Review

Current scenario of marker-assisted selection in breeding of minor oilseed crops of India

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ABSTRACT

Sunflower, safflower, castor, sesame, linseed and niger are the minor oilseed crops having potential to contribute towards achieving self-sufficiency in vegetable oil production in India. Decades of breeding research have resulted in release of high yielding cultivars with resistance to biotic stresses. However, the productivity levels are stagnated; further improvement in genetic gain requires integration of molecular tools in breeding programmes. Molecular markers, genomics and marker-assisted selection technologies are widely exploited for improvement of crops. In this review, current status of development and application of molecular markers in the oilseed crops *viz.,* sunflower, castor, safflower, sesame, linseed and niger are presented.

Keywords: Genomics, GWAS, Marker assisted selection, Molecular markers, Oilseed crops, QTL

Oilseeds play a significant role in Indian agricultural economy next to cereals. India is one of the major growers and importers of edible oils. In India, nine annual oilseed crops (rapeseed and mustard, soybean, groundnut, sesame, sunflower, safflower and niger for edible oils; castor and linseed for industrial purposes) are grown in an area of about 26 million ha with an annual production of about 31 million tonnes of seeds. Of these, major portion of oilseed production [27.8 million tonnes (90.9%) from 22.3 million ha (86.7%)] is contributed by rapeseed & mustard, soybean and groundnut whereas the remaining 2.8 million tonnes is contributed by the minor oilseeds: sunflower, sesame, niger, safflower, castor and linseed from the area of 3.4 lakh ha (average of 2015-16 to 2019-20, Directorate of Economics and Statistics, Govt. of India). The oilseed crops are largely grown in marginal lands under rainfed farming conditions, signifying their role in livelihood security of resource poor farmers. Furthermore, demand for edible oils is ever increasing in India due to rise in population and standard of living but the domestic production is adequate to satisfy only about 40% of the requirement; thus, forcing the country to rely heavily on the imports. In 2019-20, net availability of edible oils from all domestic sources was 10.7 million tonnes and the import was 13.4 million tonnes (https://dfpd.gov.in/oil-division.htm). The situation underscores the need for concerted efforts to increase the oilseed production in the country. In this context, sunflower, castor, safflower, sesame, linseed and niger assume greater significance as they have the potential to contribute for enhancing oilseed production in the country through improvements in productivity, and area expansion. In addition, these crops have huge export potential. Export of oils and by-products including oil meals, castor oil, groundnut, sesame seeds, niger seeds etc., was INR 28000 crores (3728 million USD) in 2020-21 (https://commerce.gov.in/about-us/divisions/export-products-division/export-products- agriculture/).

Low productivity is a major concern in the research and development (R&D) of minor oilseed crops. Developing high yielding cultivars adapted to biotic and abiotic stresses has been a major breeding goal in these crops to achieve higher productivity. Classical plant breeding methods have tremendously contributed for developing cultivars with high yielding potential. However, further improvements in yield potential have stagnated, mainly due to slow response to selection in breeding programmes. Low genetic variation, genetic complexity, low heritability and long selection cycle are some of the important factors that contribute for slow plant breeding response. Traditionally, plant breeding is practiced by 'hit and miss' or 'trial and error' approaches due to lack of precise selection tools, and understanding of genetics of the traits. Molecular marker technology has provided improved and precise selection tools to plant breeders. Molecular plant breeding has been recognized as the foundation for crop improvement in the 21st century to increase crop production (Moose and Mumm, 2008). In this review, current status of development and application of molecular markers in the oilseed crops *viz.,* sunflower, castor, safflower, sesame, linseed and niger is presented.

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Overview of molecular markers, trait mapping and marker-assisted selection: A variety of DNA based marker systems (RAPD, AFLP, RFLP, DArT, SSR, SNP, SRAP, TRAP, SCoT etc.,) have been developed over the years since 1980 (Kadirvel *et al.*, 2015). Recently, next generation sequencing (NGS) technologies have emerged, which offer excellent opportunities to generate a large number of markers in any crop with less cost and time. Markers are used for characterizing genetic diversity in germplasm collections, mapping and identification of genes associated with important traits, mining of superior alleles and marker-assisted selection (MAS) of desirable genes/traits in breeding programmes. Integration of markers in mainstream breeding programmes improves breeding efficiency in terms of speed, cost and accuracy. Establishing a marker-assisted breeding programme in crop plants involves a series of steps: development of genetic resources (trait specific donor germplasm, mapping populations), development of genomic resources (reference genome sequences, marker discovery, designing of marker genotyping assays, genetic linkage maps), trait mapping and QTL discovery using various strategies *viz.,* linkage mapping and association mapping (genome wide association analysis-GWAS and candidate gene based allele mining), fine-mapping and candidate gene discovery, designing of MAS protocols and application in breeding programmes by adopting MAS strategies *viz*., marker-assisted pedigree selection (MAPS), marker-assisted backcrossing (MABC), marker-assisted recurrent selection (MARS) and genome-wide selection (GWS) depending upon the traits (simply inherited or complex) under consideration (Collard and Mackill, 2008). Scheme of molecular breeding process is depicted in Fig. 1.

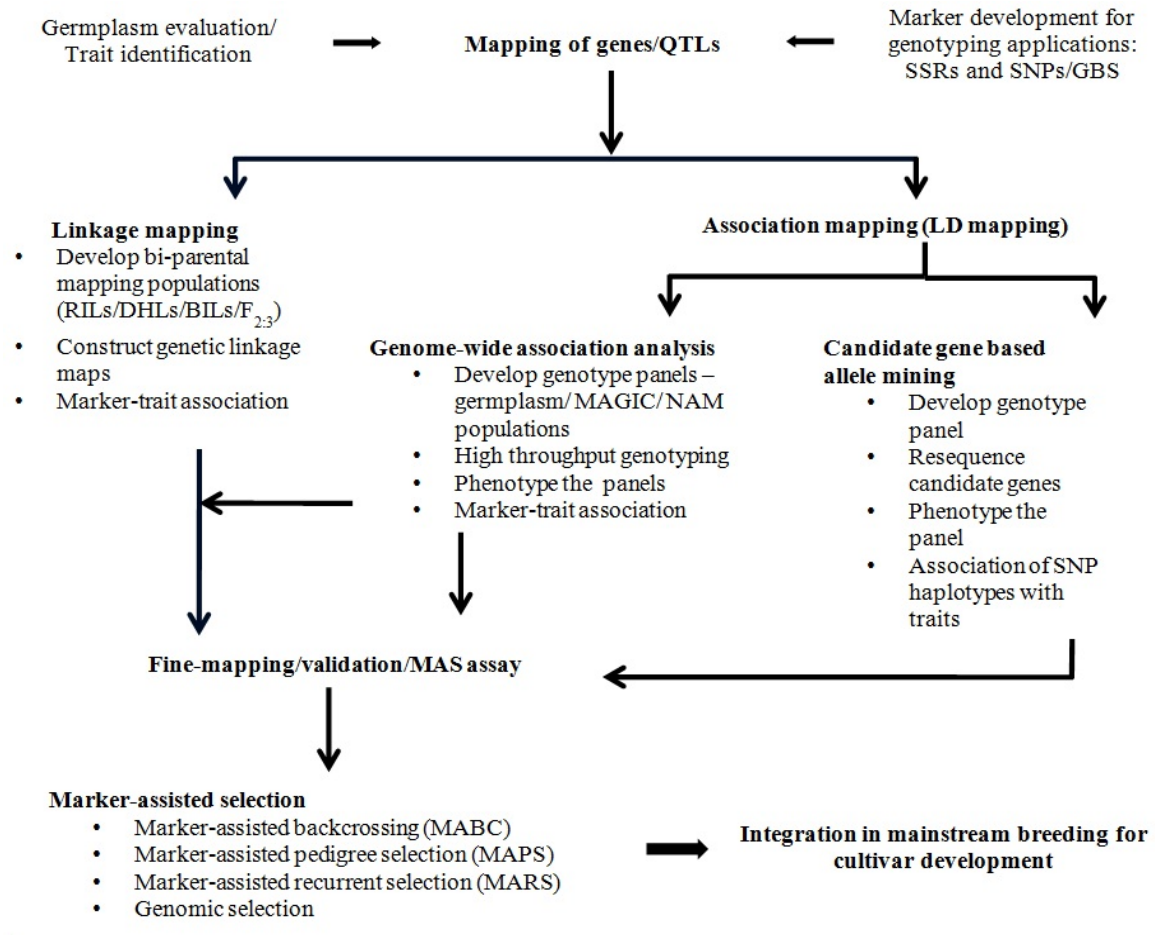

Fig. 1. Scheme of molecular breeding process in crops

Trait mapping is fundamental for establishing a molecular breeding programme in crops. Traditionally, linkage mapping [based on bi-parental mapping populations such as F_2, doubled haploid lines (DHL), recombinant inbred lines (RILs), backcross inbred lines (BILs)] has been performed to map QTLs. By this strategy, numerous QTLs have been detected for various traits in crops and several of them have been associated with candidate genes through positional cloning (Salvi and Tuberosa, 2007). Linkage mapping has been advantageous because QTLs could be roughly mapped using only a limited number of markers; subsequently, fine-mapping of the QTLs could be attempted by improving the resolution of the target QTL region. But it is restrictive with respect to capturing diversity of genes involved in complex traits because only two parents could be used at a time and a pedigree based population derived from those two parents is required. However, with the availability of genotyping by sequencing (GBS), high throughput SNP genotyping has become feasible, which has led to use of GWAS for QTL detection. GWAS can be performed directly in a diverse germplasm collection or multi-parent based populations [multi-parent advanced generation intercross (MAGIC)/nested association mapping (NAM) panel etc.,] using high density of markers (for desirable levels of linkage disequilibrium to achieve accuracy); thereby, diverse genes associated with various traits can be detected simultaneously, which would save time and resources. However, both the mapping strategies tend to throw spurious associations due to limitations in terms of phenotyping, population size, marker density, allele frequency, allelic effects etc. Therefore, the results need to be cautiously interpreted and the plausible QTLs need to be prioritized for validation and candidate gene analysis.

Sunflower: Sunflower (*Helianthus annuus* L.) is a diploid species with 2n=34 and genome size of about 3.5 Gb. The sunflower genome sequence has been published (Badouin *et al*., 2017). Being a globally important crop, substantial progress in molecular breeding has been achieved in sunflower. Genetic linkage maps using SSR and SNP markers have been developed (Tang *et al.*, 2002; Talukder *et al*., 2021). Several major genes conferring resistance to biotic stresses (downy mildew, rust and broomrape), fertility restoration, high oleic acid content, high tocopherol content and tolerance to herbicides have been identified in sunflower (Dimitrijevic and Horn, 2018). QTLs associated with several traits including domestication, self-incompatibility, flowering, male sterility, fertility restoration, seed dormancy, seed quality, oil content, high oleic acid content, tocopherol content, tolerance to drought, salinity or chilling stresses and resistance to downy mildew, rust, broomrape, chlorotic mottle virus and phomopsis stem canker have been mapped (Table 1). GWAS for flowering time, branching and *Sclerotinia* rot have been performed (Table 2). Molecular markers have been developed for the selection of fertility restoration, high oleic acid content, tocopherol content, resistance to downy mildew, rust, *Sclerotinia* white mold and broomrape and tolerance to herbicides in sunflower. Rouf *et al.* (2020) provides a detailed account of validated markers for MAS in sunflower.

In the Indian context, only a little information is available on the application of molecular markers in sunflower breeding. Nagarathna *et al.* (2011) reported validation of SSR marker associated with high oleic acid content in a collection of germplasm and parental lines being used in Indian breeding programmes. Kallamadi and Mulpuri (2020) reported three QTLs associated with resistance to powdery mildew, which require further validation. Efforts are needed to map the genes/QTLs governing resistance to necrosis, Alternaria leaf spot, downy mildew, *Macrophomina* root rot and other desirable agronomic traits to support Indian sunflower breeding programmes. Major genes associated with resistance to downy mildew, which have been reported in the exotic materials need to be validated in the Indian materials using molecular markers.

Castor: Castor (*Ricinus communis* L.) is a diploid species with 2n=20 and genome size of about 400 Mb. Draft genome sequence of castor has been published (Chan *et al.,* 2010). Senthilvel *et al.* (2019) published re-sequenced genomes of 14 diverse genotypes of castor. A chromosome scale assembly of wild castor accession has also been published (Lu *et al.,* 2021). Using the draft genome sequences, high throughput SSR and SNP markers have been developed in castor (Qiu *et al.,* 2010; Foster *et al.,* 2010; Sharma and Chauhan, 2011; Tan *et al.,* 2014; Senthilvel *et al.,* 2019; Dharajiya *et al.,* 2020). SSR based genetic linkage maps were developed by Liu *et al.* (2016) and Tomar *et al.* (2017) using F_2 populations. Senthilvel *et al.* (2019) developed high-density SNP maps using RIL populations of the crosses *viz.,* JC12 × 48-12 and DCS9 × RG1139 with more than 1000 SNP markers, which led to the development of a consensus map comprising of 1,978 SNP loci and spanning a total length of 995.8 cM with an average inter-marker distance of 0.55 cM. However, trait mapping efforts are very limited in castor. QTLs associated with resistance to Fusarium wilt (Tomar *et al.,* 2016; Shaw *et al.,* 2021) and charcoal rot (Tomar *et al.,* 2017), yield traits (Fan *et al.,* 2019), seed size and weight (Yu *et al.,* 2019) and agronomic traits (Xu *et al.,* 2021) have been reported. Candidate genes associated with cadmium tolerance (Yeboah *et al.,* 2021) and lupeol content (Li *et al.,* 2021) have been identified. A total of 69 SNPs associated with resistance to Fusarium wilt have also been identified in castor through GWAS (Shaw *et al.,* 2021). However, there are no reports published on MAS in castor till date. Details of QTL mapping and GWAS studies

performed for various traits in castor are presented in Table 1 and 2. At ICAR-IIOR, Hyderabad, important leads have been obtained in mapping resistance to Fusarium wilt in castor (Shaw *et al.,* 2021) and efforts are underway to design genotypic assays for selection of major genes//QTLs for wilt resistance (Senthilvel, unpublished). Trait mapping needs to be expedited for yield components, resistance to Botryotinia, *Macrophomina* root rot, sucking pests (leafhoppers, thrips, and whitefly) and tolerance to moisture stress, which are important for castor productivity in India.

Table 1 Reports of QTL mapping in minor oilseed crops of India

Mapping population	Marker type/Number	Traits mapped	No. of QTLs	QTL name	Linkage Group*	PVE (%)	Reference
		Sunflower					
Advanced backcross population (134 lines) derived from HA 89 (*H. argophyllus*) x Gray accession, PI 494573 cross	SNP (3110)	Basal stalk rot resistance	21	-	-	4.5-22.6	Talukder *et al.* (2021)
RILs of PS 2023 x TX16R cross	SSR (175)	Powdery mildew resistance	3	-	5, 10	-	Kallamadi and Mulpuri (2020)
F_6-RILs (164) of HA 89 x HA-R_3 cross	SNP (1,879)	Phomopsis stem canker resistance	15	-	-	5.24-17.39	Talukder *et al.* (2020)
F_2s (84) of '86-1' x 'L-1-OL-1' cross	SNP (6136)	Oleic acid content	3	OAC_1, OAC_2, OAC_3	-	5.18-12.05	Zhou *et a*l. (2018)
		Plant height	2	PH_1, PH_2		10.31-12.28	
		Head diameter	2	HD_1, HD_2	-	5.63-5.49	
		Stem diameter	1	SD_1	-	15.65	
F_4 lines of HA 300 × RHA 464 cross	SNP (2121)	Capitate glandular trichome	2	-	5, 6	11.61-14.06	Gao *et al*. (2018)
RILs (114) of PAC2 x RHA266 cross	SNP (384)	Sclerotinia head rot resistance	36	-	-	12.45-23.87	Zubrzycki *et al.* (2017)
F_2 (400) of ARG-1805 x ARG-1834 cross	SNP (530)	UV bullseye	1	-	2	20.1	Moyers *et al.* (2017)
		Flower head disc diameter	1	-	2	17.6	
		Ray ligule length	1	-	2	19.0	
		Total flower head diameter	1	-	2	21.2	
Two RIL populations derived from XRQ x PSC8 (117 F_8 RILs), and FU x PAZ2 (113 F_7 to F_{10} lines)	SSR (155), SNP (830), RGC (8)	Premature ripening	1	-	-	26.9-39.4	Bordat *et al.* (2017)
F_8 RILs (101) derived from HA89 and LR_1	SNP (951)	Resistance to broomrape (*Orobanche cumana* race F and G)	17	-	-	9.0-30.0	Louran *et al.* (2016)
F_7-RILs (106) of HA 441 x HA-439 cross	SNP (1053)	Basal stalk rot resistance	6	-	4, 9, 10, 11, 16, 17	6.4-28.9	Talukder *et al.* (2016)
BC_1 plants (975) derived from *H. debilis* ssp. *Cuccumerifolius* and *H. annuus* ssp. annuus	SNP (384)	Two fitness and 22 herbivore resistance, ecophysiological, phenological and architectural traits	110	-	-	-	Whitney *et al.* (2015)
RILs (148) derived from XRQ x PSC8 cross	SNP (2610)	Water use efficiency	9	-	-	5-7	Adiredjo *et al.* (2014)
		Carbon isotope discrimination	8	-	-	7.0	
F_8-RILs of INRA lines XRQ x PSC8 cross	SNP (235) + SSR (214)	Phytosterol traits	45	-	-	9.0-31.0	Merah *et al.* (2012)
RIL population derived from FU × PAZ2, and INEDI RIL population.	SNP SSR (451)	Downy mildew resistance	3	-	7, 8, 10	40.0-54.0	Vincourt *et al.* 2012
F_3 families (434) of CM625 x TUB-5-3234.	SSR (78)	Midstalk rot resistance	2	-	-	24.4-33.7	Micic *et al.* (2005a)

Table 1 (contd...)

Mapping population	Marker type/Number	Traits mapped	No. of QTLs	QTL name	Linkage Group*	PVE (%)	Reference
RILs (317) of NDBLOSsel x CM625 cross	SSR (41)	Midstalk rot resistance	2	-	8, 16	26.5	Micic *et al.* (2005b)
		Safflower					
F_9-RILs (98) of Mex.22-191 x Goldasht cross	AFLP (69)	Days to heading	1	qDTT_N-5-1	5	13.79	Poodineh *et al.* (2021)
		Days to heading (under stress)	1	qDTT_S-5-1	5	10.14	
		Grain yield (under stress)	1	qGY_S-4-1	4	18.18	
		Oil yield (under stress)	1	qOY_S-4-1	4	15.05	
		Harvest index	1	qHI_N-4-1	4	10.61	
		Number of branches/plant	1	qNB_N-11-1	11	13.86	
		Number of branches/plant (under stress)	2	qNB_S-7-1	7	6.73	
				qNB_S-9-1	9	6.73	
		Number of capitula/plant	2	qNC_N-3-1	3	5.87	
				qNC_N-5-1	5	19.34	
		Number of capitula/plant (under stress)	1	qNC_S-4-1	4	16.54	
		Plant dry weight	3	qDW_N-4-1	4	4.55	
				qDW_N-4-2	4	4.78	
				qDW_N-5-1	5	5.06	
		Thousand seed weight	1	qTSW_N-3-1	3	13.48	
		Days to flowering (under stress)	1	qDTF_S-2-1	2	14.08	
F_6-RILs (237) of CO-1 x EC-523368-2 cross	SSR (242)	Tolerance to aphid (days-to-wilt after aphid infestation)	2	qUc-Ct3.1	3	31.5	Jagadeeswaran *et al.* (2021)
				qUc-Ct5.1	5	9.1	
Segregating populations from Nira × *C. oxyacanthus*) and Nira × *C. palaestinus*) crosses	SSR	Resistance to Fusarium wilt	-	-	-	-	Anjani *et al*. (2018)
F_3 families (66) of Mex.22-191 × IL.111 cross	SSR and ISSR (119)	Plant height	2	qPh6_1	6	17.0	Mirzahashemi *et al.* (2015)
				qPh6_2	6	19.0	
		Branches/plant	3	qBpno4_1	4	48.0	
				qBpno 4_2	4		
				qBpno6	6		
		Capsules/plant	1	qCpno2	2	17.0	
		Dry weight/plant	3	qDw2	2	54.7	
				qDw4	4		
				qDw6	6		
		Seeds/plant	6	qSpno2	2	33.7	
				qSpno3	3		
				qSpno4	4		
				qSpno7	7		
				qSpno9	9		
				qSpno18	18		
		Seed yield/plant	2	qSyp2	2	37.0	
				qSyp9	9		

Table 1 (contd..)

Mapping population	Marker type/Number	Traits mapped	No. of QTLs	QTL name	Linkage Group*	PVE (%)	Reference
F_2 (276) of AC sunset x *C. palaestinus* cross	SNP (244)	Average leaf size	2	-	B, H	8.7-9.9	Pearl *et al.* (2014)
		Average leaf roundness	4	-	D, G, H, L	4.5-13.5	
		Spininess	3	-	E, H, L	4.5-32.7	
		Days to flower	3	-	D, H, I	5.6-11.9	
		Primary capitulum weight	7	-	A, D, H, I, L	4.5-9.9	
		Primary disc diameter	4	-	A, H, I, L	8.2-12.3	
		Number of heads	1	-	H	4.8	
		Flower colour	1	-	D	63.4	
		Stem height	3	-	E, H, I	6.3-7.8	
		Number of internodes	2	-	C, L	4.4-15.9	
		Internode length	4	-	A, E, L	4.2-7.6	
		Lowest branch height	1	-	G	5.9	
		Number of selfed seed	3	-	C, H, I	4.2-7.6	
		Achene weight	4	-	C, H, I, K	4.4-13.1	
		Achene length	4	-	C, D, I, K	5.2-12	
		Achene width	4	-	C, I, J, K	5.1-15.3	
		Seed dormancy	1	-	E, I, J, L	9.0	
		Palmitic acid	1	-	E	7.5	
		Oleic acid	3	-	C, G, H	6.3-11	
		Linoleic acid	2	-	G, H	8.6-8.7	
		Castor					
RILs (F_6) (185) of JC12 and 48-1 cross	SNP (1,090)	Resistance to Fusarium wilt based on days to wilt	1	-	7	44	Shaw *et al.* (2021)
RILs of Rc249 x Rc250 cross	SNP (2186)	Seed length	3	-	3, 5, 6	7.3-22.6	Xu *et al*. (2021)
		Seed thickness	4	-	3, 5, 6	4.5-15.9	
		Seed oil content	1	-	5	12.9	
		Single seed weight	4	-	3, 5, 6	3.7-19.8	
		Seed width	6	-	3, 4, 5, 6, 10	4.5-14.5	
F_4-RILs (200) of ZB306 x ZB107 cross	SNP (8896)	Seed length	4	qSL1	01	8.2	Yu *et al.* (2019)
				qSL3	03	7.7	
				qSL6-1	06	9.0	
				qSL6-2	06	5.1	
		Seed weight	4	qSW1	01	11.8	
				qSW3	03	6.5	
				qSW4	04	5.7	
				qSW6	06	9.1	
		Seed thickness	4	qST1	01	17.2	
				qST3	03	4.7	
				qST4	04	4.4	
				qST6	06	8.0	
		Single seed weight	4	qSSW1-1	01	6.2	
				qSSW1-2	01	4.6	
				qSSW3	03	10.9	
				qSSW6	06	20.7	

Table 1 (contd..)

Mapping population	Marker type/Number	Traits mapped	No. of QTLs	QTL name	Linkage Group*	PVE (%)	Reference
$F_{2:3}$ (190) of JI 357 x SKI 338 cross	SSR (300) + ISSR (100) + RAPD (520)	Charcoal rot resistance	3	-	2, 6, 9	11.3-71.2	Tomar *et al.* (2017)
		Sesame					
$F_{5:7}$ RILs (90) of Goenbaek x Osan cross	SNP (1657) + SSR (5)	Phytophthora blight resistance (Isolate: KACC48121)	1	qPhn-10_kacc48121	10	12.79	Asekova *et al.* (2021)
		Phytophthora blight resistance (Isolate: KACC48120)	1	qPhn-10_kacc48120	10	13.34	
		Phytophthora blight resistance (Isolate: No2526)	1	qPhn-10_no2526	10	13.34	
F_8 RILs (548) of Zhongzhi No. 13 x ZZM2748 cross	SSR (424)	Sesamin	1	qSmin_11.1	11	67.69	Xu *et al*. (2021)
		Sesamolin	1	qSmol_11.1	11	46.05	
RILs (488) of Zhongzhi No. 13 x ZZM2289 cross	SSR (81)	Leaf size	1	qLS15-1	15	5.81-27.5	Sheng *et al.* (2021)
BC_1 of Yuzhi 4 x BS cross	SLAF (3528)	Seed yield per plant	1	qSY_LG08-1	8	35-43	Mei *et al.* (2021)
		Number of capsules/plant	1	qCN_LG08	8	17.6-21.2	
		Number of seeds/capsule	2	qSN_LG04	4	12.35-15.23	
				qSN_LG08	8	14.6-16.3	
		Seed weight	1	qSW_LG04	4	9.26-13.59	
		Plant height	1	qPH_LG08	8	6.25-11.23	
		Height of the first capsule	2	qFCH_LG08-2	8	59.15-71.41	
				qFCH_LG08-1	8	23.83	
		Harvest index	1	qHI_LG05	5	6.49-10.69	
F_8 RILs (548) of Zhongzhi No. 13 x ZZM2748 cross	SSR (424)	Charcoal rot resistance	14	qCRR3.1	3	3.0-14.6	Wang *et al.* (2017)
				qCRR3.2	3		
				qCRR3.3	3		
				qCRR3.4	3		
				qCRR5.1	5		
				qCRR8.1	8		
				qCRR8.2	8		
				qCRR8.3	8		
				qCRR9.1	9		
				qCRR12.1	12		
				qCRR12.2	12		
				qCRR12.3	12		
				qCRR13.1	13		
				qCRR13.2	13		
BC_1 plants (150) of Yuzhi4 x Bengal cross	SLAF-Seq (9378)	Basal branching habit	1	qBH-LG5	5	78.64	Mei *et al*. (2017)
		Flowers/leaf axil	1	-	11	-	
$F_{8:9}$ RILs (224) of 'Miaoqianzhima' x 'Zhongzhi 14' cross	SNP SSR Indel (1230)	Plant height	2	Qph-6	6	6.0	Wu *et al*. (2014)
				Qph-12	12	5.6-9.1	
		First capsule height	3	Qfch-4	4	6.2	
				Qfch-11	11	8.2	
				Qfch-12	12	11.5	
		Capsule axis length	2	Qcal-5	5	8.1	
				Qcal-9	9	9.2	
		Capsule number/plant	1	Qcn-11	11	7.0	
		Thousand grain weight	1	Qtgw-11	11	7.7-12.3	
		Grain number/capsule	3	Qgn-1	1	6.8-11	
				Qgn-6	6	8-18.3	
				Qgn-12	12	7.9-13.6	
		Capsule length	4	Qcl-3	3	52.2-75-6	
				Qcl-4	4		
				Qcl-7	7		
				Qcl-8	8		
				Qcl-12	12		

Table 1 (contd...)

Mapping population	Marker type/Number	Traits mapped	No. of QTLs	QTL name	Linkage Group*	PVE (%)	Reference
F_3 lines (260) of COI1134 x RXBS cross	SSR (49) + AFLP (52) + RSAMPL (623)	Seed coat colour	4	QTL1-1	1	39.95	Zhang *et a*l. (2013)
				QTL11-1	11	20.61	
				QTL11-2	11	24.02	
				QTL13.1	13	30.56	
		Linseed					
F_2 (154) of JRF-4 x Chambal cross	SSR (193)	Capsules/plant	4	Qcp.nbri.2.1	2	8.2	Singh *et al*. (2021)
				Qcp.nbri.6.1	6	6.0	
				Qcp.nbri.7.1	7	8.6	
				Qcp.nbri.14.1	14	5.6	
		Capsule weight/plant	2	Qcwp.nbri.7.1	7	9.2	
				Qcwp.nbri.9.1	9	10.5	
		Seed weight/plant	2	Qsw.nbri.7.1	7	9.5	
				Qsw.nbri.9.1	9	1.0	
		Alternaria blight resistance	2	Qabr.nbri.14.1	14	9.2	
				Qabr.nbri.14.2	14	4.2	
F_2 (112) of DIANE x NY17 cross	SLAF (2339)	Plant height	1	-	1	18.77	Wu *et al*. (2018)
		Stem length	1	-	8	11.17	
		Seed yield	3	-	10, 12	10.11-19.33	
		Stem yield	3	-	5, 15	10.91-15.81	
		Fibre yield	2	-	1, 11	19.09-25.98	
		Fibre content	2	-	5, 11	13.27-15.14	
RILs (110) of Macbeth/Heiya No.14 (MH) cross; R_7 RILs (123) of P.I.249991/Heiya No.14 cross	SNP (4497)	Plant height	1	-	-	10.29-26.94	Zhang *et a*l. (2018)
		Technical length	1	-	-		
$F_{8:9}$ RILs of CDC Bethune x G1186/94 cross	SSR (91) CAPS (1)	Seed and flower colour	1	-	1	-	Sudarshan *et al.* (2017)
RILs (243) of CDC Bethune x Macbeth cross	SNP (329) SSR (362)	Palmitic acid	1	QPal.BM.crc-LG7	7	0.12	Kumar *et al*. (2015)
		Stearic acid	3	QSte.BM.crc-LG1	1	0.06	
		Oleic acid	3	QOle.BM.crc-LG3-1	3	0.13	
		Linoleic	2	QLio.BM.crc-LG3	3	0.08	
		Linolenic	1	QLin.BM.crc-LG5	5	0.10	
		Iodine value	2	QIod.BM.crc-LG5	5	0.08	
		Oil content	1	QOil.BM.crc-LG8	8	0.13	
		Seed protein	1	QPro.BM.crc-LG11	11	0.11	
		Cell wall	1	QCw.BM.crc-LG4	4	0.14	
		Straw weight	1	QSw.BM.crc-LG4	4	0.30	
		Thousand seed weight	1	QTsw.BM.crc-LG15	15	0.09	
		Seeds per boll	1	QSpb.BM.crc-LG4	4	0.20	
		Yield	1	QYld.BM.crc-LG4	4	0.08	
		Days to maturity	1	QDm.BM.crc-LG4	4	0.31	

*Linkage groups are indicated as defined by the authors and they are not comparable across studies.

Safflower: Safflower (*Carthamus tinctorius* L.) is a diploid species with 2n=24 and genome size of about 1.5 Gb. Very recently, chromosome scale reference genome of safflower has been published (Wu *et al.,* 2021). Substantial number of SSR markers have been developed in safflower through traditional EST mining, genomic library screening or NGS approaches (Chapman *et al.,* 2009; Mayerhofer *et al.,* 2010; Hamdan *et al.,* 2011; Yamini *et al.,* 2013; Lee *et al.,* 2014; Ambreen *et al.,* 2015; Usha Kiran *et al.,* 2019; Jegadeeswaran *et al.,* 2021). Only a few genetic linkage maps have been developed in safflower. Mayerhofer *et al.* (2010) first published a linkage map of safflower by using F_2 and BC_1 populations derived from interspecific crosses involving *C. tinctorius* and *C. oxyacanthus.* Subsequently, Garcia-Moreno *et al.* (2011) and Hamdan *et al.* (2012) published linkage maps of safflower involving SSR markers. Recently, Jegadeeswaran *et al.* (2021) published an SSR linkage map with 242 markers using a RIL population, which is relatively a dense SSR map of safflower to date. Bowers *et al.* (2016) published a high density linkage map with more

than two million SNPs by whole genome sequencing of a RIL population produced from the interspecific crosses involving *C. tinctorius* and *C. palaestinus.* At the moment, Bowers *et al.* (2016) map serves as a reference in safflower.

In safflower, trait mapping efforts were mainly focused on oil quality and other qualitative traits like flower colour and male sterility. Hamdan *et al.* (2008) reported that *Li* gene, controlling high linoleic acid content, was tightly linked to the nuclear male sterility gene, *Ms*, both flanked by SCAR markers. Mayerhofer *et al.* (2010) mapped a dominant gene *ctfc1* controlling yellow flower colour on to linkage group T9. Garcia-Moreno *et al.* (2011) mapped *Tph2* gene associated with high gamma-tocopherol content. Hamdan *et al.* (2012) mapped *Ol* gene associated with high oleic acid content. Anjani *et al.* (2018) reported the association of SSR markers with resistance to Fusarium wilt in interspecific crosses of Nira × *C. oxyacanthus* and Nira × *C. palaestinus.* To date, only a few reports are available on QTL mapping, which include domestication traits (Pearl *et al.,* 2014), tolerance to drought (Hussain *et al.,* 2016; Mirzahashemi *et al.,* 2015; Poodineh *et al.,* 2021) and aphids (Jegadeeswaran *et al.,* 2021). Preliminary studies on GWAS for drought tolerance (Ebrahimi *et al.,* 2008), yield, oil content and quality traits (Ambreen *et al.,* 2018), and 100-seed weight (Ali *et al.,* 2020) have been performed. Details of QTL mapping and GWAS studies performed for various traits in safflower are presented in Table 1 and 2.

To date, only one case of MAS has been reported in safflower. Liu *et al.* (2013) reported PCR based multiplex marker assay for selection of high oleic allele *'ol'* in safflower based on the mutation in the *CtFAD2-1* gene. Subsequently, Kadirvel *et al.* (2020) designed SNP genotyping assays such as Kompetitive Allele Specific PCR (KASP®) and the Amplifluor™ SNPs Genotyping System (Amplifluor®) for the prediction of *'ol'* allele. The assays were validated in segregating populations as well as in MABC scheme to introgress the *'ol'* allele in the background of popular cultivar. At ICAR-IIOR, Hyderabad, MAS for high oleic acid content trait is routinely implemented in safflower breeding programmes using these assays. Furthermore, efforts are underway to develop genetic and genomic resources and map QTLs associated with agronomic traits including yield components, oil content, resistance to Fusarium wilt and tolerance to aphids and moisture stress.

Sesame: Sesame (*Sesamum indicum* L.) is a diploid species with 2n=26 and genome size of about 950 Mb. Wang *et al.* (2014) published de novo genome sequence of sesame. SSR markers have been reported by various authors (Ke *et al.,* 2011; Wei *et al.,* 2011; Zhang *et al.,* 2012; Dossa *et al.,* 2017). SSR database namely SisatBase (Dossa *et al.,* 2017) and GinMicrosatDb (Purru *et al.,* 2018) have been developed. Kizil *et al.* (2020) reported genome-wide discovery of InDel markers using ddRADSeq. Yu *et al.* (2019) constructed pan-genome assembly based on genome assemblies of five sesame varieties including two landraces (*S. indicum* cv. Baizhima and Mishuozhima) and three modern cultivars (*S. indicum* var. Zhongzhi13, Yuzhi11 and Swetha), which serves as a rich resource for comparative genomic analyses and gene discovery in sesame research.

The first linkage map was constructed in 2009 using 220 EST-SSR, AFLP and RSAMPL (Random Selective Amplification of Microsatellite Polymorphic Loci) markers (Wei *et al.,* 2009). Zhang *et al.* (2013) developed high-density genetic linkage map in F_3 population using 724 polymorphic markers (653 SSR, AFLP and RSAMPL) corresponding to 14 linkage groups. Subsequently, RAD tag sequencing was applied on a sesame RIL population (Wu *et al.,* 2014). Uncu *et al.* (2016) identified 15,521 SNPs through genotyping by sequencing approach (GBS) and developed a linkage map with 432 markers (420 SNPs, 12 SSRs). Wang *et al.* (2017) constructed a genetic linkage map based on 424 novel polymorphic SSR markers using a RIL population.

Marker-trait associations have been reported in sesame for a few traits. Uzun *et al.* (2003) reported AFLP markers linked to closed capsule mutant. Uzun and Cagirgan (2009) identified ISSR markers linked to determinate growth habit in a segregating F_2 population of sesame derived from the cross between *dt-1* (mutant with determinate habit) and Muganli-57 (indeterminate wild type cultivar). The gene conferring recessive genic male sterility (RGMS) was mapped using AFLP markers (Zhao *et al.,* 2013). Liu *et al.* (2015) identified SSR markers associated with dominant genic male sterility (DGMS) in sesame. Liu *et al.* (2020) fine-mapped a novel locus in male-sterile mutant associated with wrinkled-leaf using bulk segregant analysis (BSA)-Seq and NGS.

QTLs associated with resistance to charcoal rot (Wang *et al.,* 2017), Phytophthora blight (Asekova *et al.,* 2021), seed oil and protein content (Li *et al.,* 2014), seed coat colour (Zhang *et al.,* 2013; Du *et al.,* 2019), yield related traits (Wu *et al.,* 2014; Du *et al.,* 2019; Mei *et al.,* 2021), leaf size (Sheng *et al.,* 2021), and sesamin and sesamolin variation (Xu *et al.,* 2021) have been reported. GWAS for seed related traits (Zhou *et al.,* 2018) and drought tolerance (Dossa *et al.,* 2019) have been performed and major effect QTLs have been detected. Details of QTL mapping and GWAS studies performed for various traits in sesame are presented in Table 1 and 2. In spite of the development of genomic resources, there is no example of MAS in sesame globally. Also, no trait mapping has been reported in sesame in India. Mapping of yield components, resistance to Phyllody, *Macrophomina* root rot and powdery mildew and tolerance to abiotic stresses including drought and flooding need to be expedited to assist plant breeding programmes in India.

Table 2 Reports of GWAS in minor oilseed crops of India

Population type/size	Marker type/number	Traits	No. of associated markers	PVE (%)	Reference
		Sunflower			
Germplasm	SNP	Rhizophagus intraradices colonization	3	-	Stahlhut *et al*. (2021)
Germplasm (601)	SNP (15483)	Docosanoic acid	53	35.4	Chernova *et al.* (2021)
		Fatty acids and oleic-linoleic acid ratio	140	-	
Germplasm (333)	SNP (8723)	Fertility restoration (*Rf7* gene)	24	-	Talukder *et al*. (2019)
		Safflower			
Germplasm (124)	SSR (93)	Oil content	5	9.7-23.4	Ambreen *et al.* (2018)
		Oleic acid	3	11.4-34.1	
		Linoleic acid	6	10.1-19.1	
		100 seed weight	2	8.9-24.52	
		Plant height	6	10-14.7	
		Number of capitula/plant	2	7.4-25.7	
		Number of primary branches	3	8.0-13.3	
		Days to 50% flowering	5	7.9-12.6	
Germplasm (100)	ALFP (341)	Seed yield (normal)	2	7.25-15.83	Ebrahimi *et al.* (2008)
		Seed yield (drought stress)	6	4.84-10.28	
		Oil yield (normal)	2	7.21-14.15	
		Oil yield (drought stress)	5	3.92-10.32	
		Oil content (normal)	3	5.75-12.12	
		Oil content (drought stress)	3	5.64-7.24	
		Number of capitula/plant (normal)	2	6.0-7.15	
		Number of capitula/plant (drought stress)	1	7.12	
		Number of seeds/capitulum (normal)	5	4.6-7.7	
		Number of seeds/capitulum (drought stress)	3	6.44-10.08	
		1000-seed weight (normal)	2	2.1-2.2	
		1000-seed weight (drought stress)	3	3.04-3.76	
		Number of branches/plant (normal)	2	8.0-9.6	
		Number of branches/plant (drought stress)	2	15.44-16.32	
		Plant height (normal)	1	2.2	
		Plant height (drought stress)	4	3.12-3.92	
		Castor			
Germplasm	SNP (3,465)	Resistance to Fusarium wilt based on days to wilt	69	0.063-0.215	Shaw *et al*. (2021)
Germplasm (175)	SSR (143)	Traits associated with cadmium tolerance - Plant height	3	7.3-15.91	Yeboah *et al.* (2021)
		Fresh weight shoot	3	10.18-13.0	
		Shoot length	5	5.63-19.43	
		Root length	1	15.11	
		Dry weight root	2	13.04	
		Fresh weight root	1	15.91	
		Dry weight shoot	2	13.26-19.43	
Germplasm (505)	SNP (23,14,859) by GBS	Plant height	2	-	Xu *et al*. (2021)
		Number of node	2		
		Diameter of main stem	9		
		Seed length	3		
		Seed width	2		
		Seed thickness	3		
		Seed area	4		
		Single seed weight	5		

Table 2 (contd..)

Population type/size	Marker type/number	Traits	No. of associated markers	PVE (%)	Reference
Germplasm (405)	SNP (1,487)	Capsule dehiscence	171	-	Fan *et al.* (2019)
		Endocarp thickness	48		
		Panicle height	24		
		Panicle length	3		
		Plant height	2		
		Ratio of male to female flowers	693		
		Seed length	37		
		Seed volume	145		
		Hundred grain weight	52		
		Sesame			
Germplasm (87)	SNP (8,883)	Phytophthora blight resistance	29	35.57-70.32	Asekova *et al.* (2021)
Germplasm (369)	SSR (112)	Oil content	8	4.0-29.0	Li *et al.* (2014)
		Protein content	9	3.0-29.0	
		Linseed			
Germplasm (200)	SNP (6,74,074)	Seed length, seed weight, 1000 seed weight	599 SNP (in 4 different environments)	-	Guo *et al.* (2020)
Germplasm (86)	SNP (10,057)	Days of 50% flowering	2		Singh *et al*. (2019)
		Seed weight/plant	2		
		Branches/plant	1	-	
		Oil content	1		
		Capsule weight/plant and seed weight	1		
Germplasm (370)	SNP (2,58, 873)	Pasmo resistance	692 unique QTNs associated with 500 putative QTLs	0.28-15.02	He *et al.* (2019)
Germplasm (200)	SNP (7,71,914)	Mucilage content	7	11.82-17.32	Soto-Cerda *et al.* (2018)
		Hull content	4	13.83-18.20	
Germplasm (224)	SNP (5,84,987)	Fruit number	1		Xie *et al.* (2018a)
		1000-grain weight	8		
		Palmitic acid content	1	-	
		Stearic acid	2		
		Linoleic acid	1		
		Linolenic acid	3		
Germplasm (224)	SNP (1,46,959)	Plant height, technical length, number of branches, number of fruits and 1000-grain weight	42	-	Xie *et al*. (2018b)
Germplasm (390)	SSR (464)	1000 seed weight	5	0.5-15.2	Soto-Cerdo *et al.* (2014)
		Start of flowering	1	7.1	
		End of flowering	1	7.6	
		Plant height	2	4.6-18.5	
		Plant branching	1	12.9	
		Lodging	2	7.1-8.9	

(QTNs: Quantitative trait nucleotides)

Linseed: Linseed (*Linum usitatissimum* L.) is a diploid species with 2n=30 and genome size of about 686 Mb. Genome sequence of fibre flax cultivar has been reported (Wang *et al.,* 2012; Dmitriev *et al.,* 2021). SSR (Ragupathy *et al.,* 2011; Soto-Cerda *et al.,* 2011; Kale *et al.,* 2012; Wu *et al.,* 2017) and SNP markers (Yi *et al.,* 2017) have been developed using NGS. QTLs associated with fatty acid composition and yield (Cloutier *et al.,* 2011; Kumar *et al.,* 2015), oil content and yield-related traits (Chandrawati and Yadav, 2017), plant height (Zhang *et al.,* 2018), fibre related traits (Wu *et al.,* 2018), seed and flower colour (Sudharsan *et al.,* 2017) and resistance to powdery mildew (Asgarinia *et al.,* 2013) have been reported. GWAS for agronomic traits

(Soto-Cerda *et al.,* 2014) and seed quality traits (Soto-Cerda *et al.,* 2014) have been performed. You and Cloutier (2020) reviewed extensively about linkage maps, trait mapping, and linked markers in flax. Till date, there is no example of MAS in linseed globally. Details of QTL mapping and GWAS studies performed for various traits in linseed are presented in Table 1 and 2. In India, work on trait mapping in linseed is very limited.

Niger: Niger [*Guizotia abyssinica* (L. f.) Cass.] is a diploid species with 2n=30 and genome size of about 7 Gb. To date, only two reports are found on the development of SSR and SNP markers. Dembewolf *et al.* (2010) developed 43 SSR markers using an EST library. These authors also sequenced the chloroplast genome of niger. Tsehay *et al.* (2020) identified SNP markers through transcriptome sequencing of two genotypes and designed KASP assays for 554 SNPs for genotyping applications in niger. There are no reports of trait mapping and MAS in niger globally.

Future prospects: Progress in development and application of molecular markers in breeding of minor oilseed crops of India (except sunflower) are very limited compared to the major oilseed crops such as rapeseed (Hu *et al.,* 2021), soybean and groundnut (Desmae *et al.,* 2019). Practical applications of MAS are not yet available in castor, sesame, linseed and niger. In safflower, MAS protocol is available only for high oleic acid content trait. Molecular breeding research in these crops must focus on the following areas: (1) developing genetic and genomic resources such as mapping populations, re-sequenced genomes, high throughput marker assays, etc. to facilitate discovery of genes/QTLs associated with agronomically and economically important traits, (2) prioritizing genes/QTLs for validation across populations and environments, (3) designing MAS protocols for routine use in breeding programmes.

In India, progress in molecular breeding in minor oilseed crops has been very slow due to the lack of adequate funding support and critical manpower. In order to bridge this gap, a new impetus has been given in R&D of sesame, linseed, safflower and niger under a mission mode programme on "Minor Oilseeds of Indian Origin" to harness the benefits of rich genetic resources through cutting-edge genomic technologies with the financial support from Department of Biotechnology, Govt. of India (ICAR-IIOR, 2020). It is expected that such initiatives would help advancing research and enhance critical manpower in the areas of genomics and marker-assisted breeding in the minor oilseed crops of India, which have been late entrants into the genomics era and have the benefit of knowledge accrued from the genomics of major crops (Siddiq and Vamireddy, 2021); therefore, rapid progress in molecular breeding of these crops is expected in the near future.

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