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Outlook on nutritional importance and breeding strategies for oil and quality improvement in sesame (*Sesamum indicum* L.)

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Abstract

Sesame (*Sesamum indicum* L.), is a pivotal crop in global agriculture due to its high oil content (50-60 %), rich in quality unsaturated fatty acids and an array of bioactive compounds like sesamin and sesamol. This review is a compilation of information on sesame nutrition, mechanism of action of bioactive principles, health benefits in terms of unsaturated fats, antioxidants and essential nutrients to combat health disorders. The genetic resources are the base for any crop improvement programs. The genetic wealth of this crop as *ex-situ* conservation world-wide, traits of importance from its wild relatives, studies on genetic diversity through agronomic and molecular techniques for quality traits are focused. Both conventional and molecular breeding methods are examined. Conventional breeding efforts covers trait variability, correlations, gene action, combining ability studies, breeding methods and varieties released. The insights into molecular biology probes the novel QTLs, discovery of candidate genes, molecular markers for quality traits, genome sequencing, advancements in gene expression studies, genetic maps and pangemone. Despite the significant progress, the lacuna and future prospects in these areas are highlighted. Integrating the information from modern genomic technologies with conventional methods is the key to maximize the crop's potential for oil and nutritional security.

Keywords

sesame; oil; nutrition; genetic resources and diversity; gene action; breeding; genes; molecular markers

Introduction

Sesame (*Sesamum indicum* L.), also known as gingelly, til and benne seed belonging to the family Pedaliaceae acclaimed as the "Queen of Oil seeds" is an annual crop mostly grown in tropical and subtropical regions (1, 2). During the past 3 decades, the worldwide area of sesame has increased from to 6.3 m. ha to 11.0 m. ha and production from 2.8 m.t to 6.2 m.t. The major production regions are Africa, Asia, America, Europe and Oceania with a share of 42.9, 39.3, 13.7, 2.1 and 0.9 % respectively, during 2022 (FAO STAT). Globally, sesame production has upscaled by 29 % in the past decade, due to the expansion of farmlands and the market values of sesame-based products. The top 5 producing countries as per FAO statistics during 2023 were Myanmar (1.05 million tonnes), India (950000 tonnes), Ethiopia (500000 tonnes), Sudan (450000 tonnes) and China (350000 tonnes). During the same period, our country witnessed a 25 % rise in production with a modest growth rate of 2 % annually. Rajasthan, Gujarat, Madhya Pradesh, Uttar Pradesh and Andhra Pradesh are the top sesame-producing states, contributing significantly to the overall national production (FAO and USDA 2023).

Sesame seed harbors up to 60 % oil which has good keeping quality among vegetable oils due to polyunsaturated fatty acids (PUFA) and natural antioxidants which impart stability to the oil by preventing oxidation and offer numerous health benefits (3). The oil fractions include oleic acid (almost~39 %) and linoleic acid, over 46 % and the total fatty acids is dominated by unsaturated fatty acid (4). While often overlooked, defatted sesame seed contains surprisingly high protein ranging from 18-25 % of its dry weight (5). This protein, rich in essential amino acids, particularly methionine and cysteine, makes sesame a valuable dietary source. The potential of sesame protein has been explored for its functional properties, demonstrating its ability to emulsify, gel and bind water and potentially enhance food textures along with nutritional delivery (6).

Sesame is an ancient oilseed crop acclaimed for its nutritional and economic purposes. Genetic gain in crop production, particularly for oil content, oil yield and quality, protein, lignans and minerals, is challenging to achieve. The genetic resources, diversity for traits and mining for traits provide novel alleles for incorporation into breeding programs. Information on genetic variability, trait correlations, gene action and combining ability supports the conventional plant breeding programmes to decide the parents for hybridization, mutation and trait selection in filial generations. DNA-based techniques stand at the forefront nowadays to bring into the limelight the information about the crop's genome and its sequences, biochemical pathways of oil synthesis, protein, bioactive and mineral accumulation, the Quantitative Trait Loci (QTL) and candidate genes involved. The discovery and designing of molecular markers linked to the genes controlling quality traits for their assisted selection in breeding programmes, transformation and gene editing tools have practical implications to bring about desired changes in the genotype.

This review will focus on the nutritional aspects of sesame seed, the health benefits of oil, genetic aspects covering genetic resources and diversity, gene action, breeding aspects, novel QTLs and candidate genes, advancements in molecular technology, constraints and future prospects in sesame breeding.

Nutritional importance of sesame

Sesame seeds, renowned for their nutty flavor and versatility, pack a powerful punch when it comes to nutritional content and functional properties. The proximate composition (%) of whole seed and defatted seed samples constitute 22.41, 40.90 crude protein, 41.29, 3.97 crude fat, 3.42, 7.82 crude fiber, and 4.27, 7.49 ash at 4.53 and 7.34 moisture content respectively (7). The major protein fraction is globulin, comprising around 95 % of 13S globulin. This protein exhibits unique properties like easy solubility in salt, high susceptibility to heat denaturation and similar in structure to soybean 11S globulin, but with more hydrophobic characteristics. While these properties render them suitable for specific applications, they may limit their use in certain food formulations like beverages. Sesame is rich in sulfur-containing amino acids but limited in lysine. It also contains significant amounts of oxalic and phytic acids, though decortication (hull removal) can significantly reduce oxalate content (8).

Sesame oil has exceptional stability and resistance to rancidity, even at high temperatures, because of its fatty acid composition with a balance of 14 % saturated, 39 % monounsaturated and 46 % polyunsaturated fatty acids (9). The optimum roasting temperature of sesame is 210˚C - 220 ˚C. At this temperature, the oxidative stability of oil, total phenol content and anti-radical activity were increased (10, 11). The high oxidative stability is due to the presence of unique unsaponifiable constituents gamma-tocopherols (a major form of Vitamin E), lignans and antioxidants like sesamol, sesamin and sesamolin (12). This profile, dominated by healthy unsaturated fats, makes it a valuable dietary fat source.

Additionally, the mineral composition (13, 14) in 100 g of seeds includes calcium (969-989 mg), phosphorous (605 -638 mg), magnesium (324-356 mg), iron (14.6-14.8 mg), zinc (5.74-7.2 mg), copper (1.58-2.5 mg) and manganese (1.24-2.5 mg).

Seeds contain 2 unique lignans namely sesamin and sesamolin and their contents vary with the genotype, growing environment and cultural practices (15). During refining, these transform into sesamol and sesaminol, which hold the key to their cholesterol-lowering effects in humans (16, 17). The antioxidant and free radical-lowering activities of sesamol have been investigated through nanosecond pulse technique (18). Unlike many oilseeds, sesame meal lacks anti-tryptic compounds, further enhancing their potential in food processing. The high polyunsaturated fat content makes it a sought-after ingredient in margarine production and cooking oils.

Potential health benefits of sesame seed and sesame oil

Numerous studies have highlighted the nutraceutical benefits of sesame and its bioactive components, showcasing a range of health benefits mentioned in the literature. Sesame seeds have demonstrated positive effects such as lowering high blood pressure, exhibiting antioxidant properties and displaying anticancer potential (5). When compared to other nuts like English walnuts and Brazil nuts, sesame seeds have a higher phytosterol content of around 400 mg/100 g (19). Sesame seeds find widespread use in addressing respiratory tract infections, infant cholera, diarrhea and various intestinal and bladder conditions. Sesame powder is utilized for managing conditions like amenorrhea, dysmenorrhea, ulcers and hemorrhagic acne (20). These bioactive ingredients are associated with benefits like reducing blood cholesterol and lipid levels, providing anti-inflammatory effects and enhancing hepatic fatty acid oxidation (21). Intake of 40 g daily of sesame seeds can decrease the total cholesterol level of the blood and more than 50 g per day leads to allergenic reactions and may cause bloating (22). The importance of the bioactive components of sesame is represented in Fig. 1 and the major bioactive components and their mechanisms are provided in Table 1.

The presence of cephalin in sesame seeds has been noted for its effective hemostatic activity. Additionally, the lecithin in seeds exhibits hepatoprotective and antioxidant properties. It has shown promise in reducing liver steatosis in individuals with prolonged parental nutrition and has been successful in treating dermatitis (23). Sesame seed proteins hold the potential for creating special foods that can both prevent and treat conditions like diabetes, cancer and heart disease (24). Studies on rats reveal that sesame proteins boost liver function and fat burning, while sesame seed consumption in humans increases vitamin E levels, a key antioxidant for cancer and heart health (25). Beyond proteins, dietary fibers offer an impressive array of benefits - antidiabetic, antitumor, anti-ulcer, heart-protective and digestive aids (26). Research even suggests promising therapeutic potential for sesame flour and cereal bars in cancer prevention (27).

Fig. 1. Bioactive components in sesame.

Table 1. Major bioactive components of sesame and their mechanisms.

Compound	Effect	Mechanism of action	References
Sesamin	Antioxidant property	Inhibits the reactive oxygen species and increases the catalase and superoxide dismutase, which protects cells from oxidative stress	(95)
	Anti-inflammatory activity	Inhibits the TNF-α- (Tumour necrosis factor) and induces pro-inflammatory cytokine mRNA expression	(96)
	Cholesterol-lowering	Down-regulates the HMGCR gene upon which the sterol transporter genes are down regulated	(97)
	Prevent cancer	Inhibits the delta -5 desaturase activity as well as cholesterol absorption	(28)
	Prevent atherosclerosis	Increases NO synthesis by stimulating endothelial NO synthase (eNOS), which improves endothelial function and causes vasodilation. Additionally, it may have an impact on macrophage activity, which affects regression and plaque stability.	(98)
Sesamol	Apoptosis induction	Causes programmed cell death of cancer cells and activates the caspases and hinders mitochondrial function leading to cell death	(55)
	Epigenetic regulation	Disturbs the methylation patterns of DNA, histone acetylation and affects the cancer cells	(99)
Sesamolin	Neuroprotective activity	Achieved *via* lowering ROS and preventing hypoxia-induced apoptosis which is advantageous for mental health.	(100)
	Anti - leukemia effects	Reduces leukemic cell numbers by almost 60 % and enhances the cytolytic activity of natural killer (NK) cells against tumor cells.	(101)
Sesaminol	Anti-cancer effects	Impacts key signaling pathways like PI3K/Akt/mTOR, often dysregulated in cancer. Interferes with the cell cycle, halting uncontrolled division and inducing arrest to limit cancer cell replication and spread	(102)
	Preventing Parkinson's disease	Activates the Nrf2-ARE pathway, enhancing cellular defense by regulating antioxidant and detoxification genes Sesaminol activation of Nrf2-ARE may boost defense against oxidative stress, linked to Parkinson's disease	(103)
Tocopherols	Anti-oxidant	α- tocopherol acts as an antioxidant by scavenging the lipid peroxy radicals and releasing the singlet oxygen	(104)
	Cancer prevention	γ-tocopherol maintains cell integrity by neutralizing the free radicals	(105)
	Maintains Cardiovascular Health	δ-tocopherols maintain cardiovascular health by removing the	(106)
Phytosterols	Anti-tumor effects	It can arrest the tumor cells cell cycle to prevent further proliferation	(107)
	Antidiabetic	Activates AMPK, an important energy metabolism regulator. Better glucose absorption and utilization result from AMPK activation, which also improves glucose regulation.	(108)
Sesame oil	Antioxidant	Increases the anti-oxidant enzymes such as SOD and reduces the lipid synthesis	(109)
	Antidiabetic	Reduction in HbA1C, glucose level, increase in insulin	(31)
	Antihypertensive	Reduction in MDA, hs-CRP, TC and LDL, TG, FBG, HOMA-IR and improves the diastolic and systolic blood pressure	(110)
	Against breast cancer	Inhibition of growth of cancer cells and apoptosis in S and G2/M phases	(111)

The polyunsaturated fatty acids (PUFAs), particularly omega-3 and omega-6 fatty acids and myristic acid present in oil contribute to cancer-fighting properties due to their ability to modulate inflammatory processes, influence cell signaling pathways regulating apoptosis and maintain a balance that supports normal cellular functions (28). Sesame oil has demonstrated significant potential in countering diazinon-induced stress, attributed to its free radical scavenging, antioxidative and anti-inflammatory properties (29). The intake of oil has demonstrated its potential to efficiently reduce cerebrovascular ischemia. Furthermore, it may synergistically work with diabetes medication, contributing significantly to the treatment of hyperglycemia (30, 31).

Sesame oil plays a vital role in the pharmaceutical industry, serving as a solvent in intramuscular injections. Renowned for its nutritional, soothing and ointment qualities, it also functions as a laxative (32). In Chinese traditional medicine, sesame oil has been utilized for centuries to address toothaches and gum diseases (33). Additionally, it is known for its effectiveness in treating conditions such as headaches, dizziness and blurred vision. In Indian culture, sesame oil is employed as an antibacterial mouthwash, offering relief from anxiety and insomnia. Its multifaceted properties make it a versatile and valued component in various traditional remedies and practices (34).

Sesame genetic resources and gene banks

The genetic diversity found in sesame crop plays a crucial foundation for identifying and selecting desirable traits in ongoing and upcoming genetic enhancement initiatives. Various National and International gene banks play a crucial role in collecting and preserving genetically diverse sesame germplasm resources comprising of wild distant relatives and closely related species, local land races, obsolete breeding lines including mutants and newly developed improved varieties, contributing to sesame improvement programmes.

The conventional belief suggested that most of the diversity in the genus *Sesamum* existed in Africa, indicating the possible origin of sesame from this continent (35). However, the evidence for the cultivation of sesame at the Indus Valley civilization dates back to 3050-3500 BC and its progenitor being *S. malabaricum* (1, 36). The diversity in sesame is rich, probably due to the adaptation of the crop to the varied environments where the crop has been reported, influenced by both long-term natural and artificial selections (1, 37). The dedicated efforts of the scientific community in collecting, characterizing and conserving sesame germplasm has resulted in an intensive collection of genetic materials in cultivated sesame and its wild relatives, presently stored at various gene banks worldwide, with much focus being placed on Asia to the tune of about 95 % and the U.S.A holding the remaining 5 %. The notable gene banks conserving sesame are mentioned in Table 2.

In wild relatives of sesame, oil content is found to be less (24.4 to 36.9 %) than in cultivated types. The elevated oil content in cultivated species has arisen from independent species-specific genomic evolution rather than environmental selection (38). In the fatty acid profile, linoleic is higher than 50 % in *S. occidentale* and *S. mulayanum*, while higher oleic than linoleic was reported in *S. alatum* (39-41). Though the % of fatty acid genes in the cultivated sesame genome is similar to that in wild *Sesamum* and other oilseed crops, copy number variations of key fatty acid genes contribute to the differences among the oilseed crops. The gene number of the ß-CT gene family (first rate-limiting enzyme in FA synthesis) in cultivated sesame was 8 times higher compared to other oilseeds and wild species, which enhances the initiation of FA synthesis and increases, seed OC (38).

Wild sesame species with resilience to biotic threats such as *Phytophthora* blight, *Alternaria* leaf spot, phyllody and leaf curl virus as well as abiotic stresses like waterlogging, drought and salinity (42), have been reported. The details are furnished in Table 3.

Genetic diversity in sesame germplasm

The conventional methods to assess the diversity in sesame germplasm for measurable traits utilize the principal component analysis, Mahalanobis D^2 statistics, and UPGMA (unweighted pair group method with arithmetic mean) hierarchical clustering. PCA simplifies complex data but might lose important information. Mahalanobis D^2 statistics assumes that data follows a multivariate normal distribution but can be affected by outliers. UPGMA clustering assume a constant evolutionary rate, which might not be true for all species. This can lead to incorrect phylogenetic relationships.

The morphological description focuses on 14 observable traits in sesame for differentiating the accessions namely stem hairiness, leaf lobes, leaf size, serration of leaf margin, plant branching and its pattern, petal color of the flower, petal hairiness, capsule hairiness, locule number per capsule, capsule shape, capsule number per leaf axil, capsule arrangement, seed coat color (43).

Table 2. Gene banks holding sesame germplasm.

Institute	Country	Accessions conserved	Web site
NBPGR (National Gene bank)	India	10517	http://www.nbpgr.ernet.in/
National Agro Biodiversity Center	South Korea	7698	http://www.rda.go.kr/foreign/ten/
Oil Crops Research Institute	China	>8000	https://www.ars.usda.gov/
USDA-ARS-PGRU	United States	1226	https://www.ars.usda.gov/
JNKVV, Jabalpur	India	2402	https://krishi.icar.gov.in/aicrp/
Total		**29843**	

Table 3. Information on wild relatives of sesame.

Crop wild relatives	Native	Chromosome number (2n)	Morphological characters	Tolerance/ resistance	Quality traits (%)	References
Sesamum angustifolium	Kenya and Sudan	26	Annual, leaves are narrow in shape, erect stem, flowers are white to pale purple in colour and capsules elongated.	Drought	Oil content - 28.9 Palmitic - 8.7 Stearic - 7.8 Oleic - 35.5	(39-41)
Sesamum laciniatum	Peninsular India	32	Perennial, profusely branching, deep purple coloured flowers with purple anthers and yellow glands are absent.	Drought and shoot webber	Oil content - 24.4 Palmitic - 8.49 Stearic - 6.52 Oleic - 35.51 Linoleic - 48.48	
Sesamum prostatum	Tropical and subtropical regions of Africa	32	Perennial, profusely branching, leathery leaves, dark purple flowers, tough capsules	Drought, soil salinity, shoot webber, phyllody and wilt	'Information not provided'	
Sesamum mulayanum	South India	26	Annual, profusely branching, purple flowers with yellowish-white anthers, thick testa with tough capsules.	*Fusarium* wilt, Gall fly, phyllody and wilt	Oil content - 27.7 Palmitic - 9.53 Stearic - 5.39 Oleic - 32.27 Linoleic - 51.24	
Sesamum radiatum	West and central Africa	64	Annual, moderately branching, broader leaves, purple flowers, purple anthers and rough seeds with thick testa.	*Fusarium* wilt, leaf blight, Phyllody, shoot webber, *Phytophthora* blight and seedling blight	Oil content - 36.2 Palmitic - 9.5 Stearic - 9.9 Oleic - 37.9 Linoleic - 40.6	
Sesamum alatum	Mostly Egypt	26	Annual, profusely branching, dark purple flowers and deeply grooved cylindrical anthers. Winged seeds with thick testa.	*Fusarium* wilt, *Phytophthora* blight, leaf blight, phyllody, powdery mildew and shoot webber	Oil content - 28.9 Palmitic - 11.5 Stearic - 5.6 Oleic - 43.2 Linoleic - 36.9	
Sesamum malabaricum	India	26	Annual, finely branching, heteromorphic and linear to 3-lobed entire leathery leaves, purple flowers and cylindrical capsules.	Heavy rainfall, powdery mildew, shoot webber	'Information not provided'	
Sesamum occidentale	Sub-Saharan Africa	64	Annual, moderately branching, yellow glands present, purple flowers with light purple coloured anthers and cylindrical anthers.	Drought and powdery mildew	Oil content - 31.7 Palmitic - 9.51 Stearic - 6.86 Oleic - 27.68	

Thus, genetic diversity analysis in sesame germplasm relied on methods such as morphological phenotyping and isozymes of isocitrate dehydrogenase (IDH) (44). These markers were gradually incorporated for evaluating genetic diversity in sesame accessions (45). Genetic markers *viz.,* Randomly Amplified Polymorphic DNA (RAPD) technique, AFLP, SSR and ISSR have been employed to assess the diversity at the molecular level through association mapping (46) as they are fast with minimum errors and provide an efficient way of linking the genotypic variations with the phenotypic variations (47). They are of great value in assisting phylogenetic relationships, parental line selection, population structure and allele distribution among germplasm lines and in designing breeding strategies. However, concerns about the instability of polymorphism were raised for these universal markers. To address this issue, researchers focused mainly on identifying species-specific markers, including Single Nucleotide Polymorphism (SNP) and Insertion/Deletion (InDel) markers. These markers are well known for their stability and were introduced into sesame breeding programs in the early 21st century (72). Advanced approaches such as RAD-seq, SLAF-seq, RNA-seq and GBS are now used in sesame research to discover single nucleotide polymorphisms (SNPs) at a large scale (48, 49). These high throughput methods provide valuable insights into sesame genetics and contribute to the improvement of positive traits.

With the availability of complete genetic information of sesame through whole-genome sequencing (WGS), SNP markers are now employed for studying sesame populations in marker-assisted breeding efforts (50). By using data from next-generation sequencing, researchers can identify SNPs that have specific characteristics-4bi-allelic (having 2 possible variations), co-dominant (both variations are expressed) and follow predictable inheritance patterns. The information about genetic diversity in recent literatures has been tabulated (Table 4).

Table 4. Genetic diversity studies in sesame.

Number of accessions studied	Genetic diversity assessed through	Traits studied	Range of quality traits (%)	References
11	UPGMA	Yield-related and nutritional composition	Oil : 53.61 - 60.50 Carbohydrate:8.81 - 28.62	(112)
70	UPGMA	Yield-related and oil-content	Mean oil content - 49.3	(113)
30	Tocher's method	Oil content and fatty acids composition	Oil: upto 36.7 Oleic acid: upto 43.87 Stearic acid: 5.36 Linoleic acid: 44.76 Palmitic acid: 10.40	(114)
32	457 AFLP markers	Morphological, yield-related and oil content	Oil: 32.3: 57.3 Oleic acid: 38.2 to 47.3 Linoleic acid: 31 to 40.9 Linolenic acid: 0.22 to 0.8 Palmitic acid: 8.8 to 12 Stearic acid: 6.3 to 8.9	(115)
10	64 RAPD markers	Morphological, yield-related and oil	'Information not provided'	(116)
38	12 RAPD markers	Morphological, yield-related and oil	'Information not provided'	(117)
46	20 ISSR markers	Morphological, yield-related and oil	'Information not provided'	(117)
96	33 polymorphic SSR markers	Morphological, yield-related and oil content	Oil: 47.74 - 61.1 Protein: 15.1 - 29.6	(47)
36	10 SSR markers	Morphological and agronomic traits	Oil: 27.89 - 58.73 Protein: 16.72 -27.79	(118)
183	25 SSR primer pairs	Yield traits, oil, protein, drought, disease and waterlogging	Oil: 44.30- 55.60 Palmitic acid: 8.31-10.23 Stearic acid: 4.73 - 5.36 Oleic acid: 36.76- 48.80 Linoleic acid: 36.56 - 47.14	(93)
369	112 polymorphic	Oil content and protein content	'Information not provided'	(67)
100	27 polymorphic SSR	Oil content and fatty acids composition	Oil: 40.83 - 61.88 Protein: 14.51- 26.76 Palmitic acid: 6.92 - 11.16 Stearic acid: 3.97 - 5.97 Oleic acid: 32.08 - 53.14 Linoleic acid: 32.95 - 52.49 Sesamin: 0.24 - 9.98 Sesamolin: 0.29 - 4.77	(119)
103	5292 SNP's	Morphological, yield and oil content	Oil: 53.61 - 60.50 Carbohydrate:18.81 - 28.62	(120)
705	1200 SNP's	Oil content, protein content and fatty	Mean Oil content:- 49.3	(71)
300	5065 silicoDArt and 5821 SNP's	Morphological, yield-related and oil content	Oil: 27.66 - 58.87	(121)

Correlation, gene action and combining ability studies

Assessing genetic variability, heritability and trait correlations is crucial in utilizing germplasm effectively (51). In general, the genetic variability in available *Sesamum* germplasm is limited due to its continuous cultivation and selection in marginal lands and genetic drift (52). In many of the literatures (53-60), oil content is reported to have low and medium coefficients of variation. High heritability for oil content coupled with high genetic advance (57, 59, 61), high and moderate heritability, but with low genetic advance (53, 54) implies the trait expression in subsequent generations of selection.

Positive association of oil content with single plant yield and thousand seed weight (62), oil content with single plant yield (63) and oil content with thousand seed weight (64) imply direct selection for yield-related traits that can enhance oil content. Contrastingly negative associations between oil content and single-plant yield (64, 65) reveal the trait complexity. Negative correlation has been reported between oleic acid and seed oil content as well as, oleic acid and linoleic acid contents (47, 66). So also, there exists a strong negative correlation between oil and protein content (67-69), positive and negative correlation between oil and protein content respectively with lignans, sesamin and sesamolin content (68, 70). This implies simultaneous improvement of oil and lignan contents, but not protein, in breeding programs. Palmitic (C16:0) and palmitoleic acid (C16:1) were strongly correlated (13). No significant associations were observed between allelic variation for seed oil content and yield traits in sesame (71), but a weak phenotypic correlation between oil content and oilseed yield was reported. Seed coat color influences oil content (71), whereby late-maturing, white-seeded cultivars had higher oil content than early, black-seeded ones (72).

Being an often-cross-pollinated crop, some degree of cross-pollination exists, offering an opportunity to leverage heterosis. Understanding combining ability and gene action is essential for successful breeding programmes aimed at breaking yield barriers and oil content. To achieve this, it is advantageous to combine genes from genetically diverse parents and techniques such as Diallel, partial Diallel and line × tester are commonly employed to evaluate genotypes in terms of their combining ability and genetic composition. Combining ability analysis provides precise insights into the nature and magnitude of gene actions governing the inheritance of quantitative traits. General combining ability (GCA) is driven by additive genetic effects and additive × additive epistasis, while specific combining ability (SCA) is impacted by non-additive dominance and other forms of epistasis. The analysis aids in identifying parents with favorable general combining ability effects and crosses with specific combining ability effects, crucial for developing desirable first filial generation materials or hybrids. Information on gene action and combining ability studies mentioned in Table 5 indicates the predominance of both additive and dominant gene action for oil content. Moreover, the lignans sesamin and sesamolin are also polygenic traits controlled by additive and dominance effects (73).

Sesame breeding and varieties

Sesame was considered an overlooked crop in terms of breeding. Most of the sesame breeding programs focus on yield improvement, tolerance to stresses, indehiscent capsules, uniform maturity followed by increased oil content. A narrow genetic base, less attention to genetic improvement and cultivation in marginal lands with poor management practices are the major constraints for increasing the yield potential. Traditional breeding techniques *viz.,* pure line selection, hybridization followed by pedigree selection, induced mutations (Fig. 2) play an important role in the diversification and improvement of new sesame types (74). In conventional breeding, good phenotypic selection requires high heritability and high genetic advancement (44). Enhancing the effectiveness of selection in sesame breeding requires a thorough understanding of the relationships between economic phenotypes. The oil content in sesame is primarily controlled by the genotype with minor effects from environment and Genotype × Environment interaction and has high heritability (38).

Through mutation, 147 sesame varieties have been released globally (75). Physical and chemical mutagenesis, particularly space mutation breeding, has been employed to create new variability. Space mutation breeding involves 3 steps: seed screening, space mutation and observation/selection. High-energy ion radiation in seeds can induce DNA change and produce 2-4 % useful mutation (37). Space mutagenesis induces morphological variations and amplified fragment length polymorphism (AFLP) markers identify DNA mutations in sesame. Notable Chinese varieties like Jiguang 2, Ezhi 2, Jinzhi 3, Zhongzhi13 and Jihangzhi 4 have resulted from mutagenesis (76).

Table 5. Gene action and combining ability studies.

Traits	Parents/Lines	Gene Action	Combining Ability	References
Oil content	12 diverse genotypes	Additive and non-additive gene action for oil content	Both GCA and SCA significant	(122)
Oil and protein content	6 parents and their 15 F_1s	Non-additive gene action for both traits	Significant SCA for both traits	(123)
Oil, protein and fatty acids	15 lines and 3 testers	Non-additive gene action for oil and quality traits	Significant SCA for oil and quality traits	(124)
Oil, protein and fatty acids	5 morphologically diverse parents	Non-additive gene action for all traits	Significant SCA for all traits	(125)
Yield and oil content	10 diverse parents and their 45 F_1s	Non-additive gene action for both traits	Significant SCA for both traits	(126)
Yield and oil content	10 diverse parental lines	Non-additive gene action for both traits	Significant SCA for both traits	(127)
Yield and oil content	28 F_1 crosses	Additive and non-additive gene action for both traits	GCA and SCA significant for both traits	(128)
Yield and oil content	7 diverse parents and their 21 F_1s	Additive and non-additive gene action for both traits	GCA and SCA significant for both traits	(129)
Yield and oil content	7 parents and their 21 F_1s	Additive and non-additive gene action for both traits	GCA and SCA significant for both traits	(130)
Yield and oil content	4 lines and 6 testers	Additive and non-additive gene action for oil content and yield	Significant GCA for oil content and significant SCA for yield	(131)
Yield and oil content	7 parents and their 21 crosses	Additive and non-additive gene action for both traits	GCA and SCA significant for both traits	(132)
Yield and oil content	8 genetically diverse genotypes	Additive gene action for oil and non-additive gene action for yield	GCA significant for both traits	(133)

GCA- General combining ability; SCA- Specific combining ability

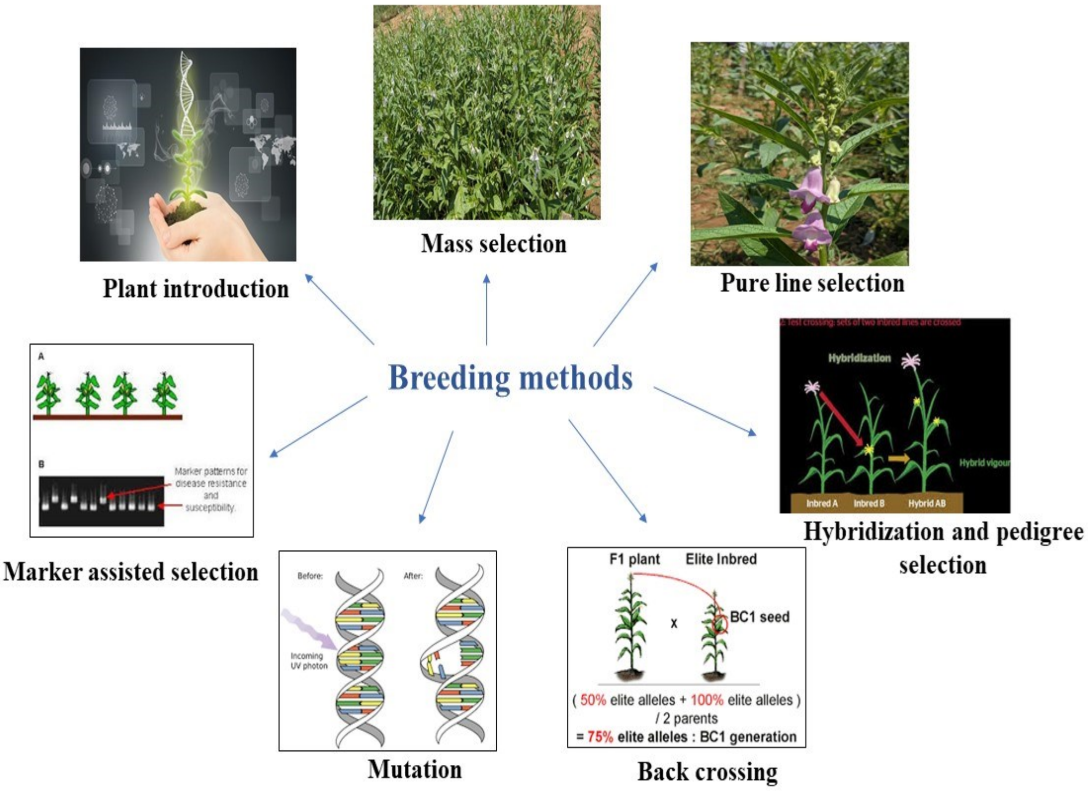

Fig. 2. Breeding methods of sesame.

Apart from China and India contributing many cultivars, Myanmar introduced 29 sesame types in 42 years, focusing on early maturity, white seeds, high yield and oil content. Notable examples include Ju-Ni-Poke and Shark-Kale, both with high yield and over 55 % seed oil. (51). Victoria, Aida, Valya and Nevena released from Bulgaria have mean yield of 1.35 tons ha^{-1} (77). All the efforts through different breeding methods have resulted in varieties with improved yields, plant type, earliness, tolerance to biotic stresses, oil content and quality. The varieties released through conventional breeding with 50 % and above oil content are mentioned in Table 6.

QTLs and genes for oil and quality

Multiple genes determine quantitative traits, each of which may have a large or small effect. QTL identification and development of molecular markers linked to useful traits can serve as a useful tool in breeding varieties by marker-assisted selection and can accelerate our breeding programmes (78). The information on 5 QTLs each for oil, protein, sesamin contents and 15 candidate genes for quality traits have been compiled (Tables 7, 8).

Table 6. Sesame varieties released through conventional breeding.

Name of the variety	Year of release	Content (%)	Name of the variety	Year of release	Content (%)
			Oil content		
TMV - 3	1943	50-52	JST -8	2001	50-53
TC - 25	1978	50-52	RT- 127	2001	50-52
TMV - 6	1980	52-54	Sekhar	2001	50-52
Kanchan (JT-7)	1980	50-53	VRI (SV)-2	2005	50-53
N - 8	1982	50-51	Tarun	2005	52-53
CO - 1	1983	50-52	Jawahar Til- 14	2008	50-53
Paiyur - 1	1990	50-52	TMV -7	2009	48-50
SVPR-1	1991	50-54	JLT - 408	2010	51-53
Varaha	1993	50-53	Zhongzhi 18	2011	56.82
Gautama	1993	50-52	Zhongzhi 19	2011	60.52
TKG- 21	1993	52-54	Yanzhuang 1	2012	59.27
VRI (SV)-1	1995	50-52	DS-5	2012	50-52
TKG - 22	1995	50-54	Yuzhi DS899	2015	51.43
Swetha Til	1997	50-52			
			Protein content		
TMV (SV)- 7	2009	24.50	Ganzhi 11	2014	25.53
Jiheizhi 2	2011	24.15	Yuzhi DS899	2015	26.75
Jinzhi 7	2012	22.52			

Source: https://www.icar-iior.org.in/sites/default/files/iiorcontent/pops/sesame.pdf and (134).

Table 7. QTLs reported in sesame for oil and quality traits.

Quality traits	QTL locus	LG position	Marker interval (cM)	References
Oil content	Qoc-1	LG1	SBN2389- SBN2485 (37.0 - 40.6)	(15, 68, 134)
	Qoc-2	LG2	SBN2776- SBN1045 (13.5- 15.2)	
	Qoc-5	LG5	SBN3585 - SBN1490 (41.5 - 52.1)	
	Qoc-9	LG9	SBN1388 - SBN145 (6.9- 9.7)	
	Qoc-16	LG16	SBN1927 - SBN3232 (22.6 - 26.6)	
Protein content	Qpc-1	LG1	SBN741 - SBN2389 (20.0 - 28.7)	
	Qpc-2	LG2	SBN2776 - SBN2749 (13.5 - 15.2)	
	Qpc-3	LG3	HS184 - SBI013(6.3 - 9.7)	
	Qpc-5	LG5	SBI007 - SBI057(62.8 - 68.4)	
	Qpc-6	LG6	SBN3210 - SBN636(94.0 - 102.4)	
Sesamin content	Qsc-4	LG4	SBI050 - SBN1100(70.7 - 73.7)	
	Qsc-5	LG5	ZHY01 - SBN1548(49.4 - 56.2)	
	Qsc-5	LG5	SBN3568 - SBI007(40.5 - 62.9)	
	Qsc-8	LG8	SBN1735 - SBN2668 (35.4 - 44.6)	
	Qsc-8	LG8	SBN1407 - SBN1140 (37.0 - 38.2)	
	qSmin_11.1	LG11	ZMM1776 - ZM918 (127 - 127.21)	
	qSmin_9.2	LG9	ZMM1135 - ZMM1133 (122.61 - 123.01)	
Sesamolin content	qSmol_11.1	LG11	ZMM1776 - ZM918 (127- 127.21)	
	qSmol_4.2	LG4	ZMM4671 - ZMM4031 (72.31 - 73)	
	qSmol_4.4	LG4	ZMM1901- ZMM1242 (83.11 - 85)	

Table 8. Genes identified for quality traits.

Candidate genes identified	Gene function	References
CXE17 (SIN_ 1003248)	Encodes a lipase involved in the breakdown of fats and contributes to oil biosynthesis in sesame.	(13, 15, 71, 135)
GDSL-like Lipase (SIN_ 1013005)	Encodes a lipase enzyme, part of the GDSL family, involved in lipid metabolism and contributes to oil biosynthesis in sesame.	
Lipid Transfer Proteins (SIN_ 1019167 and SIN_1009923)	Facilitate the transport of lipids between membranes or within cellular compartments during oil biosynthesis.	
SiPPO (SIN_ 1016759)	Mutations in SiPPO are associated with increased oil content. Specifically, varieties with mutated SiPPO alleles show higher oil accumulation. This gene is linked to protein content and it also encodes polyphenol oxidase involved in pigmentation by producing black pigments through browning reactions.	
SiNST1 (SIN_ 1005755) (SIN_1005756)	Regulates secondary cell wall formation, lignin biosynthesis and cellulose content in woody tissues. The 'A' allele is associated with increased lignin and seed coat thickness but decreased oil and protein content.	
SiKASI (SIN_ 1001803)	Involved in the synthesis of palmitic acid and influence fatty acid composition by impacting the levels of palmitic and palmitoleic acids.	
SiKASII (SIN _1024652)	Involved in palmitic acid synthesis, playing a role in fatty acid elongation and influence fatty acid composition by impacting the levels of palmitic and palmitoleic acids.	
SiACNA, SiDGAT2, SiFATA, SiFATB and SiSAD	Involved in lipid metabolism, particularly in fatty acid elongation, desaturation and export from plastids. SiDGAT2 is involved in triacylglycerol synthesis, which affects the unsaturated to saturated fat ratio.	
SiFAD2 (SIN 1009785)	Encodes an oleic acid desaturase, a key enzyme that converts oleic acid (C18:1) to linoleic acid (C18:2) in the endoplasmic reticulum. A mutation in this gene is associated with higher oleic acid content in sesame oil.	

The identified genes have a key role in increasing oil content and seed coat color (*SiPPO*), down-regulation of oil, protein, sesamin and sesamolin (*SiNST1* due to mis sense SNP), oil biosynthesis (*CXE17, GDSL*-like lipase and Lipid Transfer Proteins), lipid metabolism (*SiFATA, SiFATB, SiSAD*) and influencing fatty acid composition (***SiKASI, SiKASII, SiACNA, SiDGAT2, SiFAD2***). A missense SNP in *SiNST1*, in which, the 'A' allele was linked to higher levels of lignin and seed coat thickness but lower levels of oil, protein, sesamin and sesamolin.

Analysis of 95 modern cultivars and 404 landraces revealed that the gene *SiPPO* (*SIN_1016759*) has been favored in modern breeding programmes for its association with higher oil content as evidenced by its mutant forms. Only 2 cultivars and 98 landraces had original versions, confirmed by qRT-PCR and RNA-seq studies (71). *NAC1* transcription factors play a significant role in the regulation of fatty acid biosynthesis in developing seeds (38).

Three loci *qLignan1-1*, qLignan6-1 and *qLignan11-1* control the lignin content, specifically sesamin and sesamolin and all have additive effect that can be combined in gene pyramiding (79). The enzyme sesamin synthase is responsible for sesamin biosynthesis by encoding the gene *CYPB1Q1*, which is involved in primary and secondary metabolic pathways (80). The gene *CYP92B14* is responsible for sesamolin biosynthesis by sesamin oxidation to form sesamolin and sesaminol (81).

Recent studies (4) using microm RNA and transcriptomics revealed the genes FAD2, LOC10515945, LOC105161564 and LOC105162196 that were clustered into groups and regulated the accumulation of unsaturated fatty acid (UFA) biosynthesis in sesame. Regarding minerals,6 QTLs each related to zinc ,iron, copper and phosphorus and 4 QTLS related to potassium and 3 QTLs each related to calcium, magnesium and sulphur have been reported (82).

Population structure analysis revealed 4 fatty acids FAB55, FAB76, FAB77 and FAB118 (SiChr.3, SiChr.5 and SiChr.9) and eight R gene blocks- RB25, RB49, RB86, RB144, RB151, RB164, RB165 and RB172 (SiChr.1, SiChr.2, SiChr.3, SiChr.4, SiChr.5 and SiChr.11) enhance oil metabolism. The gene *SiNAC1* located in the nucleus was proved to have a regulatory function in fatty acid biosynthesis (38).

Molecular markers in sesame for assisted breeding

A set of 10 SSR markers were developed which was the first report to assess genetic diversity in 16 sesame accessions and significant polymorphisms were noticed (83). In 2008, researchers analyzed 3328 sesame EST sequences in NCBI, from which 50 EST-SSRs were developed. Of them, 27 (61.4 %) were highly polymorphic across 34 sesame cultivars (84). A genetic linkage map for sesame was constructed, utilizing a combination of EST-SSRs, AFLP and RSAMPLs (random selective amplification of microsatellite polymorphic loci markers (85).

Nineteen and 24 SSR markers linked to oil and protein content, of which 17 were associated with genes for the lipid pathway and 2 related to the fatty acid elongation gene were reported (67). Later, next-generation sequencing technology (NGS) has opened avenues to use genome-based markers such as SNPs and InDels, which are high throughput compared to RFLPs, RAPDs and SSRs (86). Now, high and ultra-density SNP genetic maps are available for sesame (87).

Single nucleotide polymorphisms (SNP) serves as a marker capable of detecting variations at a single location within the DNA sequence of individuals (88). Conversely, an InDel polymorphic molecular marker is a PCR-amplified marker generated from specific primers designed on both ends of the insertion/deletion sequence (89). SNPs occur more frequently in the genome, allowing for greater resolution in genetic mapping and diversity studies. They are highly informative, stable and can capture even small genetic variations. In sesame, the completion of the reference genome has facilitated the accumulation of genomics data, enabling the application of these markers. Consequently, transcriptome analysis, utilizing SNP and InDel markers based on genome data, has been employed to construct a genetic map in sesame for the examination of desired traits (90). In seeds of Zhongzhi 16 and Mishuozhima, 8404 DEGs (differentially expressed genes) for oil content and fatty acids and 20 candidate genes through whole genome sequencing were identified. Reports are on the identification of SiTPS1 is one of the key regulatory genes of fatty acids and triacylglycerol metabolism in sesame (91).

The use of molecular techniques in the improvement of various traits of sesame that enhance its production and productivity has been proposed (92, 93). Due to the limited access to technology and a lack of a centralized genetic database for crucial agronomic traits and related genes, the use of genomic techniques is still restricted (47).

Constraints

Breeding sesame for better oil, protein and nutrition faces many challenges as all are quantitatively inherited. First, the narrow genetic diversity limits access to desired traits. Simultaneous improvement of yield and quality traits like high oil, protein, lignin and minerals are governed by negative and positive relationships coupled with moderate or low heritability. Still, it is difficult to transfer the genes from wild relatives to cultivated varieties because of pre- and post-fertilization barriers. Also, the pathway behind oil and protein biosynthesis is to be fully understood, together with refinement in transformation protocols for gene editing, which needs further research. Fewer QTLs, functional markers for marker-assisted breeding and genome editing tools to improve the oil, protein and nutritional quality of sesame is in infancy but offers potential researchable area. There is also a need for more extensive research on post-harvest processing methods that can enhance nutritional quality without compromising oil extraction efficiency and loss of minerals, vitamins and anti-oxidants.

Future prospects in sesame breeding

Current crop breeding is not sufficient to meet the needs of the growing global population. Experts recommend advanced methods like germplasm characterization, genome assembly, gene function discovery and genomic breeding. These, along with gene editing, can speed up agricultural progress. Genome assembly aids in breeding and trait identification. Germplasm characterization is being taken up to identify novel alleles for agronomic traits and quality. Landraces are the source of diversity, carrying many desired alleles for genetic improvement. Compared to the GWAS and conventional QTL detection, QTL- seq is cost-effective, time-saving and informative to find useful trait-associated loci from a large number of materials evaluated at different environments to accelerate marker-assisted breeding.

The genome size of sesame is 354 Mb (76). Creating detailed maps of proteomes, metabolomes for understanding the biosynthetic pathway and gene expression is crucial. The genome assemblies of 2 landraces, Baizhima and Mishuozhima and cultivars Zhongzhi 13, Yuzhi 11, from China and Swetha from India are now available. Their genomes are valuable for comparative studies and gene discovery. A pangenome was created from these 5 genotypes with a size of 554.05 Mb. This included a core genome of 258.79 Mb and a dispensable one of 295.26 Mb, with 26472 gene clusters. Of these, 58.21 % were core genes and 15890 were unique to specific varieties. Modern varieties had genes linked to seed yield and quality, while landraces possessed genes linked to environmental adaptation (71, 92, 94).

Sesame breeding holds great potential in the future to enhance the oil, its yield and quality, protein, lignans and minerals for human nutrition. These innovations aim to meet consumer demand for code-free label oils and non-soy proteins in food. The genomic tools and bioinformatics research have helped biologists identify sesame genes useful for oil and protein. The availability of the SNPs and InDels should accelerate the QTL mapping and gene cloning of sesame. Molecular markers developed from the SNPs and InDels could become a powerful tool in molecular-assisted breeding. Addressing these challenges through the integration of breeding and molecular techniques is imperative for genetic improvement in sesame for sustaining its global supply chain and nutritional value.

Conclusion

Enormous works of literature were probed covering the aspects of sesame origin, domestication, cultivation, production, nutrition in terms of oil and its quality, protein, lignans, minerals, anti-nutritional factors, health benefits to humans, the germplasm, genetics and breeding of sesame for yield improvement, traditional techniques, modern molecular methods involving identification genes and QTLs, genome sequencing etc. for preparation of this manuscript. However, research papers integrating nutrition, health benefits, genetic resources, genetics of quality traits, genes, QTLs, trait improvement through breeding and genomic research in sesame were scanty. Hence, this review was designed to provide a whole perspective and explore the advancements in the above aspects for the benefit of researchers to identify the lacuna and potential areas for future research.

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Authors' contributions

SRVNGB drafted the manuscript, review collection, tables and figures preparation, RS involved in conceptualizing article outline, review collection, tables and figures preparation and manuscript editing, AM, MP and NM involved in the manuscript correction and supervised the process. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

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