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Inter and intra-specific crossability studies on *Mangifera* species

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ABSTRACT

Inter-specific and inter-varietal crosses were attempted using *Mangifera indica* cv. Amrapali as a female parent and *M. odorata* and *M. indica* cv. Vanraj as male donor parents (2016–19). Initial fruit set after 7 days of pollination (DAP) was 81.48%, which reduced to 2.48% at harvest. However, in inter-specific crosses, initial fruit set was 79.89%, which reduced to 0.45% at the time of harvesting. Progenies obtained from inter-varietal and inter-specific crosses were subjected to confirmation of parentage using SSR markers. Eight polymorphic SSR markers were used to estimate the paternity, maternity and new alleles in the hybrids. Based on fragment analysis, the paternity, maternity and new alleles of 12 inter-specific and 17 inter-varietal hybrids were estimated by finding a similar number of alleles between the offsprings and parents. Among inter-specific hybrids, AO2, AO7, AO11, and AO12 showed ≥50% of paternal allele inheritance, while AO1, AO2, AO4, AO5, AO7, AO8, AO9, AO10 and AO12 showed ≥50% of maternal allele inheritance. Inter-specific hybrids such as AO1, AO3, AO5, AO9, AO10 and AO11 inherited new alleles. Among inter-varietal hybrids, AV1, AV2, AV4, AV5, AV6, AV10, AV11, AV12, AV13, AV14, AV15 and AV17 possessed ≥50% paternal allele, while, AV1, AV2, AV3, AV5, AV6, AV7, AV8, AV10, AV11 and AV15 had ≥50% maternal allele. Three inter-varietal hybrids, viz. AV8, AV9 and AV16 inherited new alleles. It is concluded that SSRs markers are useful in ascertaining the parentage of hybrids obtained from inter-specific and inter-varietal crosses in mango.

Keywords: Inter-specifc crosses, Inter-varietal crosses, Mango, *Mangifera* sp.

Mango (*Mangifera indica* L.) originated in Indo-Myanmar region has 69 recognized species including the edible fruit to forest trees with fibrous and resinous fruits (Kosterman and Bompard 1993). In India, about 30 mango cultivars are being grown commercially. The majority of them possess narrow adaptability and show eco-geographical preferences for growth and yield (Yadav and Rajan 1993). Mango is considered as a difficult plant species to handle in breeding programmes owing to its long juvenile phase, high level of heterozygosity, poor understanding of the genetics of important horticultural traits (Ramachandra *et al*. 2021). Mango hybridization work attempted at the national and international levels has given more emphasis on inter-varietal hybridization. Although, there is a growing awareness among the mango breeders with regard to the utility of different *Mangifera* species, hardly any effort has been made to know about their crossability with the cultivated species. Most of the *Mangifera* species are valuable sources of the gene(s) for one or other desirable traits. These species can be utilized in crop improvement programme or as rootstocks. According to Mukherjee *et al*. (1968), successful crosses between *M. odorata* and *M. zeylanica* were made in India. Similarly, *M. laurina* has been used in Australian mango breeding programmes for imparting anthracnose resistance. *Mangifera orophila* from Malaysia and *M. dongnaiensis* from Vietnam are thriving well in forests located 100-1700 m amsl and their utilization in breeding progarmmes could extend the cultivation of mango at higher altitude. Similarly, *M. altissima* is reportedly resistant to mango hoppers, tip and seed borers could also contribute to higher productivity. The prerequisite for utilizing different *Mangifera* sp. is their availability and their crossability with *M. indica*. *M. odorata* deserves attention in breeding programmes due to its prominent flavour and fruit firmness. It is probably a hybrid of *M. indica* and *M. foetida* (Hou 1978, Kiew *et al*. 2003). In the present study, *M. odorata* and *M. indica* cv.Vanraj have been used as male donor parents and *M. indica* cv. Amrapali as female parent for investigating the crossability among them.

MATERIALS AND METHODS

An experiment was conducted at ICAR-Indian Agricultural Research Institute, New Delhi during 2016–19. In the present study, *M. indica* cv. Amrapali as a female parent and *M. odorata* and *M. indica* cv. Vanraj as male donor parents was used. Amrapali (Dashehari × Neelum) is a dwarf, precocious, highly regular, prolific bearer, and

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suitable for high-density planting. It is a preferred female parent in mango hybridization programmes worldwide as it is a good combiner. Vanraj (*M. indica* L.) is moderately vigorous and bearing is medium. Fruits are medium to large with a blush of jasper red on the shoulders and have a good aroma and long shelf-life. It is also moderately resistant to hoppers and winds (Pandey and Dinesh 2010). Vanraj can be utilized for imparting attractive peel colour in progenies. *M. odorata* has a unique feature of emitting characteristic fragrant resinous smell. Trees are medium in size and have ability to grow in areas receiving excessive rainfall and having excessive humidity. The fruits are having more firmness resulting in a long shelf-life (Jha *et al*. 2010).

Hybridization work was carried out at mango orchards of ICAR-Indian Institute of Horticultural Research, Hesaraghatta Lake, Bengaluru during 2016–19. Controlled hand-pollination was carried out by selecting healthy panicles emerging on secondary or tertiary branches following the procedure suggested by Dutta *et al*. (2013). The number of male and hermaphrodite flowers per panicle were observed at the full bloom on panicles located in all four directions of canopy. Total numbers of flowers crossed were recorded from both inter-specific and inter-varietal crosses. Fruit set percentage was recorded at 7 DAP by dividing the number of flowers showing sign of ovary enlargement by the total number of pollinated flowers and multiplied by 100. Fruit retention was recorded at 20 DAP and at harvest. The fruit growth pattern was observed in fruitlets at regular intervals. Fruits harvested at maturity were subjected to ripening under ambient conditions. Stones were extracted, washed and subjected to removal of hardcover for separation of mature seeds inside. These hybrid seeds were sown in polybags (9” h × 7” dia.) having cocopeat, sand and soil (1:1:1). After germination of hybrid seeds, the plantlets were kept for acclimatization and the number of hybrid progenies that survived during acclimatization was recorded after 60 days. The recovery of hybrid stones was calculated by dividing the number of hybrid fruits harvested by number of crossed flowers. The recovery of hybrid plantlets was calculated by dividing the number of hybrid plantlets survived post acclimatization with the number of hybrid stones obtained from crosses.

Parentage confirmation of hybrids obtained from inter-varietal and inter-specific crosses was attempted using SSR markers. Total genomic DNA was isolated from the newly emerged leaves as per the procedure suggested by Doyle and Doyle (1987). The quantity and quality of DNA were measured using NanoDrop TM spectrophotometer (Thermo Fisher, USA) and agarose gel using uncut λ DNA. Finally, the DNA was diluted to obtain a required concentration for further usage in PCR reactions (Srivastav *et al*. 2021). Initially, 12 SSR primer pairs were screened using three parents, two inter-specific and two inter-varietal hybrid progenies to check the amplification and reproducibility of the primer pairs. A total of eight SSR primers successfully amplified and showed polymorphism. Among the 8 SSR primers, two (MiIIHR31 and MiIIHR34) had tri nucleotide, 4 di-nucleotide (MiIIHR18, MiIIHR23, MiIIHR30 and MiIIHR36), and two (MiIIHR17 and MiIIHR26) had both di-and-tri nucleotide repeats (Table 1). The size of the amplification product ranged from 107 to 269 bp.

Polymerase chain reaction (PCR) was performed using Applied Biosystems Eppendorf Nexus Gradient Thermal Cycler. Each reaction mixture had 1.5 µl of reaction buffer A (*p*H 9.0, 10 mMTris with 15 mM $MgCl_2$, 50 mMKCl and 0.01% gelatin), 1.5 µl of 25 mM $MgCl_2$, 1.0 µl of 10 mM dNTPs, 1.5 µl (5 pmol) of fluorescently labeled (FAM, VIC, NED, and PET) forward primer, 1.5 µl of reverse primer (5 pmol), 0.5 µl (3 U/µl) of Taq DNA polymerase, 3 µl of template DNA and 4.3 µl of nuclease-free water.

Table 1 Details of SSR loci used for parentage analysis

Locus	Primers (5’-3’)	Repeat motif	Allelic size range (bp)
MiIIHR17[a]	F: GCTTGCTTCCAACTGAGACC R: GCAAAATGCTCGGAGAAGAC	$(GT)_{13}GAGT(GA)_{10}$	230-269
MiIIHR18[b]	F: TCTGACGTCACCTCCTTTCA R: ATACTCGTGCCTCGTCCTGT	$(GT)_{12}$	148-193
MiIIHR23[c]	F: TCTGACCCAACAAAGAACCA R: TCCTCCTCGTCCTCATCATC	$(GA)_{17}GG(GA)_6$	107-156
MiIIHR26[a]	F: GCGAAAGAGGAGAGTGCAAG R: TCTATAAGTGCCCCCTCACG	$(GA)_{14}GGA(GAA)_2$	127-171
MiIIHR30[d]	F: AGCTATCGCCACAGCAAATC R: GTCTTCTTCTGGCTGCCAAC	$(CT)_{13}$	190-213
MiIIHR31[c]	F: TTCTGTTAGTGGCGGTGTTG R: CACCTCCTCCTCCTCCTCTT	$(GAC)_6$	207-260
MiIIHR34[b]	F: CTGAGTTTGGCAAGGGAGAG R: TTGATCCTTCACCACCATCA	$(GGT)_9(GAT)_5$	203-245
MiIIHR36[d]	F: TCTATAAGTGCCCCCTCACG R: ACTGCCACCGTGGAAAGTAG	$(TC)_{17}$	210-250

[a] VIC; [b] NED; [c] FAM; [d] PET

The amplification program included an initial step of 2 min at 94°C, followed by 35 cycles of denaturation at 94°C for 30 sec, annealing at 53°C for 30 sec and elongation at 72°C for 1 min. A final extension was performed at 72°C for 5 min (Srivastav *et al*. 2021). The amplified products were analyzed using 1.5% agarose gel and the PCR products were sent for fragment analysis by capillary electrophoresis. The FSA files obtained after genotyping was analysed by the Genemarker3.0 software for scoring the amplified alleles. After scoring amplified alleles in parents and offspring, the number of alleles similar to a paternal, maternal parent and new alleles were counted manually in MS excel software. Finally, maternity, paternity and new allele per cent were calculated as:

Maternity (%) = No. of alleles similar to a maternal parent/Total number of alleles.

Paternity (%) = No. of alleles similar to paternal parent/ Total number of alleles.

New allele (%) = No. of new alleles / Total number of alleles.

Based on the allelic data tree was constructed applying UPGMA method using PAST 3.0 software.

RESULTS AND DISCUSSION

Mango being andromonoecious species differ significantly for sex ratio among cultivars and species. In present study also male and hermaphrodite flowers varied significantly among parental genotypes. Amrapali had 4.43 fold more hermaphrodite flowers than male flowers. However, Vanraj had 1.67 times more hermaphrodite flowers and *M. odorata* had 3.48 times more hermaphrodite flowers compared to male flowers. The differential number of male and hermaphrodite might be due to the genotypic effect and affected by the prevailing weather conditions during flowering up to some extent.

In the inter-specific cross, on an average 3.59 flowers per panicle of the female parent have been crossed with *M. odorata*. Among the crossed flowers, 79.89% of flowers showed signs of fruit set after 7 DAP. In the inter-varietal cross (Amrapali × Vanaraj), total of 635 panicles having 2,420 flowers were crossed. Among the crossed flowers, 81.48% of flowers showed signs of fruit set after 7 DAP. The sign of the fruit set was ascertained by observing swollen green ovary in the hand-pollinated flowers. The initial fruit set obtained in both inter-specific (Amrapali × *M. odorata*) and inter-varietal (Amrapali × Vanraj) crosses showed higher fruit set than fruit set (16.1%) reported by Pinto *et al.* (2004) in Amrapali × Tommy Atkins and 29.3% in open-pollinated Amrapali (Pandey and Kumar 2006). This indicated that there was good cross-compatibility between wild *M. odorata* and cultivated species *M. indica* cv. Amrapali. The work carried out at ICAR-Indian Agricultural Research Institute, New Delhi also suggested that Amrapali as an effective female parent owing to its better combination with number of male donor parents (Srivastav *et al.* 2014). Fruit retention after 20 DAP in inter-specific was 25.51%, which was 1.63 times more than the fruit retained under inter-varietal crosses. The fruit retention under inter-varietal crosses was 15.62% after 20 DAP. It was evident that on 7th day the there was a non-significant difference for fruit retention in inter-specific as well as inter-varietal crosses. However, fruit retention after 20 days of pollination was significantly higher in inter-specific crosses compared to inter-varietal crosses (Fig 1). In mango, signs of enlargement and change of colour of the ovary during 15 days of pollination may be due to effective fertilization or also due to endogenous auxin in the ovary which leads to swelling of ovary even in non-fertilized flowers. Therefore, the actual fruit set in mango should be considered only after 15 DAP. In the present investigation, the fruit retention on 20 DAP was higher in inter-specific crosses than inter-varietal crosses, which suggests cross-compatibility of *M. odorata* with *M. indica* cv. Amrapali. The retention of fruits up to the harvesting stage is dependent on several factors. Fruit retention at the harvest stage was higher (2.48%) in inter-varietal crosses compared to only 0.45% in inter-specific crosses. The regression analysis of fruit retention in inter-varietal and inter-specific crosses showed a positive linear relationship (R^2 = 0.975) and supports the fact that *M. odorata* has good cross-compatibility with *M. indica* cv. Amrapali as evidenced in the case of inter-varietal crosses (Fig 2). This finding provides ample opportunity for mango breeders to use *M. odorata* as one of the parents with Amrapali in cultivar improvement programmes. Observations on fruit

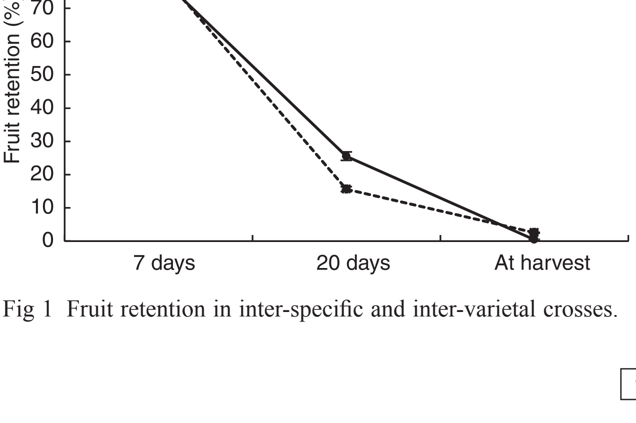

Fig 1 Fruit retention in inter-specific and inter-varietal crosses.

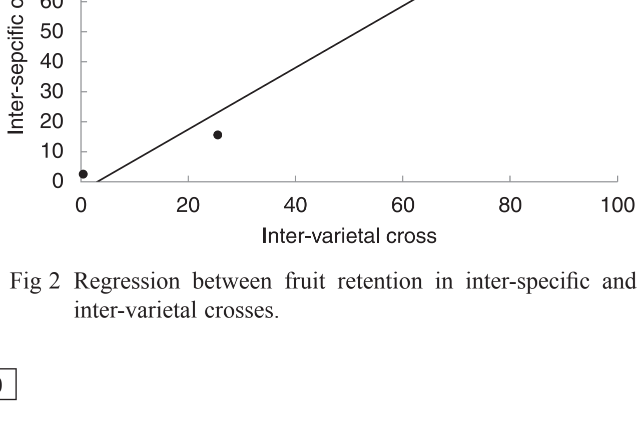

Fig 2 Regression between fruit retention in inter-specific and inter-varietal crosses.

growth of maternal Amrapali retained under inter-varietal and inter-specific crosses revealed that fruit weight, length, width and thickness were higher in fruitlets developed in response to inter-varietal crosses compared to inter-specific crosses at all fruit development stages.

Finally, 30 fruits from inter-specific crosses and 60 fruits from inter-varietal crosses were harvested. Out of 30 fruits from the inter-specific cross, only 12 stones germinated. Similarly, out of 60 fruits obtained from the inter-varietal cross, 17 stones germinated. During acclimatization, all the seedlings from both inter-specific and inter-varietal crosses survived. The final recovery of hybrid stones was 0.45% in inter-specific crosses and 2.48% in inter-varietal crosses. The hybrid stone obtained from inter-specific crosses showed higher germination (40%) compared with inter-varietal crosses (28%). A total of 12 inter-specific and 17 inter-varietal progenies were used for confirmation of parenatge. Initially, 12 SSR primer pairs were screened using three parents, two inter-specific and two inter-varietal hybrid progenies to check the amplification and reproducibility of the primer pairs. A total of eight SSR primers successfully amplified and showed polymorphism. Based on fragment analysis of amplicons, the paternity, maternity, and new allele percentages of 12 inter-specific and 17 inter-varietal hybrid progenies was ascertained by finding a similar number of alleles between the offsprings and parents. Among the inter-specific hybrids, AO2, AO7, AO11 and AO12 showed ≥50% of paternal alleles inheritance, while AO1, AO2, AO4, AO5, AO7, AO8, AO9, AO10 and AO12 showed ≥50% of maternal alleles inheritance. Inter-specific hybrids, AO1, AO3, AO5, AO9, AO10 and AO11 inherited few new alleles. It was also noted that AO2, AO7, and AO12 shared 50% alleles from both parents. Similarly, among inter-varietal hybrids, AV1, AV2, AV4, AV5, AV6, AV10, AV11, AV12, AV13, AV14, AV15 and AV17 possessed ≥50% paternal alleles, while AV1, AV2, AV3, AV5, AV6, AV7, AV8, AV10, AV11 and AV15 had ≥50% maternal alleles. Three inter-varietal hybrids, viz. AV8, AV9 and AV16 had inherited new alleles. Like inter-specific hybrids, AV1, AV2, AV5, AV10 and AV11 shared an equal percentage of alleles from both the parents (Table 2).

Table 2 Paternal, maternal and new allele percentages in inter-specific and inter-varietal hybrids of mango

Hybrid	Paternal allele (%)	Maternal allele (%)	New allele (%)
Amrapali × *M. odorata*			
AO1	25.00	50.00	25.00
AO2	50.00	50.00	0.00
AO3	33.30	33.00	33.00
AO4	33.00	67.00	0.00
AO5	25.00	50.00	25.00
AO6	0.00	0.00	0.00
AO7	50.00	50.00	0.00
AO8	42.00	57.00	0.00
AO9	33.00	50.00	16.60
AO10	17.00	50.00	33.00
AO11	57.10	28.50	14.20
AO12	50.00	50.00	0.00
Amrapali × Vanraj			
AV1	50.00	50.00	0.00
AV2	50.00	50.00	0.00
AV3	42.85	57.14	0.00
AV4	66.60	33.30	0.00
AV5	50.00	50.00	0.00
AV6	50.00	50.00	0.00
AV7	42.85	57.14	0.00
AV8	33.30	50.00	16.66
AV9	42.85	42.85	14.28
AV10	50.00	50.00	0.00
AV11	50.00	50.00	0.00
AV12	60.00	40.00	0.00
AV13	57.14	42.85	0.00
AV14	66.60	33.30	0.00
AV15	50.00	50.00	0.00
AV16	0.00	66.66	33.33
AV17	57.14	42.85	0.00

The cluster analysis based on SSR data grouped hybrids into two groups. First major group consisted of three parents, 12 inter-specific hybrids and 16 inter-varietal hybrids. Only one inter-varietal hybrid (AV17) grouped separately into the second group as out liar. The first group was further divided into two sub-groups. The sub-group Ia consisted of three inter-specific hybrids (AO10, AO11 and AO12) and 16 inter-varietal hybrids (AV1, AV2, AV3, AV4, AV5, AV6, AV7, AV8, AV9, AV10, AV11, AV12, AV13, AV14, AV15 and AV16). The second sub-group Ib consisted of nine inter-specific hybrids (AO1, AO2, AO3, AO4, AO5, AO6, AO7, AO8 and AO9). Among inter-specific hybrids, the highest genetic similarity was found between AO3 and AO4; AO6 and AO7; AO10 and AO11. However, the lowest genetic similarity was observed between AO9 with rest of the hybrids. Among inter-varietal hybrids, the highest genetic similarity was shown among AV1, AV2, AV3 and AV4 and between AV11 and AV12. In contrast, the least genetic similarity was found with AV17 with the rest of the hybrids, followed by the similarity between AV15 and AV16.

Molecular markers provide an accurate and rapid solution to overcome the drawbacks of both morphological and biochemical markers. Among a large range of molecular markers, the microsatellite markers (SSRs) are highly useful in testing parentage of hybrid progenies since they show co-dominant inheritance and relatively abundant in the genome (Powell *et al*. 1996, Kumar *et al*. 2012, Bohra *et al*. 2017). True hybrids were detected by the presence of DNA sequences corresponding to the alleles contributed by both the parents. These markers permit the early identification of true inter-specific or inter-varietal hybrids and enable early disposal of non-hybrids, thus saving time and resources in hybridization programmes (Corderio *et al.* 2001). The results showed that all the inter-specific hybrids possessed the alleles from both the parents. Among, inter-specific hybrids, AO1, AO3, AO5, AO9, AO10 and AO11 inherited few new alleles. Similarly, three inter-varietal hybrids, viz. AV8, AV9, and AV16 had inherited few new alleles. However, among inter-varietal hybrids, only AV16 had alleles from the maternal parent with new alleles. The inheritance of new alleles along with maternal and paternal alleles may be due to the high heterozygosity of mango. The UPGMA clustering based on eight SSR markers revealed the clear separation of tested genotypes into inter-specific hybrids, inter-varietal hybrids and parents. This clearly indicated the possibility of getting new recombinants by crossing two highly heterozygous parents in mango.

Kumar *et al.* (2016) screened 42 microsatellite markers (SSRs) for ascertaining the hybridity among progenies obtained from the different cross combinations in mango. Out of 42 primer pairs screened, 13 primer pairs were polymorphic and only three primer pairs, viz. LMMA 11, ESTD 9 and ESTD 10 could confirm hybridity of progenies. Ahmad *et al.* (2012) assessed the hybridity of 99 citrus hybrids using SSR markers and suggested that SSR markers are reliable and effective for early identification of true hybrids from the non-hybrid progenies in both inter-specific and inter-varietal crosses. Subashini *et al.* (2014) confirmed the parentage of inter-specific hybrids (*Eucalyptus camaldulensis* × *E. tereticornis*) by calculating the hybrid purity index (85–100%) with the help of 25 fluorescent labeled microsatellite markers and suggested that SSR markers helps in saving time and resources in breeding programmes. Based on the findings, it was concluded that wild mango species, i.e. *Mangifera odorata* had good crossability with cultivated *M. indica*. Therefore, this species can be used for imparting desirable traits in mango breeding programmes.

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