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Genome Research in Mungbean [*Vigna radiata* (L.) Wilczek] and Blackgram [*V. mungo* (L.) Hepper]

Prakit Somta and Peerasak Srinives*

Department of Agronomy, Faculty of Agriculture at Kamphaeng Saen, Kasetsart University, Nakhon Pathom 73140, Thailand.

* Corresponding author, E-mail: agrpss@yahoo.com

ABSTRACT: Mungbean [*Vigna radiata* (L.) Wilczek] and blackgram [*V. mungo* (L.) Hepper] (both 2n=2x=22) are important legume crops in Asia, which serve their roles as cash crops for farmers and as protein sources for consumers. Genome research in mungbean has long been conducted before blackgram and six genetic linkage maps were developed so far but no map contained enough markers to condense into 11 putative linkage groups. While only one linkage map was constructed for blackgram and resolved all 11 linkage groups. Thus mungbean is considered one of the most recalcitrant crops in genomic research. Comparative genome mapping between mungbean and several other legumes including azuki bean, common bean, cowpea, soybean, lablab and *Medicago trunculata* revealed various levels of macrosynteny depending on species, with the greatest upon common bean. Comparison between blackgram and azuki bean maps revealed high degree of genome colinearity. Genes or quantitative trait loci for several important traits were identified in mungbean compared to only one in blackgram. Improved genetic transformation protocols for the crops have been developed recently. High-throughput markers such as SSRs and SNPs developed for closely related legumes with mungbean and blackgram will be helpful to accelerate genome research and molecular breeding in these crops.

KEYWORDS: Mungbean, Blackgram, *Vigna radiata*, *Vigna mungo*, Legume genomics.

INTRODUCTION

Mungbean [*Vigna radiata* (L.) Wilczek] and blackgram [*V. mungo* (L.) Hepper] are important legume crops widely cultivated in Asia. The crops are utilized in several ways, where seeds, sprouts and young pods are consumed as sources of protein, amino acids, vitamins and minerals, and plant parts are used as fodder and green manure. Mungbean protein is easily digested without flatulence. It is an important protein source for people in the cereal-based society. Both legumes adapt well to various cropping systems owing to their ability to fix atmospheric nitrogen (N_2) in symbiosis with soil bacteria of *Rhizobium* spp., rapid growth, and early maturity. Trends on the demand and production of the crops are increasing[1,2]. The annual world production area of mungbean is about 5.5 million ha[3] of which about 90% is in Asia[4]. India is the biggest producer of mungbean where about 2.99 million ha are cultivated[1]. Although world blackgram production is difficult to estimate, the crop may be produced slightly lower amount than mungbean. In India alone, blackgram occupies about 3.15 million ha[1]. Considering their socioeconomic importance, the crops are neglected in breeding research, both at national and international levels, particularly in the filed of genomics. This is reflected by the fact that there have been less than two published papers per year on genome mapping in mungbean or blackgram over the last 10 years. In this paper, we provide an up to date review of genomic studies conducted on these two crops.

GENOME SIZE OF MUNGBEAN AND BLACKGRAM

Mungbean and blackgram are classified into the genus *Vigna* Savi, subgenus *Ceratotropis* (known as Asian *Vigna* or Asiatic gram), section *Ceratotropis*[5]. They are diploid in nature with 2n=2x=22. Mungbean and blackgram have small genome sizes estimated to be 0.60 pg/1C (579 Mbp) and 0.59 pg/1C (574 Mbp)[6], respectively, which are similar to those of the other *Vigna* species.

DNA MARKERS FOR MUNGBEAN

DNA markers are indispensable for genomic study. Not many genetic markers were developed specifically for mungbean or blackgram. Restriction fragment length polymorphism (RFLP) markers of both cDNA and random genomic clones of mungbean were reported by Young et al[7]. These RFLPs together with those from common bean [*Phaseolus vulagris* (L.)], cowpea [*V. unguiculata* (L.) Walps] and soybean [*Glycine max* (L.) Merr.] have been extensively used in mungbean and/or blackgram genome mapping. Only recently, microsatellite or simple sequence repeat (SSR) markers,

a marker system of choice, have been developed from mungbean[8,9,10,11]. The number of these SSRs is still very limited. However, SSRs from azuki bean [*V. angularis* (Willd.) Ohwi & Ohashi][12], common bean[13,14] and cowpea[15] can be used in both mungbean[16,17] and blackgram[17]. As high as 72.7% and 78.2% of the azuki bean SSRs amplify mungbean and blackgram genomic DNA, respectively[17]. While 60.6% of common bean SSRs amplify mungbean genomic DNA[16].

Molecular Genetic Diversity of Mungbean

A large collection of mungbean germplasm encompassing 415 cultivated (*V. radiata* var. *radiata*), 189 wild (*V. radiata* var. *sublobata*) and 11 intermediate accessions from diverse geographic regions have been characterized using 19 azuki bean SSRs[18]. The results revealed that mungbean has highest diversity in South Asia, supporting the view of its domestication in the Indian subcontinent and showing that Australia and Papua New Guinea is a center of diversity for wild mungbean. A core collection of 106 accessions representing most genetically diverse of these germplasm has been made[18]. Molecular diversity in a large collection of germplasm has never been studied in the blackgram.

Genome Mapping in Mungbean

Genetic Linkage Map

Six molecular linkage maps for mungbean have been published[19,20,21,22]. These maps were constructed from the data of F_2 or recombinant inbred line (RIL) populations from inter-subspecific crosses of VC3980 (cultivated) x TC1966 (wild from Madagascar) or Berken (cultivated) x ACC41 (wild from Australia) using mainly RFLP and/or random amplified polymorphic DNA (RAPD) markers. The population size ranged from 58 to 80 plants. The maps differ in length (737.9-1570 cM), number of markers (102-255 markers), number of linkage groups (LG) (12-14), and level (12-30.8%) and regions of marker distortion. The most comprehensive map consists of 255 loci with an average distance between the adjacent markers of 3 cM. However, none of the maps resolved 11 LGs, which is the haploid chromosome number of mungbean. To resolve 11 LGs and saturate the map, many more markers are needed. In addition, the genome coverage of the markers has yet to be determined.

Comparative Genome Mapping

Because all but one of the afore-mentioned mungbean linkage maps were developed by utilizing a number of heterologous probes from common bean, cowpea, lablab (hyacinth bean; *Lablab purpureus* L.) and soybean, comparative genomics (macrosynteny) was studied between mungbean and these legumes and the other *Vigna* species. Mungbean and cowpea share a high degree of genome similarity. Marker orders and LGs were similar in both taxa with syntenic association appeared on 10 genomic regions although duplication and rearrangement exist[23]. Mungbean and azuki bean linkage maps share several conserved genome segments without[24] or with some[25] rearrangement. Isemura *et al*.[25] showed that LG 1, 2, 3, 4, 8 and 11 of mungbean map[19] correspond respectively to LG 1, 4, 10, 8, 2 and 9 of azuki bean map[26]. Genome conservation between mungbean and common bean appears to be higher than between mungbean and cowpea[20] or azuki bean[24]. Comparison between mungbean and common bean or soybean maps revealed that mungbean genome is more conserved to common bean than soybean[20]. Linkage maps between mungbean and common bean showed extensive genome conservation (average length of colinearity of 37 cM with the maximum of 100 cM) but notable translocations in the genomes occurred as indicated by a mungbean LG was composted of different common bean LGs. While comparison between mungbean and soybean revealed that short (average colinearity length of 12-13 cM) and scattered linkage blocks are conserved and there are considerable genome rearrangements between the two species. Lee *et al*.[27] showed a higher level of genome conservation between mungbean and soybean than previously reported.

Comparative mapping in mungbean and a distantly related legume crop, lablab gave surprising results in that the two species share several large conserved genome blocks as indicated by similar marker orders and LGs[22]. However, the results also showed genome rearrangements and many deletions/duplications after divergence. In a recent study of genome conservation between a model legume *Medicago truncatula* and several other legume crops including mungbean using cross-species genetic markers, the results showed that macrosyntenic relationship between *M. truncatula* and mungbean was complicated and less informative[28]. Twenty-nine of 38 (76%) markers used between the two taxa revealed evidence of conserved gene order, whereas the remaining markers mapped to nonsyntenic positions.

Gene and QTL Mapping

Genes or quantitative trait loci (QTLs) for 8 traits encompassing 1 insect pest, 2 diseases and 5 seed-related characters were mapped with molecular markers in mungbean. Five of them are of importance for genetic improvement of this crop and thus are highlighted here.

Bruchid resistance: Bruchids or seed weevils,

especially azuki bean weevils (*Callosobruchus chinenis* L.) and cowpea weevils (*C. maculatus* F.) are the most serious pests of stored mungbean and blackgram. The genes responsible for bruchid resistance in two wild mungbean strains, TC1966 and ACC41 have been mapped. The gene conferring resistance to *C. chinensis* (*Br*) in TC1966 was located on LG 8 franked by RFLP sgA882 and mgM151 with the distance of 3.6 and 6.5 cM, respectively[7]. LG 8 was subsequently revised to LG 9[19]. The gene was narrowed down to 0.7 cM interval between marker Bng143 and Bng110[29]. *Br* was just 0.2 cM away from Bng143. This marker was at the same position to *Va*, a gene controlling the production of Vignatic acids[29] that is toxic to bruchids. Resistance to *C. chinensis* in ACC41 was located on LG 8-9[30]. The gene was linked to RAPD markers, which were then converted into sequence characterized amplified region (SCAR) markers. RFLP pR26 identified linking with the resistance gene in TC1966[7] was also found linked with the resistance gene in ACC41[30]. This probe also found associated with resistance to *C. chinensis* in rice bean [*V. umbellata* (Thunb.) Ohwi & Ohashi][31]. Recently, two sequence tagged site (STS) markers, STSbr1 and STSbr2, developed from a mungbean BAC subclone were identified linking to *C. chinensis* resistance in ACC41[32]. The latest effort involving TC1966 was to map the resistance gene using cleaved amplified polymorphic sequence (CAPs), RAPD and SCAR markers[33]. Mapping of resistance gene in cultivated mungbean is in progress[34].

Powdery mildew resistance: Powdery mildew disease caused by the fungus *Erysiphe polygoni* DC. is a common foliar disease of mungbean. The disease may cause yield loss up to 40%. Using VC3890A as a resistance source, Young *et al.*[35] found three QTLs on three different LGs associated with the resistance. These QTLs together accounted for 58% of the trait variation. Chaitieng *et al.*[36] used VC1210A as a resistance source to map the resistance gene. Initial mapping with 98 framework RFLP probes failed to identify any association with the resistance. However, subsequent identification using amplified fragment length polymorphism (AFLP) markers and bulked segregant analysis (BSA) resulted in 4 bands linking to the resistance. These bands were then cloned and used as probes for RFLP analysis of which finally 5 RFLPs were found associated with the resistance. The five RFLPs constituted a new LG. A major QTL, *PMR1*, associated with the resistance on this LG accounted for 68% of the trait variation. A main QTL was also identified in the different resistance source. Humphry *et al.*[37] found a single QTL controlling the resistance in RIL population derived from a cross between resistant line ATF3680 and susceptible cultivar Berken. Location and effect of the QTL was consistent in 2 seasons evaluated for the resistance. The QTL explained up to 86% of the variation in the resistance. However, location of this QTL did not coincide with any QTLs reported earlier by Young *et al*[35]. Efforts to identify QTLs conditioning the resistance using SSR are in progress (Kasettranun and Srinives, 2007 unpublished data).

Mungbean yellow mosaic virus (MYMV) resistance: MYMV is the most important disease of mungbean at present. The disease is characterized by yellow mosaic on leaves of infected plants that results in considerable yield losses. MYMV is caused by a bipartite begomovirus which is transmitted via whiteflies (*Bemisia tabaci*). Lambrides *et al.*[38] tagged the resistance gene from NM92 in two RIL populations, using BSA strategy. A marker generated from RAPD primer OPAJ20 was found to be distantly linked with the resistance gene. Inter simple sequence repeat (ISSR) and SCAR markers linked to the resistance in blackgram[39,40] has exerted a potential for locating the gene in mungbean. Lambrides and Godwin[4] suggested that mungbean probe Mng247 associated with soybean mosaic virus resistance[41] might be useful in identifying MYMV resistance gene. In addition, Mng247-derived SSR marker, M3Satt[41] may also be useful.

Seed weight: Seed weight is a primary component in the yield of grain legumes and is thus a main trait in breeding programs. In the first report of mapping study for seed weight in mungbean, Fatokun *et al.*[42] found four QTLs each on LG i, ii, iii, and iv (equivalent to LG 11, 1, 4 and 3, respectively, in the map of Menancio-Hautea *et al.*[19,23]) associated with the trait in an F_2 population of the cross between VC3890 and TC1966. These QTLs collectively accounted for 49% of the trait variation. The QTL on LG ii which has the most effect on seed weight appeared to be conserved in azuki bean[25], cowpea[42], and pea [*Pisum sativum* (L.)][43]. Additionally, location of the QTL on LG i is similar to that of seed weight QTL on LG 9 of azuki bean[25]. In another study, using RIL population derived from the cross between Berken and ACC41, Humphry *et al.*[44] identified eleven QTLs on LG 1, 2, 9, 10, 11 and E conditioning this trait in mungbean growing in two conditions, with 7 QTLs being common to both conditions and explaining more than 80% of the trait variation. Several QTLs in both studies located to equivalent LGs but none were co-located. QTL swB1 identified in the latter study appeared to co-localize with a seed weight QTL identified in both cowpea and soybean[44].

Hard seededness: Hard seededness in mungbean is a major problem in producing sprouts but is useful in protecting mature seed from moisture and weather damage[45]. Using the afore-mentioned material for mapping seed weight QTLs, Humphry *et al.*[44] mapped QTLs controlling hard seededness in mungbean

growing in the field and glasshouse conditions. Four QTLs were identified in the field condition while only one QTL was found in the glasshouse condition. The QTL found in the latter condition was also identified in the former condition.

Apart from these traits, resistance gene for bean bug in mungbean is being mapped using various marker types[34].

Genome Mapping in Blackgram

Genetic Linkage Map

Blackgram receives a far less attention in genome research than mungbean. As a result, only one genetic linkage map has been developed by using genetic markers of related legume species[17]. However, compared to mungbean maps, the blackgram map was constructed from a larger population (180 BC_1F_1 plants) and utilized various marker types. The population was derived from the cross between JP219132 (cultivated large-seeded mutant of *V. mungo* var. *mungo*) and TC2210 (wild blackgram *V. mungo* var. *silvestris* from India). The map comprised 148 markers (59 RFLP, 61 SSR, 27 AFLP and 1 morphological markers) and resolved 11 LGs, equivalent to the blackgram haploid genome. The 11 LGs cover a total of 783 cM with the number of markers per LG ranging from 6 to 23 and average distance between the adjacent markers varying from 3.5 to 9.3 cM.

Comparative Genome Mapping

Most of the markers utilized in the development of blackgarm genome maps[17], especially SSRs and RFLPs, were previously mapped on azuki bean[26]. Comparison of 80 common marker loci between the two maps revealed high degree (88%) of genome colinearity[17]. However, inversions, insertions, deletions, duplications and a translocation were also detected. For example, marker order on parts of LG 1, 2 and 5 is reversed between the two species.

Gene and QTL Mapping

Up to the present, only the gene for resistance to MYMV has been molecularly identified in blackgram. Resistance gene analog primer pairs RGA 1F-CG/RGA 1R was found to be linked with MYMV resistance[39]. The amplified DNA fragment associated with the resistance was sequenced and named as *VMYR1*. The sequence showed similarity to plant resistance genes or putative or partial resistance gene sequences. The predicted amino acid sequence also showed highly significant homology with the NB-ARC domain present in several gene products involved in plant disease resistance mechanism. Later, Souframanien and Gopalakrishna[40] identified ISSR linked to MYMV resistance in a RIL population derived from the parents TU 94-2 (resistant cultivar) and susceptible wild. Marker $ISSR811_{1357}$ linked to the MYMV resistant gene at 6.8 cM. A SCAR marker, YMV-1 developed from DNA sequence of $ISSR811_{1357}$ co-segregated with the original marker $ISSR811_{1357}$[40]. The primers RGA 1F-CG/RGA 1R reported by Basak *et al.*[39] was monomorphic between the parents used in this study[40].

Gene Transformation in Mungbean and Blackgram

Mungbean and blackgram have long been notorious for being recalcitrant in tissue culture and gene transformation. In mungbean, genetic transformation via microprojectile gun or *Agrobacterium*-mediated gene transfer using either cotyledonary node or axillary bud region of node has been reported,[46,47] but the efficiency was not impressive. Recently, Mahalakshmi *et al.*[48] reported development of transgenic mungbean plants through an efficient *Agrobacterium*-mediated genetic transformation method using primary leaf explants that could be induced to directly regenerate shoots via a rapid, reliable and genotype independent protocol. Sonia *et al.*[49] reported development of an efficient method of plant regeneration through direct multiple shoot organogenesis from cotyledonary node and establishment of an optimal transformation procedure and selection system that led to the introduction of the insecticidal a-amylase inhibitor and the bialaphos resistance gene for herbicide resistance in mungbean.

In blackgram, improved *in vitro* regeneration systems and genetic transformations by *Agrobacterium tumefaciens* have been recently developed. Saini *et al.*[50] reported an efficient method of plant regeneration via direct multiple shoot organogenesis from cotyledonary-node explants together with an optimal selection system. The authors also described conditions for establishing an *A. tumefaciens*-based transformation protocol for the successful production of transgenic blackgram. Later, under the same protocol but using shoot apical explants, a significant increase (from 1 to 6.5%) in production of transgenic plants has been obtained by preconditioning and wounding of small-sized shoot apices[51]. Stable transformation with 4.31% efficiency was achieved by optimizing several factors influencing tissue competence, *Agrobacterium* virulence, and their compatibility[52].

Future Perspectives

Although some progress in genome research has

been made in mungbean and blackgram, it is still far behind the other major legume crops such as soybean, cowpea, and common bean, or even their relative but less important, azuki bean. The fact that the current genetic linkage maps of mungbean and blackgram are not yet at detailed level, dense or saturated maps with 11 LGs resolved for the crops are needed. A major obstacle to achieve such maps is the lack of high-throughput SSR and SNP markers. As indicated above, the genome study in mungbean and blackgram has been made possible by using genetic markers from other related legumes, and this trend will continue since only limited genetic resources are available for further study in both crops. For example, SSRs from azuki bean, common bean and cowpea will be useful in development of mungbean linkage map with 11 LGs resolved, as in the case of blackgram. Moreover, the information obtained from sequencing of soybean genome[53], common bean ESTs[54], and genespace of cowpea[55], *M. trucatula* and *Lotus japonicus*[56] can create high-thoughput genetic markers for mungbean and blackgram. For the time being, information from a large number of soybean SSR[57,58,59] and newly developed common bean SSR[60,61] is worth investigating. In addition, a database of thousands of cowpea genespace sequences containing SSRs is now publicly available[55]. *In-silico* development of cowpea SSRs and application of those markers in mungbean and blackgram is also interesting. With many genomic tools and resources for legumes are becoming increasingly available, a more detailed and in-depth genome mapping of these two crops will be possible in the near future. By that time, genes or QTLs for important traits in the gene pool should be identified and located on genome maps such that marker-assisted selection can be practiced for the crops.

Another challenge for mungbean and blackgram genome researchers is the development and establishment of a more efficient protocol of genetic transformation to support breeding work as the use of transgenic technology is inevitable for both crops in the future. The technology will be helpful in development of cultivars resistant to serious insects and tolerance to adverse environment that no effective gene source exists in their gene pool such as legume pod borers and drought.

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