is 135-145 days

forage crop (Smartt 1991). Except for bruchid resistance, traits related to other biotic stress tolerance such as yellow mosaic virus, Cercospora leaf spot and bacterial leaf spot (Arora et al. 1980; Pandiyan et al. 2008) remain largely unexploited. There is no specific report on pre-breeding. Iangrai et al. (2017) reported a core collection developed from north east Indian genotypes which was later grouped into some qualitative classes (Pattanayak et al. 2018). Higher productivity and other economically important traits such as pod number and seed weight have been introgressed from rice bean to black gram (Singh et al. 2013). The study reported yield enhancement up to 50.31% along with resistance to mung bean yellow mosaic virus, Cercospora and bacterial leaf spots. Pandiyan et al. (2010) successfully transferred traits such as a higher number of branches per plant and pod clusters per plant from rice bean to mung bean. An attempt was made to transfer useful traits from rice bean to mung bean by developing tetraploid interspecific hybrids from sterile F_1 hybrids (Chaisan et al. 2013). The fertile tetraploid produced artificially may have a potential for improving V. reflexo-pilosa var. glabra (V. glabrescens), the only domesticated Asian *Vigna* that is tetraploid.

Genetic studies in rice bean indicated that additive genetic components played a major role in the inheritance of size of primary leaves, seedling height, plant height, days of flower, number of pods, seeds per plant and seed size (Chatterjee and Dana 1977; Gupta et al. 2009). These characters showed high heritability. Dominance components influenced green forage and dry matter yield, number of branches/plants, pod size and seed yield. All these characters showed medium to low heritability (Chatterjee and Dana 1977). Das and Dana (1981) in a partial diallele analysis involving seven homozygous lines reported that late maturing parents were good general combiners for seed yield/plant. Das and Dana (1980, 1981) also reported that seedling stem colour, pigmentation in flower bud, flower colour, days to flower, hilum ring colour, seed coast colour and pod colour genes were monogenically inherited.

Almost all available reports of variety release are from India. All India Coordinated Research Project on Potential Crops (AICRP on PC) spearheads the multilocation testing and recommendation of new varieties of rice bean. In addition, the state variety release committees also identify and recommend varieties for their states. Varieties released so far for cultivation in India are listed in Table 5. These include both grain and fodder types. Apart from released varieties, several superior germplasms were identified from the collections of northeast India. Among these, RCRB 1–6 (1.5 m height, 142 days duration and 26.32 q/ha potential yield) identified by ICAR Research Complex for NEH



Region, Meghalaya, is popular among farmers for its grainand fodder-yielding ability (Borthakur et al. 2001). Ten promising lines were also identified by Assam Agricultural University, Assam (Bepary et al. 2017), for plain areas of northeast India. Bold-seeded (length/breadth ratio is low) varieties are uncommon in India. The only bold-seeded genotype identified so far for cultivation is PCPGR 8404 (Khulbe and Panwar 2014). Variety release information from other countries is currently not available. One report (Iqbal et al. 1998) mentions about a fodder rice bean variety P.I. 2154 in Pakistan. It appears from the available literature that although several characterization studies have been done in rice bean, there is hardly any effort on pre-breeding and intraspecies hybridization. The advantage of its outcrossing nature has not been exploited.

Interspecific hybridization

The most common approach for increasing the genetic base of the crop is pre-breeding, which involves the utilization of different genetic pools of the crop through interspecific hybridization or advanced biotechnological tools. Besides widening of genetic base, interspecific hybridization also helps in introgression of traits in the related species. Based on crossability, hybrid fertility and chromosome pairing, Dana and Karmakar (1990) proposed two genome groups for Vigna species. AA genome group with Vigna aconitifolia, V. radiata, V. mungo, and V. trilobata, while A1A1 group with *V. angularis* and *V. umbellata*. This grouping indicates difficulties in hybridization among species of two groups. To overcome pre- and post-fertilization barriers, various methods such as the reciprocal cross in V. radiata x V. umbellata (Kaur and Satija 1998), use of immunosuppressant and mentor pollen in V. mungo x V. umbellata (Chen et al. 1978), embryo rescue technique in V. mungo x V. umbellata (Biswas and Dana 1975; Chen et al. 1983; Ahn 1977) and V. umbellata x V. angularis (Chen et al. 1983) have been used. In most of the reports, V. radiata and V. mungo have been reported as the most satisfactory seed parents as they cross reciprocally with V. umbellata, while V. umbellata is crosscompatible with V angularis as a seed parent only (Smartt 1990). A few successful reports of hybridization between rice bean and other Vigna species are available as on date. In most cases, efforts were directed to introgress the resistance genes and yield components from rice bean into Vigna mungo and Vigna radiata (Dar et al. 1991; Verma and Brar 1996; Singh et al. 2003; Pal et al. 2005; Pandiyan et al. 2010; Chaisan et al. 2013; Singh et al. 2013; Basavaraja et al. 2018).



Rice bean can be grown under diverse climatic conditions from hot and humid to somewhat cool conditions at temperatures ranging from 20 to 35 °C and from sea level up to at an altitude of 1500 m also (Lohani 1980). Usually, rice bean is sown during May–June although it can be planted in August for seed production only. In winter, the plants remain very dwarf and show stress flowering with small pod size (personal study, unpublished). Rice bean can be grown in different types of soils such as loam, sandy loam, clay, black and laterite soils compared to other pulses it shows more field tolerance to acid soils (Sarma et al. 1995). However, it is unsuitable for alkaline soil and marshy lands. In very loose soil, it is severely attacked by root nematodes.

Seed rate varies from 25 to 30 kg/ha. Rice bean is usually grown in less fertile soil (Khadka and Acharya 2009). However, application of 20 kg N, 40-60 kg P₂O₅ and 20-30 kg K₂O is recommended by several states in India (https://www. apnikheti.com/en/pn/ agriculture/crops/pulses/rice bean accessed on 25.03.2019). In a study carried out in Pakistan, application of 40 kg N/ha and 60 kg P/ha was reported to increase the number of pods/plants, 1000 seed weight and grain yield (Iqbal et al. 1998). Application of farm yard manure @2.0t/ha has also been recommended (Anonymous 2008). In acid soils, application of lime @ 0.4-0.6 t// ha has been reported to increase harvest index, seed yield, protein content in grain and root nodule formation (Kumar et al. 2014). Sowing method varies from broadcasting to dibbling to line sowing. Usually, dry seed is sown. Priming with water or phosphorous has been reported to improve seed yield (Kumar 2010). Row to row spacing of 30 cm and plant to plant spacing of 10-12 cm is recommended.

A single weeding in sole crop after 30 days of sowing is considered enough and economic as the crop shows luxurious growth after that. Harvesting is done when the pods change colour towards brown (Sarma et al. 1995). As cultivated rice bean is moderately indeterminate, harvesting is done in 2–3 pickings preferably in the morning to avoid pod shattering. Grains are separated from pods by manual beating after sun drying of pods.

Although rice bean has been reported to be relatively disease free (Arora et al. 1980), it is attacked by several diseases and pests (Sarma et al. 1995). Major diseases of rice bean are rust (*Uromyces spp.*) that generally appears on leaves; powdery mildew (*Oldiopsi taurica* (Lev.) Salman) which appears on leaves, stems and pods; *Rhizoctonia* blight (*Rhizoctonia solani*) and *Cercospora* leaf spot (*Cercospora spp.*) all of which appear on leaves. Among the insect pests, pod borer (*Helicoverpa armigera*) and soybean hairy caterpillar (*Spilarctia casignata*) attack rice bean. However, the most serious insect pest of rice bean is banded blister beetles



Table 6 Promising rice bean genotypes identified for India under FOSRIN

Type	States						
	Assam	Himachal Pradesh	Madhya Pradesh	Gujarat			
Grain—Rainy season	JCR-07-07	RBHP—38	RBL—6				
	JCR-08-50	RBHP—41	RBHP—38				
	JCR—55	BRS—II	BRS—II				
Grain—Pre-winter season	JCR-08-16			BRS—II			
	JCR-08-17			PRR—1			
	JCR-08-27						
	JCR-08-42						
Fodder	JR—1	RBHP—38	RBL—6				
	JCR-08-49	RBHP—14	RBHP—38				
	JCR-08-50	JR—1	BRS—II				
			JR—1				
			JCR0849				
			JCR0850				

(*Mylabris pustulata*), which severely damage rice bean flowers. Although manual control is recommended, insecticide spraying on field bunds during noon on a sunny day has been reported to be very effective (Anonymous 1993).

International research efforts for crop promotion and improvement

'Food Security through Rice bean Research in India and Nepal' (FOSRIN—http://www.ricebean.org/), a consortium project of eight partners from Europe to South Asia worked together to promote and popularize the underutilized grain legume crop, rice bean in India and Nepal. The project was funded by European Commission under its International Cooperation Programme. In the project, work was done in field sites in villages in several areas of India and Nepal. The major research components of the project were

- Supply chain, consumer demand and marketing;
- germplasm characterisation and adaptation;
- assessment of genetic diversity;
- nutrition and health.

Under the first objective, hedonic demand function and consumer preference index were developed to assist breeders in the selection of desired varieties with respect to quality characteristics that are relevant to consumers (Buergelt et al. 2010a, b). According to these indices, seed size, crude fibre, protein and fat content were found to be the desirable characteristics significantly influencing the price of rice bean. The major activity of the project was germplasm collection and characterization. Collection and evaluation of large germplasm accessions of rice bean from various locations in India and Nepal identified high-yielding genotypes.

Outcrossing, to some extent, in rice bean in the evaluation results indicated significant practical applications, including ease in breeding. The large range of crop diversity in both countries suggested great potential for improving the crop for a number of traits desired by farmers. It was suggested in the project report that there is a need to accurately catalogue the existing germplasm and make it available to plant breeders for the benefit of farmers. Genetic diversity was also studied using adzuki bean SSRs on germplasm collections of both the countries.

Through participatory varietal selection, assessment was done for traits preferred by farmers in both the countries. Based on the assessment, wide-adapted, better performing and farmer-preferred genotypes were identified (Table 6). In Nepal, landrace Seto Thulo (white, bold) was preferred while in India, all three preferred genotypes were bold seeded. The seeds of identified genotypes were multiplied and distributed to farmers. The farmers' field trials indicated clear preference for bold seeds, determinate growth habit, early to medium maturity, drought tolerance, low shattering and a plant type suited for inter or mixed crop with maize, sorghum or on terrace risers. Being a good source of high-quality protein with favourable amino acid profile and several minerals, the germplasm was profiled for nutrient content and its contribution to value-added products was assessed under the project. Efforts were made to make greater use of rice bean in improving nutrition of local populations.

Challenges and opportunities

There is a significant untapped potential for genetic improvements in rice bean, which can contribute towards sustainability of food production by providing nutritious seeds and fix symbiotic nitrogen. Rice bean has been cultivated by



indigenous communities and is an important protein source, particularly in niche areas of Asia. The crop also provides the option of growing legumes in less fertile lands and arid zones where other major legumes fail to grow. In Vigna species, bruchid and yellow vein mosaic virus are devastating pest and disease, respectively. Rice bean is the potential source of resistance to both the biotic stresses. A new gene encoding Bowman-Birk type protease inhibitor was also isolated from rice bean (Katoch et al. 2014). Besides, rice bean has a high yield potential owing to more pods per plant, pod length, number of seeds per pod, etc. in comparison to other Vigna species. However, asynchronous maturity, seed shattering, lack of ideal plant type and poor market make it unsuitable for cultivation over large areas on a commercial scale. The other undesirable feature of rice bean such as difficulty in splitting, beany flavour on cooking and high flatulence restricts its cultivation to limited areas. Conversely, excellent yield components and stress resistance make rice bean a source of useful genes for improvement of other Vigna species. The research on genetic improvement of rice bean is almost negligible and needs thorough investigations of germplasm collections initially for desirable traits based on consumers' preference. The focus on the development of varieties in the crop should not only be on agronomic attributes but also on taste and cooking as well as processing qualities. An interesting observation was made in the FOSRIN project regarding farmer preference for seed type. Contrary to the previous understanding that small-seeded genotypes are preferred in India, all genotypes liked by the farmers were bold seeded. Enhancing bio-availability of nutritional compounds by minimizing anti-nutritional compounds such as phytate and reduction of flatulence causing oligosaccharides should be looked upon on priority. Value addition of rice bean could pave the way for the development of nutritionally rich healthy foods. Comparative genomic efforts to date are insufficient and deep functional genomic studies or whole genome sequencing of rice bean is needed. The recently deciphered genome sequence of closely related species, azuki bean could help dissect the important economic traits of rice bean. Rice bean, as a traditional crop, has been selected over centuries to meet the challenges of climate and local requirement. Characterization data generated from collections made at different times may throw light on the direction of selection by farmers to make the crop climate resilient. This information may help in the breeding of other highly commercialized pulses. As rice bean is a climate-resilient crop and can thrive even in degraded soil, it needs to be tested in other parts of the tropical world where climate change mitigation is posing a serious challenge to agriculture and animal husbandry.

Way forward

Large genetic diversity has an advantage in crop breeding for the improvement of rice bean. However, accurate characterization of germplasm resources, identification of trait donors and development of mapping populations is the first priority in rice bean improvement. A number of genotypes possessing desirable traits such as earliness, high branching with higher number of pods, both bold and relatively fine grains, high seed yield and resistance to biotic stresses are available in the gene pool across collections. If these genotypes are combined together in a breeding programme, it will not only lead to improved genotypes but will also result in the development of lines for mapping of various traits. Utilization of comparative genomics for the elucidation of genetics of resistance and important agronomical characters of the crop could pave the way for the identification of genes/QTLs. Efforts at international level could help decipher the genome of rice bean, which will facilitate the identification of genes of agronomic importance and accelerate the improvement of rice bean. Transcriptome and proteome studies can further validate the sequencing results at the functional level. Research also needs to be oriented on adaptability trials, nutrient-rich value-added products, reduction of anti-nutritional compounds, consumer preference and market drivers for commercial cultivation of the crop at international level. Renewed research efforts, particularly employing next-generation genomic and phenomic technologies will help turn this orphan crop into a major pulse legume of the world. In recent years, 'Neo Domestication' (Tomooka et al. 2014) or the domestication of stress-tolerant wild species that cannot be crossed with crop species has been proposed. This process could be achieved by mutation breeding and screening of mutants through conventional and genomic tools such as TILL-ING (Takahashi et al. 2016). Recently, genome editing has been reported as an efficient tool for de novo domestication of tomato (Zsögon et al. 2018). Rice bean with many intermediate accessions is a potential candidate for this. Andersen (2012) made some very important observations, which in our opinion provide a much focused direction for rice bean improvement. His views that rice bean improvement should focus on reducing seed variability, determinate growth and improved yield with good organoleptic and cooking qualities appear to be most valid options to improve the agronomic and economic value of this crop. His suggestion that "conservation of agro-biodiversity cannot be a responsibility of poor farmers if they can find better alternatives, so the general task of genetic conservation should be left to national and global organizations



through off-farm strategies" best suits for rice bean, a crop that is struggling to get its deserving attention.

Author contribution statement AP, SR and SS prepared the overall design, contributed to introduction, germplasm collection, conservation, genomics and breeding portions, international efforts, challenges, the way forward, figure preparation and editing, and final compilation. BI and AP contributed to introduction, origin, taxonomy and nutritional aspects, and germplasm photographs. AB contributed to genomics and breeding portions, and figure preparation. SG contributed the interspecific hybridization and genetic and genomic resources portion. DCJ contributed to overall concept and design of the article, challenges, the way forward and final editing. All authors checked the final version and agreed to it.

Acknowledgements The authors are grateful to the Directors of all ICAR institutes for allowing to work in this review writing project. The authors are also appreciative of Consortium for e-Resources in Agriculture (CeRA) of ICAR through which all literature works cited here were accessed directly or indirectly. AP acknowledges funding support from ICAR through NATP for the collection and evaluation of germplasm. The authors are thankful as well to Charu Chandra Joshi of ICAR-Vivekananda Parvatiya Krishi Anusandhan Sansthan, Almora, for secretarial assistance. The authors are also obliged to the two anonymous reviewers and the guest editor for their critical and constructive comments.

References

- Ahn CS (1977) Interspecific hybridization among four species of the genus *Vigna savi*. Dissertation, Hawaii University, Honolulu, IISA
- Andersen P (2007) Food security through ricebean research in India and Nepal (FOSRIN). Report 3. In: Hollington PA (ed) Nutritional qualities of ricebean. Department of Geography, Universitet Bergen; CAZS Natural Resources, College of Natural Sciences, Bangor University, Bergen, Norway; Bangor, Wales, UK. Available from http://www.ricebean.org/publication.htm
- Andersen P (2012) Challenges for under-utilized crops illustrated by ricebean (Vigna umbellata) in India and Nepal. Int J Agric Sustain 10:164–174
- Anonymous (1993) Annual report, 1990. ICAR Research Complex for NEH Region, Barapani, p 180
- Anonymous (2008) Manual on agricultural production technology, Kharif 2008. Directorate of agriculture and food production, Bhubeneswar, pp 29–30
- Arora RK, Chandel PS, Joshi BS, Pant KC (1980) Rice bean: tribal pulse of Eastern India. Eco Bot 34:260–263
- Bajaj M (2014) Nutrients and antinutrients in rice bean (Vigna umbellata) varieties as effected by soaking and pressure cooking. Asian J Dairy Food Res 33:71–74. https://doi.org/10.5958/j.0976-0563.33.1.015
- Bajracharya J, Singh S, Dangol B, Hollington PA, Witcombe JR (2008) Food security through ricebean research in India and Nepal (FOSRIN). Report 2. Identification of polymorphic markers.

- Agriculture Botany Division, Nepal Agriculture Research Council; CAZS Natural Resources, College of Natural Sciences, Bangor University, Khumaltar, Nepa; Bangor, Wales, UK. http://www.ricebean.org/deliverables/deliverable%202%20-%20polymorphic%20markers.pdf
- Bansal R, Gupta SK, Gopalakrishna T (2012) Transferability of cowpea and azuki bean derived SSR markers to other Vigna species. J Food Legume 25:273–278
- Basavaraja T, Murthy N, Kumar LV, Mallikarjun K (2018) Studies on cross compatibility in interspecific crosses of Vigna radiata×Vigna umbellata species. Legume Res. https://doi.org/10.18805/lr-3974
- Bepary RH, Wadiker DD, Neog SB, Patki PE (2017) Studies on physico-chemical and cooking characteristics of rice bean varieties grown in NE region of India. J Food Sci Technol 54:973–986
- Bisht IS, Singh M (2013) Asian Vigna. In: Singh M, Upadhayay HD, Bisht IS (eds) Genetic and genomic resources of grain legume improvement. Elsevier, Amsterdam, pp 237–267
- Bisht IS, Bhat KV, Lakhanpaul S, Latha M, Jayan PK, Biswas BK, Singh AK (2005) Diversity and genetic resources of wild Vigna species in India. Genet Resour Crop Evol 52:53–68
- Biswas MR, Dana S (1975) Black gram×rice bean cross. Cytologia 40:787–795
- Blair MW, Pedraza F, Buendia HF et al (2003) Development of a genome- wide anchored microsatellite map for common bean (Phaseolus vulgaris L.). Theor Appl Genet 107:1362–1374
- Borthakur M, Sarma BK, Annadurai A, Verma DK (2001) Performance of rice bean genotypes (*Vigna umbellata*) in mid-altitude conditions of Meghalaya. Indian J Hill Farmg 14:150–152
- Buergelt D, Mueller RAE, Von Oppen M (2010a) Food Security through Ricebean Research in India and Nepal (FOSRIN) Report 9. Consumer preference index for ricebean. Christian Albrechts University; Centre for Advanced Research in International Agricultural Development (CARIAD), Bongor University, Kiel, Germany; Bangor, Wales, UK
- Buergelt D, Mueller RAE, Yadavendra JP, Von Oppen M (2010b) Food Security through Ricebean Research in India and Nepal (FOS-RIN) Report 8. Hedonic price function for ricebean. Christian Albrechts University; Centre for Advanced Research in International Agricultural Development (CARIAD), Bongor University, Kiel, Germany; Bangor, Wales, UK
- Burkill IH (1953) The hooker lecture. Proc Linn Soc Lond 164:12. https://doi.org/10.1111/j.1095-8312.1953.tb00664.x
- Chaisan T, Somta P, Srinives P, Chanprame S, Kaveeta R, Dumrongkittikule S (2013) Development of tetraploid plants from an interspecific hybrid between mungbean (*Vigna radiata*) and rice bean (*Vigna umbellata*). J Crop Sci Biotechnol 16:45–51
- Chandel KPS, Joshi BS, Arora RK, Pant KC (1978) Rice bean—a new pulse with high potential. Indian Farming 18:19–22
- Chatterjee BN, Dana S (1977) Rice bean (*Vigna umbellata* (Thunb) Ohwi and Ohashi). Trop Grain Legume Bull 10:22–25
- Chen NC, Parrot JF, Jacobs J, Baker LR, Carlson PS (1978) Interspecific hybridization of food legumes by unconventional methods of plant breeding. International mungbean symposium, 1977. Asian Vegetable Research and Development Centre, Shanhua, pp 247–252
- Chen NC, Baker RL, Honma S (1983) Interspecific crossability among four species of *Vigna* food legumes. Euphytica 32:925–937
- Chen H, Chen X, Tian J, Yang Y, Liu Z, Hao X, Wang L, Wang S, Liang J, Zhang L, Yin F, Cheng X (2016) Development of genebased SSR markers in rice bean (*Vigna umbellata* L.) based on transcriptome data. PLOS One 11(3):e0151040
- Dana S, Karmakar PG (1990) Species relation in *Vigna* subgenus *Ceratotropis* and its implications in breeding. Plant Breed Rev 8:19–42



- Dar GM, Verma MM, Gosal SS, Brar JS (1991) Characterization of some interspecific hybrids and amphiploids in *Vigna*. In: Sharma B, Mehra RB (eds) Golden jubilee celebration symposium on grain legumes. Indian Society of Genetics and Plant Breeding, New Delhi, pp 73–78
- Das ND, Dana S (1980) Linkage in rice bean. Indian J Genet Plant Breed 40:105–116
- Das ND, Dana S (1981) Genetics of some qualitative characters in rice bean. Indian J Genet Plant Breed 41:401–405
- de Carvalho NM, Vieria RD (1996) Rice bean [Vigna umbellata (Thunb) Ohwi and Ohashi]. In: Nkowolo E, Smart J (eds) Legumes and oilseeds in nutrition. Chapman & Hall, London, pp 222–228
- Doi K, Kaga A, Tomooka N, Vaughan DA (2002) Molecular phylogeny of genus *Vigna* subgenus *Ceratotropis* based on rDNA ITS and atpB-rbcL intergenic spacer for cpDNA sequences. Genetica 114:129–145
- Duke JA (1981) Handbook of legumes of world economic importance. Plenum Press, New York, p 345
- Eyzaguirre P, Padulosi S, Hodgkin T (1999) IPGRI's strategy for neglected and underutilized species and the human dimension of agrobiodiversity. In: Padulosi S (ed) Priority setting for underutilized and neglected plant species of the Mediterranean region. Report of the IPGRI conference proceedings. ICARDA, Aleppo
- Fan W, Lou HQ, Gong YL, Liu MY, Wang ZQ, Yang JL, Zheng SJ (2014) Identification of early al-responsive genes in rice bean (Vigna umbellata) roots provides new clues to molecular mechanisms of Al toxicity and tolerance. Plant Cell Env 37:1586–1597
- FAO (1982) Legumes in human nutrition. FAO, Rome
- Fatokun CA, Danish D, Young ND (1993a) Molecular taxonomic relationships in the genus Vigna based on RFLP analysis. Theor Appl Genet 86:97–104
- Fatokun CA, Danish D, Young ND, Stewart EL (1993b) Molecular taxonomic relationships in subgenus *Ceratotropis* (genus Vigna) as revealed by RAPD analysis. Euphytica 88:17–24
- Gaitan-Solis E, Duque MC, Edwards KJ, Tohme J (2002) Microsatellite repeats in common bean (Phaseolus vulgaris): isolation, characterization, and cross- species amplification in Phaseolus ssp. Crop Sci 42:2128–2136
- Gautam R, Kumar N, Yadavendra JP, Neog SB, Thakur S, Khanal A, Bhandari B, Joshi KD, Hollington PA (2007) Distribution of rice bean in India and Nepal. Project Report 1, Food Security through Rice bean Research in India and Nepal. European Commission 6th Framework Programme, Project no. 032055
- Gopinathan MC, Babu CR, Chatterjee SR, Abrol YP (1987) Nutritional potential of *Vigna minima* (Roxb.) Ohwi and Ohashi: I seed protein content and amino acid composition. Plant Food Human Nutr 36:345–355
- Gruére G, Guilani A, Smale M (2006) Marketing underutilized plant species for the benefit of the poor: a conceptual framework. EPT discussion paper. IFPRI, Washington
- Guerra-Sanz JM (2004) New SSR markers of *Phaseolus vulgaris* from sequence databases. Plant Breed 123:87–89
- Gupta SK, Gopalakrishna T (2010) Development of unigene-derived SSR markers in cowpea (*Vigna unguiculata*) and their transferability to other *Vigna* species. Genome 53:508–523
- Gupta S, Kozak M, Sahay G, Durrai AA, Mitra J, Verma MR, Pattanayak A, Thongbam PD, Das A (2009) Genetic parameters of selection and stability and identification of divergent parents for hybridization in rice bean (*Vigna umbellata* Thunb, (Ohwi and Ohashi)) in India. J Agric Sci 147:581–588
- Gupta S, Gupta DS, Anjum T, Pratap A, Kumar J (2013) Transferability of simple sequence repeat markers in black gram (Vigna mungo L. Hepper). Aust J Crop Sci 7:345–353

- Heslop-Harrison JS (2000) Comparative genome organization in plants: from sequence and markers to chromatin and chromosomes. Plant Cell 12:617–635
- Iangrai B, Pattanayak A, Khongwir DEA, Pale G, Gatphoh EM, Das A, Chrungoo NK (2017) Development and characterization of a new set of genomic microsatellite markers in rice bean (Vigna umbellata (Thunb.) Ohwi and Ohashi) and their utilization in genetic diversity analysis of collections from North East India. PLoS One 12:e0179801. https://doi.org/10.1371/journal.pone.0179801
- Iqbal K, Tanveer A, Ali A, Ayub M, Tahir M (1998) Growth and yield response of rice bean (Vigna umbellata) fodder to different levels of N and P. Pakistan J Biol Sci 1:212–214
- Isemura T, Kaga A, Tomooka N, Shimizu T, Vaughan DA (2010) The genetics of domestication of rice bean, *Vigna umbellata*. Ann Bot 106:927–944. https://doi.org/10.1093/aob/mcq188
- Jaaska V, Jaaska V (1990) Isozyme variation in Asian beans. Bot Acta 103:281–290
- Javadi F, Tun YT, Kawase M, Guan K, Yamaguchi H (2011) Molecular phylogeny of the subgenus Ceratotropis (genus Vigna, Leguminosae) reveals three eco-geographical groups and Late Pliocene-Pleistocene diversification: evidence from four plastid DNA region sequences. Ann Bot 108:367–380
- Jayasundara S (2015) Harvest index of three grain legume crops grown in Canada, calculated by two approaches. https://www.researchgate.net/post/How_is_harvest_index_estimated_especially_in_indeterminate_pulses. Accessed 23 April 2019
- Kaga A, Ishii T, Tsukimoto K, Tokoro E, Kamijima O (2000) Comparative molecular mapping in Ceratotropis species using an interspecific cross between azuki bean (Vigna angularis) and rice bean (V. umbellata). Theor Appl Genet 100:207–213
- Kajiwara H, Tomooka N (1998) Comparative analysis of genus Vigna seeds using antiserum against synthesized multiple antigenic peptide. Electrophoresis 19:3110–3113
- Kashiwaba K, Tomooka N, Kaga A, Han OK, Vaughan DA (2003) Characterization of resistance to three bruchid species (*Callosobruchus* spp., Coleoptera, Bruchidae) in cultivated rice bean (*Vigna umbellata*). J Econ Entomol 96:207–213
- Katoch R (2013) Nutritional potential of rice bean (*Vigna umbellata*): an underutilized legume. J Food Sci 78:C8–C16
- Katoch R, Singh SK, Thakur N, Dutt S, Yadav SK, Shukle R (2014) Cloning, characterization, expression analysis and inhibition studies of a novel gene encoding Bowman-type protease inhibitor from rice bean. Gene 546:342–351
- Kaur D, Kapoor AC (1992) Nutrient composition and antinutritional factors of rice bean (Vigna umbellata). Food Chem 43:119–124
- Kaur M, Kawatra BL (2000) Effect of domestic processing on flatus producing factors in rice bean (Vigna umbellata). Nahrung 44:447–450
- Kaur R, Satija CK (1998) Study of incompatibility barriers between interspecific hybrids of Vigna radiata x V. uumbellat. Crop Improv 23:213–216
- Khadka K, Acharya BD (2009) Cultivation practices of ricebean. Local initiatives for biodiversity. Research and Development (LI-BIRD), Pokhara, p p28
- Khulbe RK, Panwar RK (2014) Large seeded rice bean accession from Garhwal region of Uttarakhand, India. Int J Basic Appl Agric Res 12:458–459
- Kihara H (1924) Zytologische und genetische Studien bei wichtigen Getreidearten mit besonderer Rücksicht auf das Verhalten der Chromosomen und die Sterilität in den Bastarden. Mem Coll Sci Kyoto Imp Univ B 1–200
- Kumar N (2010) Effect of P priming on the yield of rice bean intercropped with maize. Conference proceeding. http://ricebean.org/ publication.htm Accessed on 25 Aug 2018
- Kumar R, Chatterjee D, Kumawat N, Pandey A, Roy A, Kumar M (2014) Productivity, quality and soil health as influenced by lime



in ricebean cultivars in foothills of northeastern India. Crop J 2:338–344

- Li CD, Fatokun CA, Ubi B, Singh BB, Scoles GJ (2001) Determining genetic similarities and relationships among cowpea breeding lines and cultivars by microsatellite markers. Crop Sci 41:189–197
- Liu MY, Lou HQ, Chen WW et al (2018) Two citrate transporters coordinately regulate citrate secretion from rice bean root tip under aluminum stress. Plant Cell Environ 41:809–822. https://doi.org/10.1111/pce.13150
- Lohani SN (1980) Agricultural crops of Nepal. In: Lohani D, Chabahil M (eds) Agricultural crops of Nepal. Nepal, Kathmandu, pp 282–285
- Mal B (1994) Underutilized grain legumes and pseudocereals. Their potential in Asia. RAPA/FAO report no. 14, Bangkok
- Malhotra S, Malik D, Singh K (1988) Proximate composition and antinutritional factors in rice bean (*Vigna umbellata*). Plant Food Hum Nutr 38:75–81
- Mohan VR, Janardhanan K (1994) Chemical composition and nutritional evaluation of raw seeds of six ricebean varieties. J Indian Bot Soc 73:259–263
- Muthusamy S, Kanagarajan S, Ponnusamy S (2008) Efficiency of RAPD and ISSR markers system in accessing genetic variation of rice bean (*Vigna umbellata*) landraces. Electronic J Biotechnol, 11(3). https://doi.org/10.2225/vol11-issue3-fulltext-8. http://www.ejbiotechnology.cl/content/vol11/issue3/full/8/index.html
- Noda A (1951) Studies on native (primitive) varieties of crop plant: observations on a climbing variety of adzuki bean native to San'in district, Japan (1). Japan J Crop Sci 21:134–135 (in Japanese with English summary)
- Pal SS, Sandhu JS, Singh I (2005) Exploitation of genetic variability in interspecific cross between *Vigna mungo* × *V. umbellata*. Indian J Pulses Res 18:9–11
- Pandiyan M, Ramamoorthi N, Ganesh SK, Jebraj S, Pagarajan P, Balasubramanian P (2008) Broadening the genetic base and introgression of MYMY resistance and yield improvement through unexplored genes from wild relatives in mungbean. Plant Mut Rep 2:33–38
- Pandiyan M, Senthil N, Ramamoorthi N, Muthiah AR, Tomooka N, Duncan V, Jayaraj T (2010) Interspecific hybridization of *Vigna radiata* x 13 wild *Vigna* species for developing MYMV donor. Electron J Plant Breed 1:600–610
- Pattanayak A, Ingrai B, Khongwir DEA, Gatpoh EM, Das A, Chrungoo NK (2018) Diversity analysis of rice bean (*Vigna umbellata* (Thunb.) Ohwi and Ohashi)) collections from North Eastern India using morpho-agronomic traits. Sci Hort 242:170–180
- Rajerison R (2006) *Vigna umbellata* (Thunb.) Ohwi & Ohashi. In: Brink M, Belay G (eds) Cereals and pulses. PROTA1, Wageningen, Pays Bas, Netherlands
- Rodriguez MS, Mendoza EMT (1991) Nutritional assessment of seed protein in ricebean [Vigna umbellata (Thunb) Ohwi and Ohashi]. Plant Food Hum Nutr 41:1–9
- Saharan K, Kheterpaul N, Bishnoi S (2002) Anti-nutrients and protein digestibility of faba bean and rice bean as affected by soaking, dehulling and germination. J Food Sci Technol 39:418–422
- Saikia P, Sarkar CR, Borua I (1999) Chemical composition, antinutritional factors and effect of cooking on nutritional quality of rice bean [Vigna umbellata (Thunb) Ohwi and Ohashi]. Food Chem 67:347–352
- Sarma BK, Singh M, Pattanayak A (1991) Evaluation of ricebean (*Vigna umbellata*) germplasm in upland terraces of Meghalaya. Indian J Agril Sci 61:182–184
- Sarma BK, Singh M, Gupta HS, Singh G, Srivastava LS (1995) Studies in rice bean germplasm: research bulletin No. 34. ICAR Research Complex for NEH Region, Barapani Meghalaya, India, pp 35

Sears ER (1941) Chromosome pairing and fertility in hybrids and amphidiploids in the Triticinae. Mo Agri Exp Stn Res Bull 337:1–20

- Seehalak W, Tomooka N, Waranyuwat A, Thipyapong P, Laosuwan P, Kaga A et al (2006) Genetic diversity of the *Vigna* germplasm from Thailand and neighbouring regions revealed by AFLP analysis. Genet Resour Crop Evol 53:1043–1059
- Shafiqul I, Dutta M, Shachi S, Kumar P, Bhatt KV (2017) Assessment of genetic diversity of ricebean [(Vigna umbellata) (Thunb.) Ohwi & Ohashi)] varieties and their narrow leaf cross derivatives using RAPD markers. Int J Agric Env Biotechnol 10:415–421
- Singh KP, Monika Sareen PK, Kumar A (2003) Interspecific hybridization studies in *Vigna radiata* L. Wilczek and *Vigna umbellata* L. National J Pl Improv 5:16–18
- Singh M, Bisht IS, Sardana S, Gautam NK, Hussain Z, Gupta S et al (2006) Asiatic Vigna. In: Dhillon BS, Saxena S, Agrawal A, Tyagi RK (eds) Plant genetic resources: food genetic resources. Narosa Publishing House Pvt Ltd, New Delhi, pp 275–301
- Singh I, Sandhu JS, Gupta SK, Singh S (2013) Introgression of productivity and other desirable traits from rice bean (*Vigna umbellata*) into black gram (*Vigna mungo*). Plant Breed 132:401–406
- Smartt J (1990) Grain legumes: evolution and genetic resources. Cambridge University Press, Cambridge
- Smartt J (1991) Grain legumes: evolution and genetic resources. Cambridge University Press, Cambridge, pp 140–175
- Somta P, Kaga A, Tomooka N et al (2006) Development of an interspecific Vigna linkage map between Vigna umbellata (Thunb) Ohwi & Ohashi and V nakashimae (Ohwi) Ohwi & Ohashi and its use in analysis of bruchid resistance and comparative genomics. Plant Breed 125:77–84
- Sudha M, Anusuya P, Ganesh NM, Karthikeyan A, Nagarajan P, Raveendran M, Senthil N, Pandiyan M, Angappan K, Balasubramanian P (2013a) Molecular studies on mungbean (Vigna radiata (L.) Wilczek) and rice bean (Vigna umbellata (Thunb.) interspecific hybridization for Mungbean yellow mosaic virus resistance and development of species-specific SCAR marker for ricebean. Arch Phytopathol Plant Prot 46:503–517
- Sudha M, Karthikeyan A, Anusuya P, Ganesh NM, Pandiyan M, Senthil N, Raveendran M, Nagarajan P, Angappan K (2013b) Inheritance of resistance to Mungbean yellow mosaic virus (MYMV) in inter and intra specific crosses of mungbean (Vigna radiata). Am J Plant Sci 4:1924–1927
- Takahashi Y, Somta P, Muto C, Iseki K, Naito K et al (2016) Novel genetic resources in the genus Vigna unveiled from gene bank accessions. PLoS One 11:e0147568
- Thakur S, Bhardwaj N, Chahota RK (2017) Evaluation of genetic diversity in rice bean [Vigna umbellata (Thunb.) Ohwi and Ohashi] germplasm using SSR markers. Electronic J Plant Breed 8:674–679
- Tian J, Isemura T, Kaga A, Vaighan DA, Tomooka N (2013) Genetic diversity of the rice bean (Vigna umbellata) as assessed by SSR markers. Genome 56:717–727
- Tomooka N, Lairungreang C, Nakeeraks P, Egawa Y, Thavarasook C (1991) Mung bean and the genetic resources. The final report of the Cooperative Research Work between Thailand and Japan submitted to the National Research Council of Thailand, March 1991. Tropical Research Centre, Tsukuba, Japan
- Tomooka N, Kashiwaba K, Vaughan D, Ishimoto M, Egawa Y (2000) The effectiveness of evaluating wild species, searching for sources of resistance to bruchid beetle in the genus *Vigna* subspecies Caratotropis. Euphytica 115:27–41
- Tomooka N, Maxted N, Thavarasook C, Jayasuriya AHM (2002a) Two new species, new species combinations and sectional designations in *Vigna* subgenus Ceratotropis (Piper) Verdcourt (Leguminosae, Phaseoleae). Kew Bull 57:613–624



Tomooka N, Yoon MS, Doi K, Kaga A, Vaughan D (2002b) AFLP analysis of diploid species in the genus Vigna sub- genus Ceratotropis core collection. Genet Resour Crop Evol 49:521–530

- Tomooka N, Naito K, Kaga A, Sakai H et al (2014) Evolution, domestication and neo-domestication of the genus *Vigna*. Plant Genet Resour 12:S168–S171
- Upadhayay MP (2010) Status of ricebean in Nepal. http://www.ricebean.org/publication.htm. Accessed 28 Aug 2018
- Vaillancourt RE, Weeden NF (1993) Lack of isozyme similarity between *Vigna unguiculata* and other species of genus *Vigna* (*Leguminosae*). Can J Bot 71:586–591
- Verma MM, Brar JS (1996) Breeding approaches for increasing yield potential of mungbean. In: Asthana AN, Kim DH (eds) Recent advances in mungbean research. Indian Soc Pulses Res Dev, Kanpur, pp 102–123
- Vir R, Jehan T, Bhat KV, Lakhanpaul S (2010) Genetic characterization and species relationships among selected Asiatic Vigna Savi. Genet Resour Crop Evol 57:1091–1107
- Wang XW, Kaga A, Tomooka N, Vaughan DA (2004) The development of SSR markers by a new method in plants and their application to gene flow studies in adzuki bean (*Vigna angularis* (Willd.) Ohwi and Ohashi). Theor Appl Genet 109:352–360
- Wang LX, Chen HL, Peng B, Wu JX, Wang SH, Blair MW, Cheng XZ (2015) The transferability and polymorphism of mung bean SSR markers in rice bean germplasm. Mol Breed 35:77. https://doi. org/10.1007/s11032-015-0280-y

- Wang L, Kim KD, Gao D, Chen H, Wang S, Lee S et al (2016) Analysis of simple sequence repeats in rice bean (*Vigna umbellata*) using an SSR-enriched library. Crop J 4:40–47. https://doi.org/10.1016/j.cj.2015.09.004
- Yang JL, Zhang L, Li YY, You JF, Wu P, Zheng SJ (2006) Citrate transporters play a critical role in aluminium-stimulated citrate efflux in rice bean (Vigna umbellata) roots. Ann Bot 97:579–584
- Yu K, Park SJ, Poysa V, Gepts P (2000) Integration of simple sequence repeat (SSR) markers into a molecular linkage map of common bean (*Phaseolus vulgaris* L). J Hered 91:429–434
- Zhong M, Cheng XZ, Wang LX, Wang SH, Wang XB (2012) Transferability of mung bean genomic-SSR markers in other Vigna species. Acta Agron Sin 38:223–230
- Zsögon A, Čermák T, Naves ER, Notini MM, Edel KH, Weinl S, Freschi L, Voytas DF, Kudla J, Peres LEP (2018) De novo domestication of wild tomato using genome editing. Nat Biotechnol 36:1211–1216

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

