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A Review: Molecular Markers in Jackfruit (*Artocarpus heterophyllus* Lam.)

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ABSTRACT

Jackfruit being a perennial fruit crop, the crop improvement using marker assisted selection plays an important role in developing best cultivars for various applications. Although markers play a significant role in selection of traits of commercial importance, their application in jackfruit is limited due to tetraploid nature of the crop. However, efforts have been made by several workers to identify the markers linked to fruit quality traits (soft and firm fleshed types, fruit cracking and pulp color). Thus there is a need for whole genome sequencing in jackfruit to identify the marker sequence linked to the traits of commercial importance such as fruit size and shape, pulp color, age of fruit bearing. In this review article, effort has been made to compile the studies conducted on molecular markers in jackfruit.

Keywords Molecular markers, Jackfruit, *Artocarpus heterophyllus*, Fruit quality traits.

INTRODUCTION

Jackfruit (*Artocarpus heterophyllus* Lam.) belongs to the family Moraceae. It is believed to have originated in the South Western rain forests of India (Naik 1949) and has been introduced and cultivated in many tropical countries. Besides India, jackfruit is commonly grown in many parts of Southeast Asia (Rahman et al. 1999), in the evergreen forest zone of West Africa, in Northern Australia (Azad et al. 2007) and in South Florida as well (Schnell et al. 2001). Jackfruit is a medium - sized evergreen tree, typically reaching 8–25 m in height and its fruit is the largest among all cultivated plants. The succulent and aromatic flavored fruits are eaten fresh or preserved in many forms. The fruit contains high levels of minerals such as potassium, phosphorus, calcium, iron and zinc with moderate levels of protein, carotenoids and riboflavins. Being protoandrous and crosspollinated and propagated mainly by seed, jackfruit shows wide variability in many characters including age of first bearing and the texture, flavor and color of the fruit. Jackfruits are generally classified into two main types (Odoemelam 2005) : Those having fruits with small, fibrous, soft and spongy flakes with very sweet carpels called as

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"Koozhachakka" in Malayalam ; "Biluva" or Ambli in Kannada. The other type being crunchy though not as sweet, with crisp carpels and of high quality called as "Varikka" in Malayalam ; "Bakke" in Kannada. So far, there are few developed varieties namely PLR-1, PLR-2 and PP1-1 from TNAU, Mottam Varikka and Sendhura from KAU, Swarna from UAS, Bengaluru and Konkan Prolific from BSKKV, Dapoli. Some exotic varieties such as J-33, Dang Surya and Nang Dak from Malaysia and Vietnam super early from Vietnam have been introduced. However in different localities, local varieties have different names based on their variability in yield, fruit shape and size, rind color, pulp color, number of flakes, texture of flakes, total sugars and many other characters.

Taxonomy and cytology

Artocarpus heterophyllus Lam., belongs to the family Moraceae, along with *Ficus* spp. and *Morus* spp. (mulberry) (Chandler 1958, Popenoe 1974). It crosses freely with *A. integer*, *A. lanceaefolius* and *A. rigidus* which are believed to be are closely related species of *A. heterophyllus* (Kanzaki et al. 1997). Moraceae family encompasses about 1,000 species in 67 genera, mostly tropical shrubs and trees, but also a few vines and herbs (Bailey 1949, Merill 1912). The genus Artocarpus comprises about 50 species, 11 of which are known to produce edible fruits (Barrau 1976, Campbell 1984, Corner 1988). Very little information is available on the cytology of *A. heterophyllus* genepool. Darlington and Wylie (1956) have reported that it is tetraploid with a somatic chromosome number of 56 (2n=4x=56), thus the basic chromosome number (x) is 14. In contrast, in a study carried out by Zhuanying et al. (2015) pertaining to ploidy and genomic size determination of jackfruit lines it was reported that the ten jackfruit lines under the study were diploid (2n=2x=56). The genome size of soft fleshed type (1902 ± 8.08) was larger than that of the firm fleshed types (1243.75 ± 9.21 to 1540 ± 3.55) indicating that the firm fleshed jackfruit genotypes have been evolved from the soft fleshed types. These cytological complexities related to the ploidy level and the genome sizes have made the application of the molecular markers in jackfruit as a cumbersome process.

Morphological markers

Morphological markers are detected with naked eye and their inheritance can be monitored visually without specialized biochemical or molecular techniques. In jackfruit, several morphological traits like trunk character, leaf shape and size, fruit shape and size, latex content in ripe fruits and pulp color can act as the morphological markers. For example, Rudhrakshi type of jackfruit has typical round fruit shape with flat spines that are hexagonally arranged on the rind of the fruit. The pulp color varieties from white, creamish yellow, yellow, orange and red. The red types are preferred in market for its attractive color and they are popular as Chandhra Halasu in Karnataka. The morphological markers are affected by environment their expression altered by epistatic and pleiotropic interactions. The morphological markers are limited in number ; their alleles interact in a dominant-recessive manner, thereby making it impossible to distinguish the heterozygous individuals from homozygous individuals. Many of these traits are of polygenic inheritance and expressed only long juvenile phase (Hamrick et al. 1992). However, characterization of genotypes at the genetic level, supplemented by phenotypic characters, provides the first step towards more efficient conservation, maintenance and utilization of existing genetic diversity (Prakash et al. 2002).

Biochemical markers

The phenotypic approach to characterize plant population has been criticized because it does not provide genetic information (Simpson and Withers 1986). Biochemical markershelp in assisting selection of superior types and to find out the extent of genetic diversity within the selected clones. However, Pushpakumara et al. (2005) tried isozyme analysis jackfruit which showed low levels of polymorphism. The study revealed low level of polymorphism and only two out of sixteen (12.5%) enzymes were polymorphic. There was no evidence to distinguish soft fleshed and firm fleshed genotypes. The success of biochemical markers may also depend on the stage at which the plant material is used for extraction of enzymes, since enzyme expression at early stages (Embryo ; leaf tissues in seedling) may not be the same as at later

stages (Tissue from ripening syncarps). Further, fifty accessions of Bangladhesh were evaluated by Azad et al. (2007) for four enzyme systems. The isozyme patterns were determined on the basis of number and position of loci. They discovered that, morphological traits such as weight, length, girth of the fruits and percentage of pulp correlated poorly with environmental factors, suggesting that these characters are more likely genetically controlled.

Peroxidase and esterase isozymes were investigated from leaf tissue samples of forty four selected (superior) jackfruit genotypes of West Bengal by Wangchu et al. (2011). These selected genotypes were collected following jackfruit IPGRI descriptors (IPGRI 2000) after surveying 1500 trees in the districts of Nadia, 24 Parganas (N) and Coochbehar in West Bengal. Polymorphism was observed in both the enzyme systems studied. In the peroxidase assay, 7 loci were identified among the forty four genotypes and the relative mobility (Rm) values of the loci ranged between 0.29 and 0.50. Whereas, in the esterase assay 6 loci were identified and the relative mobility (Rm) values of the loci ranged between 0.22 and 0.65. Moreover, it was observed that genotypes collected from nearby locations did not show similar banding patterns indicating several causes for genetic diversity viz. geographical origin, exchange of genetic stocks, genetic drift, spontaneous variation, natural and artificial selection, cross pollination and seedling origin of the plant. In this study, both the young and mature leaves were used for biochemical extraction and it was found that the mature leaves gave better and clear banding patterns as compared to young ones. However, the isozyme markers are also known to be affected by both environment and post-translation modification and their practical uses are limited (Akashi et al. 2002).

Molecular markers

A molecular marker is a DNA sequence which is readily detected and whose inheritance can easily be monitored. They rely on DNA assay incontrast to morphological markers based on visible traits and biochemical molecular markers based on protein products. Hence, DNA is an ideal molecule for studying polymorphism. These molecular markers can be linked to important traits and used for early selection of potentially desirable genotypes. Molecular markers are capable of producing patterns that are unique for each individual genotype.

Random amplified polymorphic DNA (RAPD)

RAPD variation was assessed in sixty five accessions of jackfruit from Leizhoupeninsula, Southern China (Ye et al. 2005). About 78 loci detected by 16 RAPD primers and among them 69 were polymorphic. The cluster analysis categorized the genotypes into three groups. However, this could not distinguish the genotypes based on their bearing behavior and latex content.

Genetic diversity in twelve high-yielding jackfruit accessions obtained from different locations in Southern India was estimated with RAPD markers (Simon et al. 2007). About 171 amplified fragments were obtained using 23 random primers of which, 115 (67.3%) were polymorphic and shared between at least two individuals, while 46 (26.9%) were monomorphic and common to all the individuals. Only ten (5.8%) were polymorphic and unique. The genetic dissimilarity matrix revealed a maximum genetic distance of 7.9% between a clone of 'Mottamvarikka' and 'Chandrahalasu' from distant locations, while the minimum genetic distance (5%) was between 'Mottam Varikka' and 'Kerala', indicating their similar geographical origin. Ward's method of cluster analysis grouped all individuals on the dendrogram into two major clusters according to their geographical location.

Prasad et al. (2014) screened two RAPD primers OPA-9 and OPA-8 in five different jackfruit genotypes. The marker assay yielded 57 amplified fragments of which primer OPA-9 had higher polymorphism (24%) than OPA-8 (22%).

Anu et al. (2015) screened 30 RAPD primers to realize the genetic relationship among six superior jackfruit selections. Among them, ten primers good amplification which could be reproduced. The primer OPA-4 (AATCGGGCTG) gave the maximum number of polymorphic loci (14) and OPD–19 (CTGGGGACTT) produced least (9). Four major clusters were

obtained for genotypes which followed geographical separation.

Sequence characterized amplified region (SCAR)

An attempt to develop trait specific marker to differentiate between the soft fleshed and firm fleshed fruit types of jackfruit was tried by Pushpakumara and Harris (2007) using the RAPD markers in Sri Lanka. These two types of fruit could be found in jackfruit varying in the firmness of the edible flesh of the ripened fruit (Acedo 1992, Yaacob and Subhadhrabandhu 1995, Pushpakumara et al. 1997). Variation in flesh texture between the two fruit types has not been consistent through generations and seeds planted from either fruit type yields a mixture of both. However, little is known about their pattern of segregation. The seedlings of these two types cannot be morphologically differentiated and is possible only when ripe syncarps are produced, which generally takes eight to ten years from planting. Identification of fruit types of jackfruit at the seedling stage is useful in the management of genetic resources for conservation and genetic improvement programs (Pushpakumara 1997). The two fruit types of this species are not consistently distinguishable on the basis of morphological traits of mature trees (Pushpakumara 1997, Soepadmo 1991). Furthermore, apart from firmness of the ripened flesh no morphological or phenological differences were observed between two fruit types in a study carried out on flowering and fruiting morphology and phenology (Pushpakumara 1997). Pushpakumara and Harris (2007) revealed that the two fruit types may be distinguished from one RAPD product, namely OPB-01 with fragment size of 123 kb for firm fleshed genotypes which were absent in soft fleshed genotypes. About 100 primers were screened and only five primers showed polymorphism for fruit type and were considered as useful markers to differentiate fruit types of jackfruit. The reproducibility test was carried out for those five primers with 30 trees of each type.

The occurrence of two fruit types in jackfruit may also be a result of different enzyme activities, or the inhibition of an enzyme / set of enzymes at fruit ripening. In many plant species, the process of fruit ripening and softening is largely the result of enzyme-mediated physico-chemical changes, which are genetically and developmentally regulated (Brady 1987). Therefore, differential gene expression patterns that are correlated with changes in growth and physiology have been a source of concern in many studies (Christofferson et al. 1982, Oh et al. 1995). Results of such studies have revealed that fruit ripening occurs under the control of genes expressed during the ripening process. Studies on biochemical changes during the ripening of the firm and soft fleshed fruit types of jackfruit revealed a common process of ripening in both the fruit types (Rahman et al. 1995, Selvaraj and Pal 1989). It was also suggested that the texture of the flesh of the ripened syncarps are related to the degree of change of activities in enzymes such as pectin esterase and polygalacturonase towards the early ripening stage. These changes were more marked in the soft-fleshed type and either arrested or delayed in the hard-fleshed fruit type. Although such evidence supported the developmental expression of enzymes (hence genes), little is known about the gene expression during fruit ripening in jackfruit (Pushpakumara et al. 2005). Cloning, sequencing and conversion of the RAPD marker to a SCAR marker for verification of the result and development of highly reproducible and easy markers can assist the effective identification of fruit types at the early stage of growth.

Another such trial to develop trait specific marker was undertaken by Singh et al. (2011) to identify the SCAR marker related to fruit cracking in some jackfruit genotypes. The RAPD primer OPC-7 produced polymorphic loci of 810 bp in fruit cracking genotypes. The result was confirmed for reproducibility. Further, the marker was sequenced and homology search was done using BLASTX. The gene sequence has been deposited in gene bank (NCBI). This can be used as a marker to identify the jackfruit genotypes with fruit cracking character at the seedling stage.

Amplified restriction fragment length polymorphism (AFLP)

AFLP markers are reported to be the best markers for genetic diversity studies due to their ability to scan the whole genome with two distinct types of

primer sequences. The AFLP technique was adapted by Schnell et al. (2001) for genetic diversity analysis in twenty six accessions collected from 8 countries. They screened 30 primers of which, 12 primers produced good quality polymorphic fragments with moderate level of polymorphism (49.2%) among the genotypes. Cluster analysis and principal component analysis (PCA) grouped all of the jackfruit accessions with Southeast Asian origin into one major cluster with little bootstrap support for groupings within the cluster. The Indian accessions were grouped in a different cluster, as did the hybrid and the bread fruit accession.

AFLP markers were used to investigate genetic diversity of fifty jackfruit accessions collected from different parts of South India by Shyamalamma et al. (2008). They selected 8 primers from the 16 primer pairs evaluated for screening of genotypes. These primer combinations amplified 5976 loci of which, 1267 (22%) were polymorphic. Among the jackfruit accessions, the similarity coefficient ranged from 0.137 to 0.978 ; the accessions also shared a large number of monomorphic fragments (78%). Three major clusters were obtained by cluster analysis and principal component analysis. The genotypes growing in regions with very dry conditions and in locations having medium to heavy rainfall grouped in different clusters and a good correlation between genetic and geographical data were found.

Similarly, the Li et al. (2010) analyzed the genetic diversity of fifty jackfruit accessions from three provinces in China using AFLP marker. A total of 320 unambiguous loci were produced by eight primer combinations and 65 (20.3%) of them were polymorphic. The dendrogram revealed five groups which could not distinguish the genotypes based on geographical origin, fruit quality and bearing behavior.

Simple sequence repeats (SSRs)

SSR markers for jackfruit diversity estimation were developed by partial genome sequencing of jackfruit (Kavya et al. 2019). The primers thus obtained were used to estimate the genetic diversity among the twenty jackfruit genotypes collected from different parts of Karnataka to differentiate the genotypes of jackfruit with distinct pulp colors. Based on the color of the jackfruit pulp, the twenty genotypes were classified into four types viz., red, orange, yellow and cream. A total of twenty two SSR primers gave good amplification in twenty jackfruit genotypes and only nine primers were found to be polymorphic. The similarity matrix generated from the marker data showed correlation between pulp color and genotypes in such a way that the genotypes with similar pulp color had high similarity index. All the genotypes with red color pulp were closely related among themselves and also a bit closely related to the orange color genotypes. The cream color genotypes had similarity with the yellow color genotypes rather than orange and red colored ones. Three major clusters were obtained by the dendrogram where in the cluster 1 grouped three genotypes with cream color pulp. Cluster II was further classified into two sub-clusters IIa and IIb, which comprised two cream and two yellow pulp colord genotypes. Cluster III comprised large number (thirteen) of the genotypes with yellow, orange and red pulp color. The genotypes with red color pulp were closely linked to orange color pulp irrespective of the place of collection indicating the genetic relations for the pulp color rather than the place of cultivation. Further studies were recommended to screen and find out the sequences linked to pulp colors.

Thumilan et al. (2016) developed and validated 206 EST (Expressed Sequence Tags) derived SSR markers using transcriptome data generated from leaf tissue of a drought tolerant mulberry (Moraceae) genotype, Dudia white. A total of 264 primers to the most appropriate repeat regions were designed, of which 206 were locus specific out of which 60 (29%) were transferable to jackfruit.

Inter-simple sequence repeats (ISSRs)

Sane et al. (2009) distinguished eighteen accessions of jackfruit maintained in the field gene bank of Indian Institute of Horticultural Research Bangalore by ISSR analysis. The cluster diagram depicting genetic relationships between accessions revealed that the accessions Gumless, Dorichandra and Tenvarike were the most divergent ones. The morphological characters when collated with DNA profiles of these

accessions showed that Tenvarike, which is a divergent accession, had desirable fruit characters such as low latex exudation and low flake fiber content.

A study was under taken to assess the molecular difference between clonal and seedling progenies collected from two distinct mother plants known to produce good quality fruits. The clonal progenies were propagated by grafting from a single mother plant and the seedling progenies were raised from seeds of elite mother plant known for quality fruits. The major objective was to elucidate molecular variations between the clonal and seedling progenies using ISSR markers using ISSR markers among twenty five progenies of jackfruit (Wann et al. 2013). Out of 25 ISSR primers used, only 6 gave good amplification. Higher polymorphism (34.78%) was exhibited by primer 823 and lower (10.00%) by primer 815. The cluster analysis grouped the progenies of seedling and clonal origin into four groups wherein, cluster I, II, III and IVb grouped all the clonal progenies and cluster IVa contained all the seedling progenies.

Maturase K (matK gene)

Maturase K (matK) is a plant plastidial gene (Zoschke et al. 2010) and the protein it encodes is an intron maturase, a protein that splices introns. Amongst other maturases, this protein retains only a well conserved domain and remnants of a reverse transcriptase domain (Mohr et al. 1993). Universal matK can be used for DNA barcoding of angiosperms (Yu et al. 2011). The level of genetic diversity and genetic relationships among six varieties of jackfruit were assessed using 'matK gene' based on PCR technique and RFLP markers (Prem et al. 2017). The partial sequence of 'matK' gene of six different jackfruit varieties was used to analyze their level of genetic diversity and genetic relationships. The size of amplified products was approximately 700 bp. After sequencing and sequence editing, sequence information on a 674 bp region was finally obtained for analysis. The alignment of sequences revealed two haplotypes out of 674 sites. The nucleotide frequencies were 30.00% (A), 37.69% (T/U), 17.93% (C) and 14.39% (G). The sequence of the Singapore varikka variety had change in a single nucleotide in the 654th base pair locus with adenine (A) whereas all the other five genotypes had cytosine (C).

CONCLUSION

The molecular marker studies carried out in jackfruit using RAPD, SCAR, AFLP, SSR and ISSR has been a preliminary work and the efforts made by various workers reveals association of some markers for the traits of interest. However, these markers need to be verified to confirm their application in crop improvement program.

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