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Genetic variation in soybean (Glycine max (L.) Merrill) germplasm

Reda H.Sammour[1,2]*, Abd El-Zahar Mustafa[1,2]

[1]Botany & Microbiology Department, Faculty of Science, King Saud University, Riyadh, (SAUDI ARABIA)

[2]Botany Department, Faculty of Science, Tanta, (EGYPT)

E-mail : reda_sammour@yahoo.com; rsammour@ksu.edu.sa

INTRODUCTION

Glycine max (L.) Merrill is recognized as one of the most important grain legume in theworld in terms of total production and international trade[1]. It is animportant source of protein and oil. Thousands of breeding lines andhundreds of elite cultivars are developed yearly in *Glycine max* (L.) Merrill hybridization programmes over the world. The developing of these breeding lines increased genetic uniformity in the frame of *Glycine max* (L.) Merrill. Therefore, the genetic basis of these released cultivars is rather narrow. To widen the genetic basis of these cultivars, we must introduce new sources of genetic variation. To do this, criteria for parental stock selection need to be considered not only by agronomic value, butalso from the point of view of their genetic dissimilarity. Therefore, the evaluation ofgenetic variation in *Glycine max* (L.) Merrill is a very important task not only for population genetics but also for plantbreeders. The study of genetic variation has fallen within population genetics which hasfocused on analyzing, measuring and partitioning genetic. The genetic variation can beanalyzed by agronomic and biochemical traits, and molecular marker polymorphisms. Its analysis enables estimation of the mating system and monitoring ofgenetic changes caused by factors affecting the reproductive biology of a species. Utilization of exotic germplasm for characteristics such as disease resistance or agronomic traits is the ultimate goal of assessing genetic diversity in plant crops including *Glycine max* (L.) Merrill.

ORIGIN AND DIVERSIFICATION CENTER

Scholars generally agree that cultivated soybean (*Glycine max*) has originated in the easternhalf of North China in the eleventh century B.C. or perhaps a bit earlier[2,3]. It is believed on world wide scale that soybean has been domesticated from theannual wild soybean *Glycine soja* Sieb.et Zucc. China is the origin and diversification center of the cultivated soybean. This was inferred from many studies based on old Chinese literature,the geographic distribution of the wild ancestral species, the levels and types of geneticdiversity of soybean varieties and the archeological evidence[2,4,5]. There are many evidences that China is the origin and main center ofdiversity of soybean. These evidence are (1) soybean has been found in unearthed artifacts; (2) soybeans cultivated in different countries in the world were introduced directly or indirectly from China; (3) the distribution of *G. soja* in China is the most extensive in termsof the numbers and diversity of types; (4) China has the earliest written records of soybeancultivation, about 4500 years ago;and (5) the pronunciation of the word of soybean in many countries is about thesame as the Chinese 'Shu'; for instance, it is pronounced 'soya' in England, 'soy' in the USA,and in other languages.

The scholars have different viewpoints on the original areas of soybean domestication. One of these views is the theorythat soybean originated from northeast China[2], being based on theobservations that there are large numbers of soybean varieties that possess 'primitive' characteristics,such as small black soybean

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germplasm that extensively distributed in the lower and middlereaches of the yellow river North provinces. The second viewpoint is that soybean cultivationoriginated in South China[6]. The scholars who adopted this theory based there evidences on the wide distribution of wildsoybean in this area, extensive presences of primitive soybean varieties such as Nidou,Maliao Dou, Xiao Huangdou, and the close relatedness between cultivated soybeans in southernChina, to wild soybeans in genetic terms based on botanical traits, biochemical and molecular markers[7,8]. In the third theory, it has beenthought that the origin of soybean was the eastern part of northern China (i.e. the lowerreaches the Yellow River)[4]. The evidences for his thought are the sameblooming dates for both wild soybean and cultivated soybean at 35°N, confirming thatcultivated soybean varieties may have been derived from local wild soybean at around35°N. In addition, the protein content of cultivated soybean is close to that of wild soybeanat 34–35°N. The fourth theory stated that the cultivated soybeans have multiple origins[9]. The evidences for that postulation are (1) the ancients of both South and North used local wild soybeanas food and did not domesticated wild soy-beans into cultivated ones; (2) the occurrence and the successful cultivation ofboth wild soybean and cultivated soybean in different regions across China; and (3) the geographical distribution of theshort-day character of wild soybean indicates the possibility of multiple origins of cultivatedsoybean.

EVALUATION OF GENETIC DIVERSITY AT THE BIOCHEMICAL LEVEL

The genetic markers have made evaluation of the genetic andenvironmental components of variation more accurate. The biochemical markers are ones of the interestingmeasures of genetic diversity. They include protein techniques and isozymes[10-15]. The proteintechniques are practical and reliable methods for cultivars and species identification becauseseed storage proteins are largely independent of environmental fluctuation[20-24]. They are less expensive as compared to DNAmarkers. SDS-PAGE is one of these techniques, widely used to describe seed proteindiversity of crop germplasm[25-36]. SDS-PAGE[34,37,38] and discontinuous polyacrylamide slab gel electrophoresis[39] were used very successfully in evaluating the genetic diversity andidentifying soybean (Glycine max) cultivars. Malik et al.[36] evaluated the geneticvariation in 92 accessions of soybean collected from five different geographical regionsusing the electrophoretic patterns of seed proteins. The accessions from various sourcesdiffered considerably, indicating that there is no definite relationship between geneticdiversity and geographic diversity. Similar results were reported by Ghafoor et al.[20]. Based on the results of Ghafoor et al.[40] and Malik et al.[36], SDS-PAGE cannot beused for identification of various genotypes of wild soybean at the intra-specific level,because some of the accessions that differed on the basis of characterization and evaluationexhibited similar banding patterns. However, it might be used successfully to study interrather than intra-specific variation[28,15,40,44]. 2-D electrophoresis can be used to characterize the genotypes exhibitedsimilar banding patterns[20].

Allozyme markers have been used in soybean to evaluate genetic diversity in accessions from diverse geographic regions[15,16], wild soybean innatural populations from China, Japan and South Korea[17,28], and Asian soybean populations[19,33]. From ananalysis of the Kunitz trypsin inhibitor (Ti) and beta-amylase isozyme (Sp1 = Amy3),Hymowitz & Kaizuma[19] defined seven soybean germplasm pools in Asia: (1) northeastChina and the USSR, (2) central and south China, (3) Korea, (4) Japan, (5) Taiwan and southAsia, (6) north India and Nepal and (7) central India. Hirata et al.[33] compared thegenetic variation at 16 isozyme of 781 Japanese accessions with the genetic variations of 158Korean and 94 Chinese accessions, detecting a number of region-specific alleles thatdiscriminated Japanese from Chinese accessions. The presence of alleles specific to theJapanese population suggested that the present Japanese soybean population was not solelya subset of the Chinese population.

EVALUATION OF GENETIC DIVERSITY USING MOLECULAR MARKERS

Introduction

The soybean genome is consisting of around 1115 Mbp, much smaller than the genomes ofmaize and barley, but larger than the genomes of rice and Arabidopsis[41]. Soybean is a tetraploid plant, evolved from a diploid ancestor (n=11), wentaneuploid loss

(n=10), followed by polyploidization (n=20) and diploidization (chromosomepairing behavior)[42]. As a result of polyploidization soybean has asignificant percentage of internal duplicated regions distributed among its chromosomes. Sequence diversity in cultivated soybean is relatively low compared toother species leading to a major challenge in the improvement of this important crop. Toefficiently broaden the genetic base of modern soybean cultivars, we have a detailed insightinto genetic diversity of soybean germplasm. Such insight could be achieved throughmolecular characterization using DNA markers, which are more informative, stable andreliable, compared to pedigree analysis and traditionally used morphological markers. Thegenetic markers include RFLP, RAPD, SSR and AFLP markers were used to probe thegenetic differences between wild and cultivated soybeans or for the origin anddissemination of soybeans[43,45-48]. These studies have revealed higher levels of geneticdiversity in wild soybean.

RFLP (Restriction Fragment Length Polymorphism)

This analysis exploits variation in the occurrence of restriction sites in genomic sequenceshybridizing to a cloned probe. Originally, RFLP analysis required Southern blotting andhybridization, making the method fairly slow and laborious. This technique is still used togenerate ''anchor'' markers, used by many scholars to make consensus recombinationalmaps, though it is often implemented with the polymerase chain reaction (PCR) to generatethe polymorphic fragments[49].

Chung et al.[16] evaluated levels of genetic diversity in USDA soybean germplasm (107accessions), originated from six provinces in central China, using RFLP analysis. Theydetected significant genetic differentiation among the six provinces (mean GST = 0.133). These results suggest that Chinese germplasm accessions from various regions or provincesin the USDA germplasm collection could be used to enhance the genetic diversity of USCultivars.

AFLP (Amplified Fragment Length Polymorphism)

AFLP is an anonymous marker method, detects restriction sites by amplifying a subset of allthe sites for a given enzyme pair in the genome by PCR between ligated adapters. To someextent, it like RFLP detects single nucleotide polymorphisms (SNPs) at restriction sites. Ude et al.[50] analyzed the genetic diversity within and between Asian and NorthAmerican soybean cultivars by AFLP. They found that the average genetic distance betweenthe North American soybean cultivars and the Chinese cultivars was 8.5% and between theNorth American soybean cultivars and the Japanese cultivars was 8.9%, but the Chinesesoybean was not completely separated from the Japanese soybean. They also revealed thatJapanese cultivars may constitute a genetically distinct source of useful genes for yieldimprovement.

RAPD (Random Amplified Polymorphic DNA)

RAPD analysis uses conserved or general primers that amplify from many anonymous sitesthroughout the genome. It is indeed rapid, and need only short primers of randomsequence, but suffers from low polymorphism information content (PIC), poor correlation with other marker data, and problems in reproducibility due to the low annealingtemperatures in the reactions.

The genetic diversity in the wild soybean populations from the Far East region of Russiawas analyzed using RAPD markers[51]. The results obtained suggest that genetically different groups of wild soybean have active development, level ofpolymorphism was significantly higher than in the cultivated soybean, andgeographically isolated subpopulations showed maximum distance from the mainpopulation of wild soybean. The high level of polymorphism between the wild andcultivated soybean accessions was also reported by Kanazawa et al.[52] in their study onsoybean accessions from the Far East using RAPD profiles of mitochondrial and chloroplastDNA. Pham Thi Be Tu et al.[53], An et al.[54] confirmed the results ofKanazawa et al.[52] and Seitova et al.[51] in terms of the high genetic variation betweenthe wild and cultivated soybean accessions. They also found that the diversity of *G. soja* washigher than that of *G. max*; and environmental factors may play important roles in soybeanevolution. Furthermore, they revealed that accessions within each species tend to form subclustersthat are in agreement with their geographical origins, demonstrating that anextensive geographical genetic differentiation exists in both species. Consequently, it wasindicated that geographical differentiation plays a key role in the genetic differentiation ofboth wild and cultivated soybeans. The relationship between geographical differentiationand genetic diversity appeared in the work of Chen &

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Nelson[55] who identifiedsignificant genetic differences between soybean accessions collected from differentprovinces in China. Their data provided pronounced evidence that primitive cultivars ofChina were generally genetically isolated in relatively small geographical areas. Similarresults were obtained by Li & Nelson[46] in their study on soybean accessions from8 provinces in China using a core set of RAPD primers with high polymorphism in soybean[56]. On the contrary, Brown-Guedira et al.[43] did not find anassociation between origin and RAPD markers among soybean lines of more modern origin. It is likely that these genotypes have been dispersed by human intervention from the areasof actual origin. The relationship between genetic differentiation and origin of 120 soybean accessions fromJapan, South Korea and China was evaluated with RAPDs[40]. They foundthat the Japanese and South Korean populations were more similar to each other, whereasboth were genetically distinct from the Chinese population, suggesting that the S. Koreanand Japanese gene pools might be probably derived from a relatively few introductionsfrom China. Li et al.[47] compared the genetic diversity of ancestral cultivars of the N. American (18) as well as the Chinese soybean germplasm pools (32) using RAPD markers,the N. American ancestors have a slightly lower level of genetic diversity. Cluster analysesgenerally separated the two gene pools. In particular, a great genetic variability wasdetected between the ancestors of northern U.S. and Canadian soybeans and the Chineseancestors.

Chowdhury et al.[58] examined the level of genetic similarity among forty-eight soybeancultivars imported out of their country Thailand using DNA (RAPD) markers. They foundhigh level of genetic similarities between these cultivars. Cluster analysis of the obtaineddata classified the 48 cultivars into four groups at 0.57 similarity scale, even though thecultivars are morphologically or geographically very close. Comparing agronomicperformance and RAPD analysis via dendrogram, a total of 11 cultivars can be useful tosoybean breeders in Thailand who want to utilize genetically diverse introductions insoybean improvement. Baranek et al.[59] evaluated the genetic diversity within 19soybean genotypes included in the Czech National Collection of Soybean Genotypes byRAPD method. The polymorphism among the studied genotypes was 46%. Presentedresults enable the selection of genetically distinct individuals. Such information may beuseful to breeders willing to use genetically diverse introductions in soybean improvementprocess.

SSRs (Simple sequence repeats)

SSRs molecular markers have been widely applied in the genetic diversity studies of thesoybean germplasm[48,60-64]. The advantages of SSR over other typesof molecular markers are that they are abundant, have a high level of polymorphism, arecodominant, can be easily detected with PCR and typically have a known position in thegenome. High levels of polymorphism at SSR loci have been reported for both the numberof alleles per locus and the gene diversity[48,60,61,65,66].

Wang et al.[66] used 40 SSR primer pairs to study genetic variability in 40 soybeanaccessions of cultivars, landraces and wild soybeans collected from China. These resultsindicated that wild soybeans and landraces possessed greater allelic diversity than cultivarsand might contain alleles not present in the cultivars which can strengthen furtherconservation and utilization. The UPGMA (Unweighted Pair Group Method withArithmetic) results also exhibited that wild soybean was of more abundant genetic diversitythan cultivars.

A total of 2,758 accessions of Korean soybean landraces were profiled and evaluated forgenetic structure using six SSR loci[64]. The accessions within collections wereclassified based on their traditional uses such as sauce soybean (SA), sprouted soybean (SP),soybean for cooking with rice (SCR), and others-three different Korean *Glycine max*collections and for groups distinguished by their usage, such as SA, SP, and SCR. Nei'saverage genetic diversity ranged from 0.68 to 0.70 across three collections, and 0.64 to 0.69across the usage groups. The average between-group differentiation (Gst) was 0.9 amongcollections, and 4.1 among the usage groups. The similar average diversity among threecollections implies that the genetic background of the three collections was quite similar orthat there were a large number of duplicate accessions in three collections[64]. The selection from the four groups classified based upon usage may be a useful way toselect accessions for developing a Korean soybean landrace core collection at the RDA genebank.

Hudcovicova et al.[67] analyzed allelic profiles at 18 SSR loci of 67 soybean genotypes ofvarious origins. Six only of SSR markers differentiated all 67 geno-

types each from otherssuccessfully. Guan et al.[68] investigated the genetic relationship between 205 Chinesesoybean accessions that represent the seven different soybean ecotypes and 39 Japanesesoybean accessions from various regions using 46 SSR loci. Cluster analysis with UPGMAseparated the Chinese accessions from Japanese accessions, suggesting that soybean in thesetwo countries form different gene pools. It also showed that (1) accessions from China havemore genetic diversity than those from Japan, (2) studied germplasm was divided into threedistinct groups, "corresponding to Japanese soybean, Northern China soybean, SouthernChina soybean and a mixed group in which most accessions were from central China", and (3) Japanese accessions had more close relationship with Chinese northeast spring andsouthern spring ecotypes. This study provides interesting insights into further utilization ofJapanese soybean in Chinese soybean breeding.

Abe et al.[48] analyzed allelic profiles at 20 SSR loci of 131 accessions introduced from Asian countries. UPGMA-cluster analysis clearly separated the Japanese from the Chineseaccessions, suggesting that the Japanese and Chinese populations formed differentgermplasm pools; showed that Korean accessions were distributed in both germplasmpools, whereas most of the accessions from south/central and southeast Asia were derivedfrom the Chinese pool; indicated that genetic diversity in the southeast and south/centralAsian populations was relatively high; and exhibited the absence of region-specific clustersin the southeast and south/central Asian populations. The relatively high genetic diversityand the absence of region-specific clusters in the southeast and south/central Asianpopulations suggested that soybean in these areas has been introduced repeatedly andindependently from the diverse Chinese germplasm pool. Therefore the two germplasmpools can be used as exotic genetic resources to enlarge the genetic bases of the respectiveAsian soybean populations.

Chotiyarnwong et al.[69] evaluated the genetic diversity of 160 Thai indigenous andrecommended soybean varieties by examining the length polymorphism of alleles found in18 SSR loci from different linkage groups. UPGMA-Cluster analysis and principalcomponent analysis (PCA) separated Thai indigenous varieties from recommended soybeanvarieties. However, the genetic differentiation between the indigenous and recommendedsoybean varieties was small.

Shi et al.[70] performed genetic diversity and association analysis among 105 food-gradesoybean genotypes using 65 simple sequence repeat (SSR) markers distributed on 20soybean chromosomes. Based on the SSR marker data, the 105 soybean genotypes weredivided into four clusters with six sub-groups. Thirteen SSR markers distributed on 11chromosomes were identified to be significantly associated with oil content and 19 SSRmarkers distributed on 14 chromosomes with protein content. Twelve of the SSR markerswere associated with both protein and oil QTL. A negative correlation was obtainedbetween protein and oil content.

Mimura et al.[71] investigated SSR diversity in 130 vegetable soybean accessionsincluding 107 from Japan, 10 from China and 12 from the United States. Eighteen of the 130accessions were outliers, and the rest of the accessions were grouped into nine clusters. Themajority of food-grade soybean cultivars were released from Japan and South Korea becauseof the market availability and demands. However, the genetic diversity of South Koreafood-grade soybean remains unreported[71].

Nguyen et al.[82] used 20 genomic SSR and 10 EST-SSR SSR to explore the geneticdiversity in accessions of soybean from different regions of the world. The selection of thethirty SSR primer-pairs was based on their distribution on the 20 genetic linkage groups ofsoybean, on their trinucleotide repetition unit and on their polymorphism informationcontent. All analyzed loci were polymorphic. A low correlation between SSR and EST-SSRdata was observed, thus genomic SSR and EST-SSR markers are required for an appropriateanalysis of genetic diversity in soybean. They observed high genetic diversity whichallowed the formation of five groups and several subgroups. They also observed a moderaterelationship between genetic divergence and geographic origin of accessions.

Xie et al.[73] analyzed genetic diversity of 158 Chinese summer soybean germplasm, fromthe primary core collection of G. max using 67 SSR loci. The Huanghuai and Southernsummer germplasm were different in the specific alleles, allelic-frequencies and pairwisegenetic similarities. UPGMA cluster analysis based on the similarity data clearly separatedthe Huanghuai from South-

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ern summer soybean accessions, suggesting that they weredifferent gene pools. The data indicated that Chinese Huanghuai and Southern summersoybean germplasm can be used to enlarge genetic basis for developing elite summersoybean cultivars by exchanging their germplasm.

Most diversity studies on cultivated soybean published by now have focused on NorthAmerican[53,71,84] Asian[48,60,62,64,73] aswell as South American[75] soybean germplasm. In several studies only afew genotypes of European origin have been represented among germplasm studied[43,61,74,76]. Baranek etal.[59] evaluated genetic diversity of 19 Glycine max accessions from the Czech NationalCollection using RAPD markers. Recently, Tavaud-Pirra et al.[77] evaluated SSR diversityof 350 cultivated soybean genotypes including 185 accessions from INRA soybean collectionoriginating from various European countries and 32 cultivars and recent breeding linesrepresenting the genetic improvement of soybean in Western Europe from 1950 to 2000.

They found the genetic diversity of European accessions to be comparable with those of theAsian accessions from the INRA collection, whereas the genetic diversity observed inEuropean breeding lines was significantly lower. Breeding material and registered soybeancultivars in southeast European countries are strongly linked to Western breedingprograms, primarily in the USA and Canada. There is little reliable information regardingthe source of germplasm introduction, its pedigree and breeding schemes applied. Consequently, use of these genotypes in making crosses to develop further breeding cyclescan result in an insufficient level of genetic variability. Assessing the genetic diversity of thisgermplasm at genomic DNA level would complement the knowledge on the Europeansoybean gene pool (germplasm) and facilitate the utilization of the resources fromsoutheastern Europe by soybean breeders. Ristova et al.[78] therefore assess geneticdiversity and relationships of 23 soybean genotypes representing several independentbreeding sources from southeastern Europe and five plant introductions from WesternEurope and Canada using 20 SSR markers. Cluster analysis clearly separated all genotypesfrom each other assigning them into three major clusters, which largely corresponded totheir origin. Results of clustering were mainly in accordance with the known pedigrees.

EST (Expressed Sequence Tags)

The use of functional molecular markers, such as those developed from EST allows directaccess to the population diversity in genes of agronomic interest that they represent codingsequences, facilitating the association between genotype and phenotype. Nelson andShoemaker[79] identified approximately 45,000 potential gene sequences (pHaps) fromEST sequences of Williams/Williams 82, an inbred genotype of soybean (Glycine max L.Merr.) using a redundancy criterion to identify reproducible sequence differences betweenrelated genes within gene families. Analysis of these sequences revealed single basesubstitutions and single base indels are the most frequently observed form of sequencevariation between genes within families in the dataset. Genomic sequencing of selected lociindicates that intron-like intervening sequences are numerous and are approximately 220 bpin length. Functional annotation of gene sequences indicates functional classifications arenot randomly distributed among gene families containing few or many genes. Theidentification of potential gene sequences (pHaps) from soybean allows the scientist to get apicture of the genomic history of the organism as well as to observe the evolutionary fates ofgene copies in this highly duplicated genome.

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