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Review article

Advances in genome mapping in orphan grain legumes of genus *Vigna*

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Abstract

The genus *Vigna* contains many important grain legumes that provide an inexpensive source of dietary protein for humans. With recent advancement in molecular marker technology, there has been a surge in the genome mapping studies in crop plants. Although, a significant amount of genetic studies has been carried out in *Vigna* species, genome mapping research in *Vigna* species is far behind the other major grain legumes such as common bean and soybean. This article presents a comprehensive review on the recent advances in genome mapping research in *Vigna* species with emphasis on four important grain legumes *viz*., cowpea, mungbean, azuki bean and blackgram. The reviewed areas include genetic linkage maps, comparative genome mapping, genes/QTLs mapping for agronomically important traits and availability of genomic resources, which can be used to accelerate molecular breeding in genus *Vigna*.

Key words: *Vigna*, molecular markers, genetic linkage map, QTL mapping, genomic resources

Legumes are members of the family Fabaceae and constitute the third largest family among the higher plants, and are second only to cereals in agricultural and economic importance. This family contains about 750 genera and 20,000 species, and includes major grain legumes, oilseed, forage, medicinal, ornamental crops and agroforestry species [1]. Taxonomically, it has been divided into three sub-families: the Mimosoideae, the Caesalpinioideae and the Papilionoideae. Most of the economically important grain legumes (also known as pulses or food legumes) belong to the two major clades of the sub-family Papilionoideae: Galegoid or cool season/temperate legumes and Millettoide or warm season/tropical legumes. Galegoid clade includes the important grain legumes like pea (*Pisum sativum* L.), chickpea (*Cicer arietinum* L.), lentil (*Lens culinaris* Medik.) and faba bean (*Vicia faba* L.). Millettoide clade includes the important grain legumes like soybean (*Glycine max* L.), pigeonpea [*Cajanus cajan* (L.) Millsp.], common bean (*Phaseolus vulgaris* L.), cowpea [*Vigna unguiculata* (L.) Walp.], mungbean [*Vigna radiata* (L.) Wilczek], blackgram [*Vigna mungo* (L.) Hepper] and azuki bean (*Vigna angularis* (Willd.) Ohwi and Ohashi). These grain legumes are primarily grown for their edible seeds or grains and are mainly cultivated in the developing countries of South America, Africa and Asia. The seeds of grain legumes contain about 20-40% protein and provide about one-third of the dietary protein for human consumption [2]. Proteins of grain legumes are generally high in lysine, but deficient in sulphur containing amino acids i.e. methionine and cysteine [3]. Therefore, grain legumes form a perfect diet of energy and protein when mixed and consumed with cereals.

In grain legumes, many crops like soybean and common bean have been well studied and a large number of genetic and genomic resources are available for them. However, there is dearth of such resources in other grain legumes and therefore these legumes are often called orphan grain legumes [4]. Cowpea, mungbean, blackgram and azuki bean are four important orphan grain legumes cultivated in the South

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American, African and Asian countries and are an inexpensive source of dietary protein. These crops are also valued as fodder, cover and green manure. All these four crops are diploid, belong to the genus *Vigna*, and have the same number of chromosomes (2n = 2x = 22). However, strong reproductive isolation barrier exists between these species [5]. The total productivity in these grain legumes is low and has been stagnating for the last few decades. A large number of biotic and abiotic factors affect the quality and yield potential of these crops. Therefore, the prime breeding objective is to cope with these stresses and increase the productivity. Till recently, morphological and biochemical markers were used to trace the inheritance of a target gene. However, these markers are limited in number and are strongly influenced by the environmental factors. One of the most significant developments in biology is the detection and analysis of naturally occurring DNA sequence variation using DNA markers or molecular markers, which have many advantages over morphological and biochemical markers. These molecular markers provide an indispensable tool for the construction of genetic linkage maps and tagging of agronomically important traits for use in marker assisted selection (MAS). The aim of this review is to summarise the progresses made in genome mapping studies in the genus *Vigna* with emphasis on the four important grain legumes *viz*., cowpea, mungbean, azuki bean and blackgram.

Genetic linkage map

Construction of the genetic linkage map is of fundamental importance for the efficient exploration and exploitation of the plant genetic potential. Many genetic linkage maps have been constructed in these grain legumes and a list of the important genetic linkage maps available is given in Table 1. The genetic linkage maps developed in important *Vigna* species are discussed below.

Cowpea

The preliminary genetic linkage maps in cowpea were developed based on RFLP markers using an F_2 inter-subspecific mapping population [6, 7]. However, these maps were not saturated and markers were distributed on more than 11 linkage groups. With the advent of PCR based molecular markers techniques, improved genetic linkage maps were developed in cultivated cowpea using a recombinant inbred (RI) population and a combination of AFLP, RFLP and RAPD markers [8, 9]. Later on Muchero *et al*. [10] constructed a high density consensus genetic linkage map in cowpea using 741 RI lines from six different mapping populations and 928 EST-derived SNP markers. This map spanned 680 cM of cowpea genome with 11 linkage groups and an average marker density of 0.73 cM. In asparagus bean (*V. unguiculata* spp. *sesquipedialis*), a distinctive subspecies of cowpea, a genetic linkage map was constructed using 375 marker loci (SNPs and SSRs) distributed into 11 linkage groups [11]. Map covered a length of 745 cM with an average marker density of 1.98 cM. Andargie *et al.* [12] constructed a genetic linkage map in cowpea with 202 SSR markers distributed in 11 linkage groups using a RI population. This map spanned a total distance of 677 cM, with an average marker distance of 3 cM. Recently, an improved consensus genetic linkage map was developed using 1293 individuals representing 13 mapping populations [13]. A total of 1107 EST-derived SNP markers were mapped on 11 Linkage groups and the map covered a distance of 680 cM.

Mungbean

In mungbean, the preliminary genetic linkage maps were developed using RFLP markers and an F_2 inter-subspecifc mapping population derived from a cross between genotype 'VC3890' (an improved cultivar) and 'TC1966' (*V. radiata* ssp*. sublobata*) [6, 7]. Lambrides *et al.* [14] developed two genetic linkage maps in mungbean with RFLP and RAPD markers. The first map constructed from 67 F_2 individuals consisted of 110 markers (52 RFLP and 56 RAPD) that grouped into 12 linkage groups and spanned a total map distance of 758.3 cM. Another genetic map was based on 67 RI individuals and was composed entirely of 115 RAPD markers distributed in 12 linkage groups and spanned a total map distance of 691.7 cM. Humphry *et al.* [15] developed a genetic linkage map with RFLP markers using an inter-subspecifc RI population derived from a cross between cultivated mungbean genotype 'Berken' and a wild mungbean genotypes 'ACC41' (*V. radiata* ssp. *sublobata*). Using the same mapping population, Zhao *et al.* [16] constructed a genetic linkage map based on SSR, RFLP, RAPD and STS markers distributed in 12 linkage groups with a total length of 1831.8 cM and an average marker density of approximately 10 cM. However, all these maps were low-density genetic linkage maps and none of them resolved into 11 linkage groups, which is the haploid chromosome number in mungbean. Recently, Isemura *et al*. [17] constructed a genetic linkage map using 430 SSR markers from mungbean

Table 1. Some important genetic linkage maps developed in *Vigna* species

Crop	Mapping population	No. of markers	Type of markers	Map size in cM (Total linkage groups)	References
Cowpea	58 F_2 from 'IT2246' x 'TVN1963'	97	RFLPs	684 (10)	Menancio-Hautea *et al.* 1993
	94 RILs from 'IT84S-2049' x '524B'	181	RAPDs, RFLPs, AFLPs	972 (12)	Menendez *et al.* 1997
	94 RILs from 'IT84S-2049' x '524B'	423	RAPDs, RFLPs, AFLPs	2670 (11)	Ouédraogo *et al.* 2002
	741 RILs from six mapping populations	928	SNPs	680 (11)	Muchero *et al*. 2009
	127 RILs from 'IT93K503-1' x 'CB46'	306	AFLPs	643 (11)	Muchero *et al*. 2009
	114 RILs from 'ZN016' x 'Zhijiang282'	375	SNPs and SSRs	745 (11)	Xu *et al.* 2011
	159 RILs from '524B' x '219-01'	202	SSRs	677 (11)	Andargie *et al.* 2011
	1295 individuals from 13 mapping populations	1107	SNPs	680 (11)	Lucas *et al.* 2011
Mung bean	58 F_2 from 'VC3890' x 'TC1966'	171	RFLPs	1570 (14)	Menancio-Hautea *et al.* 1993
	67 F_2 from Berken x ACC41	110	RFLPs, RAPDs	758.3 (12)	Lambrides *et al.* 2000
	80 RILs from Berken x ACC41	255	RFLPs	737.9 (13)	Humphry *et al.* 2002
	202 RILs from Berken x ACC41	179	SSRs, RFLPs, STS	1831.8 (12)	Zhao *et al.* 2010
	250 BC_1F_1 from JP211874 x JP229096	430	SSR	727.6 (11)	Isemura *et al.* 2012
Azuki bean	80 F_2 from *V. angularis* x *V. nakashimae*	132	RAPDs, RFLPs	1250 (14)	Kaga *et al.* 1996
	86 F_2 from *V. angularis* x *V. umbellata*	188	RFLPs, RAPDs	1702 (14)	Kaga *et al.* 2000
	187 BC_1F_1 from *V. angularis* x *V. nepalensis*	486	SSRs, AFLPs, RFLPs	832.1 (11)	Han *et al.* 2005
	188 F_2 from JP110658 x JP109685	233	SSR, AFLP	771.9 (10)	Kaga *et al*. 2008
Blackgram	180 BC_1F_1 from JP219132 x TC2210	148	SSRs, RFLPs, AFLPs	783 (11)	Chaitieng *et al.* 2006
	104 RILs from TU94-2 x *V. mungo* var. *silvestris*	428	RAPDs, ISSRs, AFLPs, SSRs	865 (11)	Gupta *et al.* 2008

and its related species that resolved into 11 linkage groups spanning a total distance of 727.6 cM with an average marker density of 1.78 cM.

Azuki bean

The first genetic linkage map of azuki bean was constructed with RAPD and RFLP markers using an

F_2 population of an inter-specific cross between azuki bean and its wild relative *V. nakashimae* [18]. A total of 132 molecular markers were distributed into 14 linkage groups and the map covered a distance of 1250 cM with an average marker density of 10.6 cM. Subsequently, a genetic linkage map using an F_2 inter-specific cross between azuki bean and rice bean consisting of 14 linkage groups spanning 1702 cM of the genome with an average marker density of 9.7 cM was developed [19]. A more saturated genetic linkage map using a backcross mapping population of azuki bean and the wild relative *V. nakashimae* was developed with 486 molecular markers (205 SSR, 187 AFLP and 94 RFLP markers) distributed into 11 linkage groups [20]. This map spanned 832 cM of the genome and the average marker density was reduced to 1.85 cM. Recently, a genetic linkage map in rice bean, a close relative of azuki bean, was constructed with SSR and AFLP markers using a BC_1F_1 mapping population derived from a cross between cultivated and wild rice bean [21]. A total of 326 markers were mapped on 11 linkage groups covering 796.1 cM of rice bean genome at an average marker density of 2.5 cM.

Blackgram

The first genetic linkage map in blackgram was developed using a BC_1F_1 population derived from a cross between a cultivated genotype and a wild relative (*V. mungo* var. *silvestris*) [22]. In this map, about 148 molecular markers (SSR, RFLP and AFLP) were distributed in 11 linkage groups and the map covered 783 cM of the blackgram genome with an average marker density of 5.7 cM. Subsequently, a more saturated genetic linkage map was developed using an inter-subspecific RI population with 428 molecular markers (SSR, AFLP, RAPD and ISSR markers). This map had 11 linkage groups spanning a total distance of 865.1cM with an average marker density of 2 cM [23].

Gene/QTL mapping

The productivity of crops is constantly threatened by many biotic and abiotic factors. One of the most important applications of genetic mapping is the identification of linked molecular markers for agronomically important traits so that the inheritance of the desired trait can be traced in the segregating populations. In *Vigna* species, many agronomically important traits have been mapped for use in marker-assisted selection (Table 2). Mapping of some of the important traits in *Vigna* species are discussed here.

Mungbean yellow mosaic virus resistance

Mungbean yellow mosaic virus (MYMV) disease caused by a Gemini virus is a major disease of mungbean and blackgram. It is transmitted through whiteflies (*Bemisia tabaci*), and under severe conditions can cause up to 100% damage. The source of resistance for this disease has been reported in the cultivated germplasm collections. In mungbean, resistance to MYMV is under the control of a single recessive gene [24, 25] or two recessive genes [26]. In blackgram, resistance to MYMV is governed by one or two recessive genes [27-29]. For use in MAS, MYMV resistance genes have been tagged with RAPD [30] and SCAR markers [25] in mungbean. In blackgram, MYMV resistance genes have been mapped using resistance gene analog (RGA), ISSR and SCAR markers [29, 31, 32]. However, in all these mapping studies, either the marker are loosely linked to the trait (>5 cM), or proper linkage or validation studies were not performed. Therefore, there is an urgent need to develop and validate tightly linked molecular markers for MYMV resistance gene so that MYMV resistance can be rapidly transferred to susceptible mungbean and blackgram genotypes though MAS.

Powdery mildew resistance

Another major destructive disease of mungbean and blackgram is the powdery mildew caused by an obligate fungal parasite *Erysiphe polygoni*. Severe infection occurs in cool, dry months and can reduce the crop yield upto 20-40% [33]. Genetic resistance has been identified for powdery mildew in the cultivated gene pool and genetic studies have suggested that several mode of inheritance may exist [33-37]. Many studies have been performed on mapping the powdery mildew resistance in mungbean [36-39]. Young *et al.* [36] identified three QTLs that together explained upto 58% of the phenotypic variation for the partial resistance to powdery mildew. Similarly, Chaitieng *et al.* [37] and Humphry *et al.* [38] identified a single major QTL that explained 65% and 86% of the variation in resistance to powdery mildew, respectively. Zhang *et al.* [39] used a RFLP marker (VrCS65) closely linked to powdery mildew resistance locus to screen a mungbean bacterial artificial chromosome (BAC) library and developed four PCR based markers (including two SSRs and two STSs) that co-segregated with the original RFLP marker VrCS65. These mapping studies would help in the development of powdery mildew resistance cultivars in mungbean through MAS.

Table 2. Important genes/QTLs for biotic stresses mapped with molecular markers in *Vigna* species

Crop	Trait	Gene/QTL	Linked markers	References
Cowpea	*Striga gesnerioides* resistance	*Rsg1* *Rsg2, Rsg4*	AFLPs, SCAR AFLPs	Boukar *et al.* 2004 Ouédraogo *et al.* 2001
	Aphid resistance	*Rac1*	RFLPs	Myers *et al*. 1996
	Cowpea bacterial blight resistance	QTL	SNPs	Agbicodo *et al.* 2010
Mung bean	Mungbean yellow mosaic virus (MYMV) resistance	MYMV resistance locus	RAPDs SCAR	Selvi *et al*. 2006 Dhole and Reddy, 2012
	Powdery mildew resistance	QTLs	RFLPs RFLPs, AFLPs RFLPs	Young *et al*. 1993 Chaitieng *et al.* 2002 Humphry *et al*. 2003
		PM resistance locus	SSRs, STS	Zhang *et al.* 2008
	Bruchid resistance	*Br*	RAPDs, RFLPs STS RAPDs, SCAR, CAPs	Kaga and Ishimoto 1998 Miyagi *et al*. 2004 Chen *et al.* 2007
	Cercospora leaf spot resistance	QTL	SSRs	Chankaew *et al.* 2011
Blackgram	Mungbean yellow mosaic virus (MYMV) resistance	MYMV resistance locus	RGA ISSR, SCAR	Basak *et al.* 2004; Maiti *et al.* 2011 Souframanien and Gopalakrishna 2006
	Bruchid resistance	QTL	AFLPs, ISSR, SSRs	Souframanien *et al.* 2010
Azuki bean	Bruchid resistance	QTL	RFLPs, SSRs SSRs	Somta *et al.* 2006 Somta *et al.* 2008

Bruchid resistance

Bruchid beetle or weevils (Coleptera:Bruchidae), particularly the azuki bean weevils (*Callosobruchus chinensis* L.) and cowpea weevils (*C. maculates* F.) are the principal and most destructive post-harvest pest of *Vigna* species [40]. Bruchid beetles occur wherever the crop is grown and frequently infests up to 100% of the stored seeds within 3 to 5 months under ordinary storage conditions. The genetic resistance to bruchids has been identified in cowpea [41], mungbean [42], wild mungbean (*V. radiata* var. *sublobata*) [43], wild blackgram (*V. mungo* var. *silvestris*) [44], rice bean (*V. umbellata*) and wild relative of azuki bean (*V. nepalensis*) [45]. In mungbean, inheritance of bruchid resistance is governed by single dominant locus [42]. RFLP markers linked at a distance of 3.6 cM to bruchid resistance locus have been identified in a wild mungbean relative, TC1966 [46]. Using similar resistance source, Kaga and Ishimoto [47] identified six RAPD and one RFLP markers within a distance of 0.7 cM from the bruchid resistance locus. For use in MAS, PCR-based STS markers [48] and CAPS markers [49] closely linked with a major bruchid resistance locus also have been developed in mungbean.

Bruchid resistance was found to be a quantitatively inherited trait in *V. mungo* var. *silvestris* [50], *V. umbellata* [51] and *V. nepalensis* [52]. For QTL analysis, bruchid resistance is generally measured using two specific phenotypes namely percentage of seeds damaged by bruchids (or percentage of adult emergence) and the time taken for adult bruchids to emerge from seeds (or developmental period). QTLs for percentage adult emergence and developmental period have been mapped in *V. mungo* var. *silvestris* [50], *V. umbellata* [51] and *V. nepalensis* [52]. In all these studies, some QTLs were localized on similar positions in the linkage maps, suggesting the conservation of bruchid resistance loci in these species. These markers will be invaluable in facilitating the introgression of bruchid resistance into breeding lines as well as further characterization of the resistance locus.

Resistance to other biotic stresses

Other biotic factors, which are responsible for decreasing the productivity of *Vigna* species, are *Cercospora* leaf spot (CLS), bacterial blight, parasitic weed *Striga gesnerioides* (Willd.) and aphids. CLS caused by the fungus *Cercospora canescens* is an important foliar disease of mungbean in Asia. CLS infection results in premature defoliation and reduction in the size of pods and seeds with yield losses up to 50% [53]. A major QTL that explained 65.5-80.5% of the phenotypic variation for CLS resistance was mapped with SSR markers in mungbean [54].

In cowpea, parasitic weed *Striga gesnerioides* is a major constraint to cowpea production and causes severe chlorosis, wilting, and stunting resulting in yields losses. Five *Striga* resistance genes (*Rsg1-1, Rsg2-1, Rsg3-1, Rsg994-1, Rsg4-3*) have been identified in cowpea and these genes have been mapped using AFLP and SCAR markers for use in MAS [9, 55, 56]. Other major biotic factors affecting cowpea productivity are bacterial blight (CoBB) disease caused by *Xanthomonas axonopodis* pv. *vignicola* (*Xav*) and aphids (*Aphis craccivora* Koch). Locus conferring genetic resistance to aphids has been mapped using RFLP markers [57]. Three QTLs associated with CoBB resistance have also been mapped in cowpea using an SNP based genetic linkage map [58].

Resistance to abiotic stresses

Productivity of *Vigna* species is also affected by many abiotic stresses, particularly drought and heat. However, very little efforts have been put to understand the genetics and genomics of resistance to these abiotic stresses in *Vigna* species. Although, cowpea is most drought tolerant among *Vigna* species, periodic droughts still limit its productivity. Significant differences in response to drought stress exist among cowpea genotypes [59-61]. Muchero *et al*. [62] have identified ten QTLs for seedling drought-induced senescence in a RI population derived from seedling drought tolerant line 'IT93K503-1' and susceptible line 'CB46'. Subsequently, using the same mapping population, Muchero *et al*. [63] applied candidate gene mapping strategy to identify gene-derived molecular markers co-locating with drought stress-induced premature senescence QTLs in cowpea. To further understand the molecular basis of drought tolerance, Barrera-Figueroa *et al*. [64] identified 44 drought associated microRNAs (miRNA) through deep sequencing of small RNA reads from two cowpea genotypes that were grown under well water and drought stress conditions, indicating that miRNA may play an important role in determining the drought tolerance in cowpea. For heat tolerance, five genomic regions/QTLs, which represent 9% of the cowpea genome, were identified using a RI population [65]. These regions explain 11.5 to 18.1% of the phenotypic variation and were mapped with SNP markers, which will help in breeding heat tolerant cowpea genotypes.

Seed weight

Seed weight is the most important parameter to measure the yield. In *Vigna* species, the first QTL for seed weight was mapped in mungbean and cowpea with RFLP markers using F_2 populations [6]. Two major QTLs in cowpea accounting for 52.7% of variation and four QTLs in mungbean accounting for 49.7% of variation in seed weight were identified. The major QTL for seed weight in both the species spanned the same genomic region suggesting the conservation of seed weight loci during evolution. Later on, Humphry *et al.* [66] identified 11 QTLs in mungbean for seed weight collectively accounting for over 80% of the phenotypic variation in a RI population. However, none of these QTLs co-localize with the QTL identified by Fatokun *et al.* [6].

Other domestication related traits

The traits related to the size of various plant parts (like seeds, pods, leaf and stem), plant habit (stem and branch), life cycle (flowering time), color (seed, epicotyl and stem), pod dehiscence and seed germination are all known to differ between wild and cultivated plants and, therefore, are considered to be directly or indirectly the result of changes associated with domestication. In *Vigna* species, mapping of domestication related traits has been performed using the interspecific mapping populations to understand the genetics of domestication.

In yardlong bean (*V. unguiculata* ssp. *unguiculata*), a vegetable form of cowpea, domestication related traits were mapped using linkage maps developed from the cross between yardlong bean accession 'JP81610' and wild cowpea accession 'TVnu457' [67]. Twenty-four domestication related traits were investigated in the study and 21 quantitative traits were dissected into 153 QTLs. This study showed that domestication-related traits are controlled by a few major and many minor QTLs in yardlong bean,

and QTLs were co-localized on the several narrow genomic regions on almost all the linkage groups.

In mungbean, Isemura *et al.* [17] mapped 105 QTLs and genes for 38 domestication related traits with SSR markers using 250 BC_1F_1 individuals developed from a cross between a wild mungbean accession 'JP211874' and a cultivated mungbean accession 'JP229096'. As in other crops, a few major genes plus some minor genes control domestication-related traits in mungbean. Twenty major QTLs for domestication-related traits were distributed on seven of the 11 linkage groups and 53 QTLs with small effects were found on each linkage group. The useful QTLs for seed size, pod dehiscence and pod maturity that were not found in other Asian *Vigna* species were also identified and should be useful for improvement of mungbean and related legumes.

In azuki bean, two studies on genetics of domestication related traits are reported. In one study, Isemura *et al.* [68] evaluated 33 domestication related traits. In another study, Kaga *et al.* [69] analyzed 162 QTL for 46 traits related to domestication. In azuki bean, most of the traits were controlled by few QTLs, but several traits such as pod dehiscence were controlled by single gene. Most of the QTLs for domestication were distributed in clusters on a limited number of linkage groups and a large number were positioned in proximity to the breakpoint of a presumed translocation. The results also revealed that domestication of azuki bean has involved a trade-off between yield and seed size with fewer but longer pods and fewer but larger seeds selected at the expense of the overall yield. Similarly in rice bean, 31 domestication-related traits were dissected into 69 QTLs [21]. The differences between cultivated and wild parents were controlled by only a few major QTLs.

Comparative genomic studies

The comparative genome mapping facilitates the mapping of orthologous DNA sequences among related plant species and increase the knowledge of organization and evolution of plant genomes. Comparative mapping studies have been performed in *Vigna* species by utilizing the common RFLP and SSR markers. Menancio-Hautea *et al.* [7] performed comparative mapping study between cowpea and mungbean using common RFLP markers and found multiple linkage groups that were conserved between mungbean and cowpea, indicating a high degree of genomic similarity between the two genomes. Comparative mapping among mungbean, common bean and soybean indicated high conservation between genomes of mungbean and common bean and substantially more genome rearrangement between soybean and mungbean or common bean [70]. Conserved genome blocks distributed in most of the linkage groups with small insertions, deletions and rearrangements have also been found between mungbean and lablab [15], and between mungbean and azuki bean [19]. Comparative studies between azuki bean and blackgram using common SSR markers showed a high degree of colinearity between the two genomes with some chromosomal rearrangements [22, 23]. Comparative study between rice bean map [21] and azuki bean map [69] revealed high level of genome synteny between rice bean and azuki bean, and also facilitated QTL comparison between the two species.

Based on sequence comparison between cowpea unigenes harboring a mapped SNP and reference genome sequences of soybean and medicago (*Medicago truncatula*), Muchero *et al.* [10] observed regions with extensive macrosynteny, microsynteny and colinearity between cowpea, soybean and medicago, although synteny was reduced in medicago compared with soybean. Based on comparative analysis, large scale genome conservation was observed and all cowpea 11 linkage groups were found syntenic with asparagus bean linkage groups, conveying the close relatedness of the two subspecies [11]. Lucas *et al.* [13] also observed synteny and colinearity between cowpea, soybean and medicago by using an SNP based improved consensus genetic linkage map of cowpea. The comparative mapping studies are effective in increasing the number of markers, as well as in increasing the coverage of genetic linkage maps. Comparative mapping also allows the use of molecular markers/QTLs linked to the traits in one species to be used in a related species. For example, based on comparative mapping between common bean and mungbean, a putative orthologue for *Phs* locus, which encodes the most abundant seed storage protein (phaseolin), was identified in mungbean [71].

Availability of genomic resources

The cDNA libraries and large insert bacterial artificial chromosome (BAC) libraries are an important genomic resource for the genetic mapping, physical mapping and positional cloning of genes. These libraries also provide an important resource for the development of

molecular markers and to integrate the genetic and physical maps.

During the past few years, considerable progress has been made in the establishment of core genome resources for cowpea. A Cowpea Genespace/ Genomics Knowledge Base (CGKB) was developed under the Cowpea Genomics Initiative program [72]. CGKB database has about 298,848 cowpea gene-space sequences (GSS) isolated by methylation filtering of genomic DNA and is an integrated and annotated resource for cowpea GSS with features of homology-based and Hidden Markov Model (HMM)-based annotations, enzyme and pathway annotations, GO term annotation and a large number of other facilities to perform complex queries (http:// cowpeagenomics. med. virginia. edu/ CGKB/).

Sequencing of the gene rich hypomethylated portion of the cowpea genome had generated about 250,000 gene-space sequence reads (GSRs) which contain a large number of SSRs and provide a rich source for the design of primers for SSR markers [73]. Many cDNA libraries also have been constructed to generate large number of EST sequences in cowpea [10]. Harvest:Cowpea (http://harvest.ucr.edu/), an EST database based software for cowpea researchers facilitates oligonucleotide designing, physical mapping, genetic mapping and comparative genome analysis. These EST sequences provided a valuable genomic resource for the development of gene based molecular markers like SNPs (10), SSR markers [11, 74], and intron length polymorphic (ILP) markers [75]. In addition, BAC library has been developed in cowpea and a large number of BAC-end sequences (BES) have been generated. These BACs and BES have been used to generate a physical map, which has been anchored to the cowpea genetic linkage map via SNP loci [76].

In mungbean, a cDNA library and four cDNA subtractive libraries for early development and stress response were developed and 811 non-redundant uniESTs were identified [77]. Miyagi *et al*. [48] have developed a BAC library in mungbean that represent an estimated 3.5X coverage. This library has been successfully used to develop PCR based molecular markers closely linked to a bruchid resistance locus in mungbean. In another study, Barkley et al. [78] used EcoTILLING to identify SNPs and small insertions/ deletions (INDELS) in a collection of *Vigna radiata* accessions. Tangphatsornruang *et al.* [79] characterized a total of 470,024 genome shotgun sequences covering 100.5 Mb of the mungbean genome using 454 sequencing technology and identified 1493 SSR motifs. Similarly, through transcriptome sequencing of cDNA libraries in two mungbean genotypes, a large number of SSR motifs and SNPs have been identified [80]. In mungbean and azuki bean, SSR enriched libraries and public sequence databases also have been for the development of SSR markers [81-84].

Future prospects

In recent times, although much progress has been made in the genomics of *Vigna* species, still it is far behind the other grain legumes like common bean and soybean. Most of the *Vigna* species have a narrow genetic base resulting in limited marker polymorphism within the cultivated germplasm. Due to this major limitation, most of the genetic linkage maps in *Vigna* species have been constructed using inter-specific or inter-subspecific crosses to increase the level of polymorphism. However, such maps have limited utility in breeding programs that exploit genetic variation within the cultivated genepool. Further, the numbers of markers mapped on most of these genetic maps are quite less and of low-to-moderate density. Therefore, there is a need to develop dense genetic linkage maps in *Vigna* species based on intra-specific mapping populations.

Limited genomic resources are the main hurdles in the improvement of *Vigna* species. Although, efforts have been made to develop molecular markers in *Vigna* species, the number of molecular markers available is still very less. With decrease in the cost of sequencing, increasing number of genome and transcriptome sequencing are routinely becoming available. Therefore, efforts should be made to develop a large number of molecular markers in *Vigna* species and utilize them for molecular breeding. Because of extensive synteny in the genus *Vigna*, these molecular markers would also show high transferability to related *Vigna* species, thereby expediting their use in genetic and comparative mapping studies. To further speed up the construction of high density genetic linkage maps, there is a need for the development and implementation of high throughput genotyping techniques. Allele-specific oligonucleotide microarrays [85] and single-feature polymorphism (SFP) [86] provide a rapid and cost effective method for genotyping at high density. Das *et al.* [87] have demonstrated that Affymetrix soybean genome array can be successfully used for the identification of SFPs

in cowpea and could also be used for other orphan crops.

High-throughput next generation sequencing (NGS) technologies provide a powerful tool for detecting large numbers of DNA variation within a short time frame. However, sequencing the whole genome for marker discovery is still a costly affair. Therefore, methods that can detect DNA variation in a fraction of genome should be advantageous. One such tool is sequencing of restriction site associated DNA (RAD) tags on the massively-parallel NGS platform to rapidly detect large number of DNA polymorphisms from multiplexed reduced genomic representations that could be used for direct genotyping of individuals [88, 89]. The use of these high throughput marker genotyping techniques must provide the required thrust for increasing the genomic resources in *Vigna* species and in future detailed in-depth genome mapping in these *Vigna* species will be possible. Further, the whole genome of Korean mungbean cultivar, 'Sunwhanokdu' has been sequenced and *de novo* assembled into contigs and scaffolds [90]. In addition, completed whole genome sequences of soybean, medicago and lotus (*Lotus japonicus*) will provide a vast genomic resource for comparing the genomes and transferring the information from these model legumes to *Vigna* species. This would also help in the fine mapping and cloning of genes and QTLs for agronomically important traits and in the breeding of elite cultivars resistant to biotic and abiotic stresses through MAS.

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