Biotechnological Approaches for Genetic Improvement of Sesame (*Sesamum indicum* L.)

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Abstract

Sesame (*Sesamum indicum* L.) is an important oilseed crop cultivated since the ancient past for its healthy and quality oil. However, it is only in the recent past that modern genomic tools have been developed in sesame and deployed in sesame crop improvement. Knowledge of biotechnological tools and techniques developed in sesame in the post-genomics era would help to bridge the long-stagnated yield barrier and relieve the crop from a range of biotic and abiotic stresses. In this context, an attempt has been made to collect, analyze, organize, and present information on biotechnological approaches for sesame crop improvement. Further, in the foreground of the immediate research attention required for sesame crop improvement and the background of works accomplished so far, future perspectives have been discussed. The present chapter is intended to educate stakeholders of sesame research ecosystem: researchers, academicians, scientists, policymakers, research funders, students, etc.

Keywords

Sesame · *Sesamum indicum* · Biotechnology · Molecular biology · Genomics · Genetic improvement · Crop improvement · Tools and techniques

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11.1 Introduction

Sesame (*Sesamum indicum* L.) is an annual herbaceous diploid plant ($2n = 2X = 26$) belonging to the family Pedaliaceae of the Tubiflorae order (Nayar and Mehra 1970). The only cultivated species among 37 species in the genus *Sesamum* has been cultivated for its unique oil, which has industrial-scale utility in culinary, pharmaceuticals, nutraceuticals, cosmetics, etc. (reviewed by Pusadkar et al. 2015). Sesame enjoys sobriquets "queen of oilseeds" and "seeds of immortality" due to the long shelf life of its seed oil, caused by resistance to oxidation and rancidity (Bedigian and Harlan 1986). The crop is grown in three regions: the Indian subcontinent, the African continent, and the Far East subcontinent (Kobayashi 1991). Globally, 70% of the sesame seeds are utilized for extracting oil and cake, whereas 30% is used for edible seeds (reviewed in Kumaraswamy et al. 2015).

The world produced 68.04 million tons of sesame seeds from 13.97 million hectares, with an average yield of 487.2 kg per hectare. The maximum production of sesame seeds was contributed by Sudan (1.53 mt), whereas Myanmar (0.74 mt) and India (0.66) occupied second and third positions, respectively. In terms of area under sesame cultivation, Sudan (5.17 Mha) occupied the first place, followed by India and Myanmar with 1.52 Mha and 1.5 Mha, respectively. While Lebanon realized the world's highest productivity of 3298.2 kg of sesame seeds per hectare, Jordan and Israel recorded the second and third highest yield levels of 2375 kg per hectare and 2041.7 kg per hectare, respectively (FAOSTAT 2020).

Even though sesame is an important oilseed crop from nutritional, industrial, and pharmaceutical viewpoints, sesame cultivation is facing numerous challenges, including biotic and abiotic stresses and stagnation of yield levels. Recent advancement in molecular biology and biotechnology is yet to be harnessed in sesame crop improvement. Development of high-density linkage maps, consensus linkage maps, marker-trait association studies, and deployment of genome editing is required to be focused as a high-priority area of research at the global level, and concerted efforts are needed worldwide to develop plant idiotypes suitable for mechanical harvesting and high-density planting; plant types with engineered quality seed oil and value addition with bioactive compounds; and sesame genotype resistance or tolerance to abiotic as well as biotic stresses. In this chapter, recent advances in sesame research, particularly from the genetic improvement point of view, are comprehensively discussed as to how they can be harnessed to enhance sesame productivity and production including genetic engineering and genome editing for securing nutritional benefits from sesame seed and seed oil.

11.2 Background

11.2.1 Sesame Origin and Evolution

The first report on the origin of sesame was made by Hilterbrandt (1932). According to him, Africa was the origin of cultivated sesame (*Sesamum indicum* L.), and the same view was concurred subsequently by Nayar and Mehra (1970), Seegler (1983), Burkill (1997), and Mehra (2000). However, a subsequent hypothesis based on archaeobotanical evidence illuminates that the Harappan civilization was the place of the first domestication of sesame and that it was subsequently spread to Egypt and Mesopotamia (Fuller 2003). In 2011, Bedigian showed that sesame originated in India and reached other parts of the world, moving along a trade route called "silk route" (Bedigian 2011, 2014). However, consensus regarding the origin and evolution of sesame species is yet to be established. Analysis of morphological, cytological, and comparative genomics may provide some convincing evidence on the origin and phylogeny of sesame (Zhang et al. 2013).

Based on the fact that India contains maximum genetic variability for cultivated species of sesame, it is believed that India is likely to be the center of origin for *Sesamum indicum* (L.), according to Bhat et al. (1999). In the present scenario, India occupies the major place in the world sesame seed export map (Ranganatha et al. 2014). The preferred seed quality parameters in the world sesame seed export market are free from pesticide residues, lack of pest infestation, high (>830 mg/100 g seed) lignan content, less than 2% free fatty acid, less than 1% oxalic acid content, the boldness of the seeds with white seed coat color, and uniform lustrousness (Ranganatha et al. 2014). The demand in the international market for sesame seeds is on an increasing trajectory. This calls for concerted efforts to improve sesame, taking advantage of recent genomics and molecular biology advancements.

Its oleaginous seed is rich in omega-6 fatty acids but lacks omega-3 fatty acids. Therefore, there is a need to undertake oil quality engineering through a genome editing approach to alter the desaturase enzyme pathways (reviewed by Pusadkar et al. 2015). Sesame seeds, as well as seed oil, contain nutrients, both mineral and vitamins: phosphorus, iron, zinc, copper, calcium, magnesium, manganese, dietary fiber, and vitamin B1, vitamin K, and vitamin E in sesame seeds (Pathak et al. 2014); and omega-3 fatty acids, sesamin, and lecithin were also found in the oil extracted from sesame seeds (Shivhare and Satsangee 2012).

11.2.2 Sesame Cytogenetics

The study of cytogenetic aspects of cultivated sesame (*Sesamum indicum* L.) is challenged by two facts: firstly, chromosomes ($n = 13$) are relatively smaller in size, varying between 1.106 μm and 3.871 μm; and secondly, they lack the morphological variations (subtelocentric, metacentric, or submetacentric (Zhang et al. 2012)). These chromosomal and morphological indistinctness further constraints investigations into structural aspects of chromosomes and evolutionary details of

sesame genome (Zhang et al. 2012; Nyonggesa et al. 2014). Based on the diploid number of chromosomes, there exists three sesame species: *S. radiatum* and *S. schinzianum* with $2n = 64$; *S. indicum* and *S. alatum*, having $2n = 26$; and *S. prostratum* and *S. angolense*, where $2n = 32$ (Nimmakayala et al. 2011; Ashi 2006). Genus *Sesamum* has two types of basic chromosome number, $X = 8$ and $X = 13$ (Ashi 2006; Zhang et al. 2013).

The genome size of cultivated sesame (*Sesamum indicum* L., $2n = 13$) was determined indirectly by deploying the flow cytometry technique and comparing it with the known genome size of other species, in addition to that of *Arabidopsis thaliana*. Based on an indirect approach, it was found to be 369 megabase pairs (Mb), whereas according to sequence data, it was observed to be 354 Mb (Yi and Kim 2011; Zhang et al. 2013).

11.2.3 Sesame Phylogenetics

Genome sequence data analysis revealed the phylogenetic position of *Sesamum indicum* (L.), where it belonged to asterids clade forming a part of core eudicotyledons that constituted the second phylogeny group of angiosperms (AGP 2, The-Angiosperm-phylogeny-group et al. 2003). Further, phylogenetic analysis using the chloroplast genomic sequence information showed that sesame (*Sesamum indicum* L.) falls under Pedaliaceae family and is a sibling genus to *Jasminum* and *Olea* (members of Oleaceae family) clade. Therefore, sesame seems to have the core lineage of the Lamiales families (Yi and Kim 2011).

11.3 Sesame Improvement in the Genomics Era

In this chapter, we tried to comprehensively summarize the recent developments in biotechnological/genomic approaches for sesame crop improvement. Omics studies and functional genomics in sesame have been reviewed explicitly by Dossa et al. (2017) and Wei et al. (2017). This chapter provides an overview of recent developments in sesame biotechnology and genomics and their potential applications in sesame crop improvement.

Research initiatives and developments in the sesame crop improvement research can be broadly viewed under three eras: (1) collection of wild and cultivars and genebank creation (Prior to 2000); (2) genetics and traditional breeding (2000–2013); and (3) genomics and omics (Since 2013, reviewed in Dossa et al. 2017). Sesame is also a very good model crop for conducting genomic research and functional genomic analyses of oilseed crops, which can be attributed to its small-sized diploid genome (Wei et al. 2015) of 354 Mb (Wei et al. 2017; Wang et al. 2014a). An overview of various resources, tools, techniques, strategies, and approaches that are deployable in sesame biotechnology are graphically illustrated in Fig. 11.1.

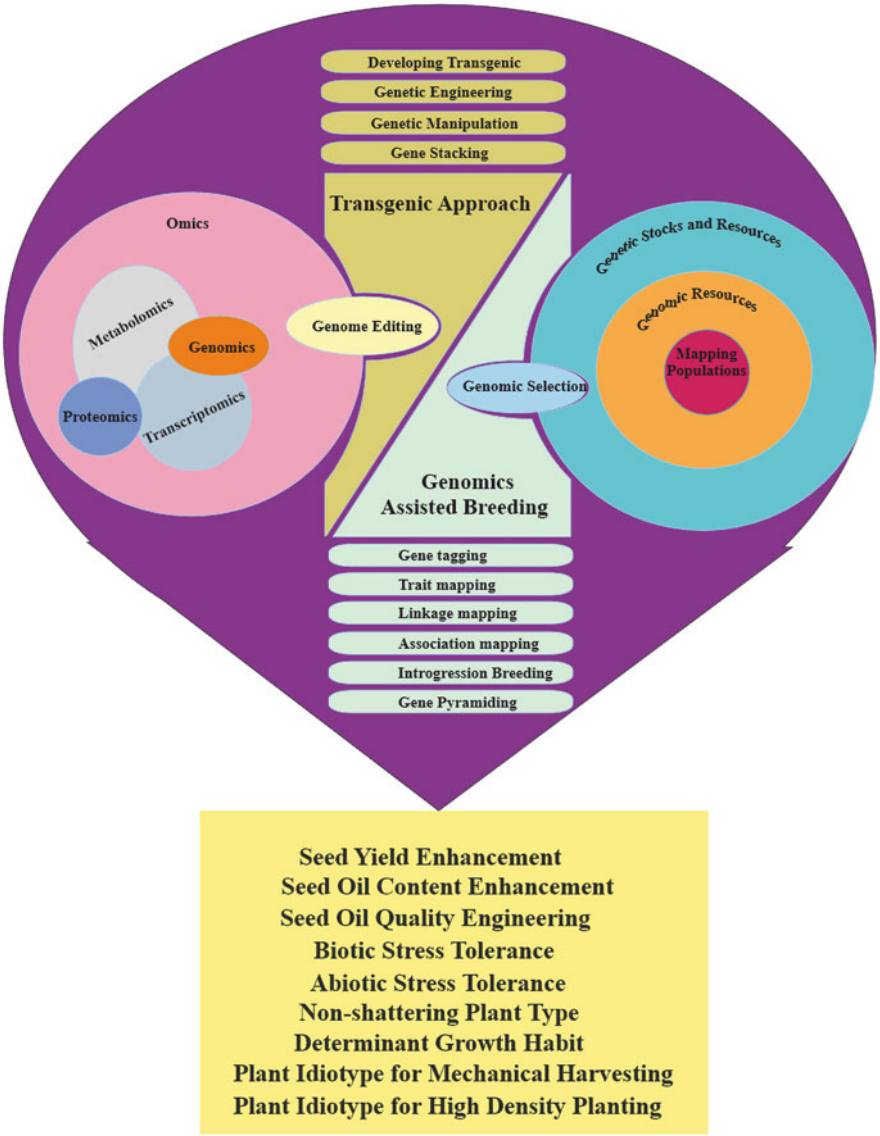

Fig. 11.1 Interrelationship among numerous genomic tools, resources, techniques, and strategies useful for sesame breeding programs

11.3.1 Sesame Genetic Resources

As stated by Murray (2017), for genetic material to be qualified as a plant genetic resource, it must be of value as a resource for present and future generations of humans. The world germplasm collection has 35,000 lines in its sesame basket, of

Fig. 11.2 Sesame crop raised under field conditions: The inserts show flowers (bottom-left) and a closeup of capsules (the right half); a closeup of a plant showing capsules is given on the right side of the figure

which 4000 are in India and China alone (Hodgkin et al. 1999). Large intra-population variations and rich phenotypic and genotypic diversity offer huge potential, and immense opportunities for genomic-assisted crop improvement in sesame are attributable to rich genotypic and phenotypic diversity with greater extent of intra-population variations (Wei et al. 2016, 2017). An aerial view of the sesame crop raised under field conditions is given in Fig. 11.2.

11.3.2 Sesame Genomic Resources

Yi and Kim (2011) sequenced the chloroplast genome of sesame for the first time. Subsequently, another chloroplast sequencing was performed from *S. indicum* cv. Yushi 11 (Zhang et al. 2013). In the same year, Wei et al. (2011) developed 86,222 unigenes, of which 46,584 showed significant similarity with protein sequences of Swiss-Prot database and NCBI nonredundant protein database. Transcriptome sequencing using the paired-end technology of Illumina led to the sequencing of 42,566 unitranscripts (Wei et al. 2011; Zhang et al. 2012). Two libraries, 57,600 BAC clones and 80,000 BIBAC clones having insert sizes of 85 kb and 120 kb, covering 13-fold and 27-fold genomes, respectively, are developed by Zhang and his team (Zhang et al. 2013). EST database of NCBI contains 45,093 sequences from *S. indicum*-expressed sequence tags. Including one full-length cDNA library of 300,000 clones, there are two seed-specific cDNA libraries of *S. indicum* (Ke et al. 2011; Suh et al. 2003). In 2009, Wei and his team constructed a first linkage map of sesame involving 284 microsatellite loci (Wei et al. 2009) which has been subsequently augmented with other 653 simple sequence repeat (SSR) markers, single nucleotides (SNPs), amplified fragment length polymorphism

(AFLP), and random selective amplification of microsatellite polymorphic loci (RSAMPL) assorted to 14 linkage groups (Zhang et al. 2013).

Expressed sequence tag-based simple sequence repeats (EST-SSRs), also called microsatellite markers, have been developed in sesame using transcriptome sequence information (Wei et al. 2011). Wang et al. (2012a) developed and characterized 59 polymorphic cDNA-based microsatellite markers; genic-SSR markers were developed and validated by Zhang et al. (2012) using RNA sequence information; 218 polymorphic SSR markers were developed by Wei et al. (2014) using genome-wide survey. They observed that 23,438 simple sequence repeats had at least 5 repeats, and the most common (84.24%) repeat motif had 2 nucleotides, while 3 nucleotide, 4 nucleotide, 5 nucleotide, and 6 nucleotide repeats comprised 13.53%, 1.65%, 0.3%, and 0.28% of the SSRs, respectively.

The sesame genome working group utilized these genomic resources for sequencing and assembling sesame genome (Zhang et al. 2013). Whole-genome sequence information (Wang et al. 2014b) is available in the public domain for both landrace and cultivated varieties (Wei et al. 2016). Based on what has been covered in the literature under the umbrella term "genomic resources," Kumaraswamy et al. (2022) attempted to define the term "genomic resources" as the sum total of biological samples and/or the information that provides the foundation for further study of the biological processes and genomic mechanisms of an organism aimed to be exploited for the benefit of mankind including ecological and environmental gain.

11.3.3 Development of DNA Markers and Sesame Genomic Diversity

The term "genome," initially coined by Winkler (1920), was described by Kihara (1930) as "a set of chromosomes that forms a fundamental and physiological unit which is indispensable for normal housekeeping metabolism, growth and development of the plant or organism." Subsequently, in the last decade of the twentieth century, the field of genome and genomics advanced impactfully.

The available of reports on genomic diversity studies on crop species suggests that the following criteria can be employed for genetic diversity analyses: morphological traits (Schut et al. 1997; Maric et al. 1998; Casadesus et al. 2007; Zarkti et al. 2012; Malik et al. 2014), molecular markers (Karp et al. 1996; Rao and Riley 1994; Manifesto et al. 2001; Pagnotta et al. 2005; Gogoi et al. 2018; Bhattacharjee et al. 2019; Kahsay et al. 2020), pedigree analysis (Barret et al. 1998), biochemical markers (Cox et al. 1985; Metakovsky and Branlard 1998), and

11.3.3.1 Morphological Markers

Among different markers, morphological markers are the first kind of markers available to plant breeders. They can be easily and visually characterized, for instance, pigmentation in any part of the plant, including corolla color, growth habit, seed shape, hairiness, etc. In the traditional plant breeding approach, plant breeders usually prefer to select wanted plants for advancing to subsequent generations only based on visual and/or directly measurable attributes. If any

morphological features are co-inherited with the traits of importance, then such markers are used to select the concerning traits indirectly. However, the morphological markers are not widely applicable owing to their environmental influence, low polymorphism, limited availability, pleiotropism, expressivity, etc.

The first problem in diversity studies solved by molecular marker was establishment of variability among functionally similar but structurally different proteins as allozymes synonymous with isozymes (Schlotterer 2004) which was extensively deployed by Hamrick and Godt (1990) in studying population genetics. Molecular marker property of the allozymes (or isozymes) was imparted and empowered by their ability to move differentially under gel electrophoresis according to their net charge and tertiary structure. Allozyme-based diversity enjoyed the monopoly field of molecular markers serving various purposes, including fingerprinting of plant genetic resources, assessment of genetic diversity, taxonomic and phylogenetic delineation, developmental biology and population genetics, and plant breeding (Bretting and Widrlechner 1995).

Isozymes originate due to amino acid alterations, which cause changes in net charge or the spatial structure (conformation) of the enzyme molecules and, therefore, their electrophoretic mobility. Isozyme analysis has been used for over 60 years in biology to delineate phylogenetic relationships, estimate taxonomy, and study population genetics and developmental biology (Bretting and Widrlechner 1995). Like in the case of the morphological markers, the biochemical markers are also impacted by the environmental factors and phenological (developmental) stages of the organism (Winter and Kahl 1995), apart from being not abundantly available in nature.

11.3.3.2 DNA/Molecular Markers

Plant DNA-level variations form the basis of variations in its morphological traits and can be analyzed using various types of DNA markers. Molecular markers are the DNA sequence variations that can be readily detected and whose inheritance can be monitored easily. The development and deployment of deoxyribonucleic acid (DNA) marker technology for detecting and exploiting DNA sequence diversity is one of the marvels in the advancement of molecular genetics (Semagn et al. 2006). DNA extraction can be accomplished using any parts of the plant taken from any developmental stage, and its analysis can be cheaper and non-laborious (Kumar et al. 2009). It has also been proved to be helpful in studying the genetic relationships, evolutionary trends, and fingerprinting of varieties.

The term "marker" was coined by Stansfield in 1986 (Stansfield 1986). In general, DNA markers mean any segment (locus) of genomic DNA with a defined nucleotide sequence that can be used as a reference point to specify other nearest locations (loci) on the same chromatin or the chromosome. Suppose the marker locus varies among different copies of genomes (individuals) in terms of the nucleotide sequence. In that case, the marker is said to be a polymorphic marker and is useful to distinguish the species' individuals or cultivars/genotypes. Individuals having two copies of the genome are called diploids and carry two copies of the marker locus. Two copies of the marker locus are called alleles if and only if they occur at the same

locus in the genome. Otherwise, they constitute multi-locus segments and are not useful for marker analysis. However, in terms of the nucleotide sequence, two alleles can be the same (identical) or different (non-identical). If a diploid individual carries the identical alleles of the marker, it is called homozygote for the marker locus, and the condition of the marker is called homozygosity. Otherwise, if it carries non-identical alleles of the marker locus, the individual is called heterozygote for the marker locus, and the marker locus is said to be in heterozygous condition.

Microsatellite or simple sequence repeat (SSR) markers are abundant throughout the genome. There is a possibility of high variations in their loci due to the inherent nature of their origin: replication slippage and crossing-over events. Therefore, SSR markers have been utilized for a wide spectrum of applications in plant genetic and genomic research. The most commonly applied fields of research include (1) population and evolutionary studies, (2) genome mapping, (3) genetic diversity analyses and phylogenetic relationships, (4) DNA fingerprinting and cultivar identification, and (5) gene tagging and marker-assisted selections. Various types of DNA marker-based diversity studies in different panels of sesame genotypes and the salient findings are summarized in Table 11.1.

After the entry of sesame into the omics era, various types of DNA markers, including SSRs, SNPs, and indels, have been discovered in sesame, paving new horizons for genomics-assisted sesame improvement programs (Dossa et al. 2017).

11.3.4 Genome Sequence-Driven Sesame Genomics

Genome-level variations form the basis for variability in every biological process and trait, including genetic control, biochemical processes at the cellular level, and physiological attributes at the organism level. Therefore, genome sequence information is vital to understanding and manipulating traits of agronomic and economic importance in crop species, including sesame. In addition, sesame genome sequence information is of paramount importance in understanding the genome's organization, evolution, structure, and size, which helps study comparative genomics of sesame.

After the genome sequencing (Wang et al. 2014a) was accomplished in the Chinese cultivar "Zhongi No. 13" of cultivated sesame, deep sequencing (Wang et al. 2014b) was carried out; this resulted in the dawn of sesame omics and subsequent development of a comprehensive database called SINBASE (Wang et al. 2014c). Subsequently, other cultivars and landraces were sequenced, including a cultivar "Swetha" from India (Purru et al. 2018), which led to the development of a dedicated microsatellite database "GinMicrosatDb" (Purru et al. 2018).

Table 11.1 Molecular marker-based genetic diversity studies in sesame

SN.	Marker type (number)	Genotypes (number)	Remarks	Reference
1	RAPD (24)	58 accessions from India and 22 exotic collections	Highly diverse accessions were from Rajasthan and northeastern states and low diversity among exotic lines	Bhat et al. (1999)
2	ISSR (14)	75 Korean genotypes	Narrow genetic diversity existed in Korean accessions	Kim et al. (2002)
3	RAPD (12)	38 Turkish genotypes	Analysis of molecular variance (AMOVA) revealed the presence of more variations within the region than among the region	Ercan et al. (2004)
4	SSR (50)	16 germplasm accessions	Ten of 50 SSRs showed polymorphism with PIC values: 0.34–0.8	Dixit et al. (2005)
5	AFLP (457)	32 germplasm lines	Ninety-three percent AFLPs showed polymorphism, and Jaccard's similarity coefficients ranged between 0.38 and 0.85	Laurentin and Karlovsky (2006)
6	AFLP (21)	96 accessions collected from East Asia and South Asia	Clustering of East Asian and South Asian accessions into two separate groups suggested the geographical identity	Ali et al. (2009)
7	RAPD (75)	10 lines collected from different regions of Sudan	Sixty-four of 75 primers gave reproducible amplicons of which 10 primers gave unique bands in each of the ten lines	Abdellatef et al. (2008)
8	RAPD (5) and morphological markers (20)	20 lines belonging to different agroecological zones of India genotypes obtained from Slovakia	Phenotypic markers (with a genetic similarity index of 0.88–0.99) were more discriminative than the RAPD markers (with a genetic similarity index of 078–095). Morphological grouping was similar to DNA-based grouping, based on principal coordinate analysis (PCA)	Kumar and Sharma (2009)
9	ISSR (14)	10 accessions	ISSRs discriminated the accessions with PIC values: 0.50–0.85 with an average of 0.67	Anitha et al. (2010)
10	Morphological, phenological, and reproductive traits (24); RAPD markers	27 lines (14 exotic accessions and 13 from Iran)	While morphological typing indicated the existence of a high spectrum of genetic variability in both exotic and Iranian genotypes, RAPD markers could decipher higher variability in Iranian genotypes than in exotic lines	Tabatabaei et al. (2011)
11	SSR (16)	150 sesame collected from 22 countries	One hundred twenty-one alleles were detected in the range of 2–18; average number of alleles were 7.6 per locus. The genotypes were clustered into three groups	Cho et al. (2011)
12	SSR (207)	9 genotypes	Forty-six of 150 markers were polymorphic and revealed the genetic similarity coefficient ranging from 76 to 92%. The genotypes were grouped into four clusters and one clade, revealing the presence of good variability and diverse origin of the genotypes	Rao et al. (2012)

13	SSR (156)	49 genotypes	Twenty of 156 markers showed polymorphism, with PIC values ranging from 0.49 to 0.90 with an average of 0.72	Yepuri et al. (2013)
14	SSR (14)	70 lines (43 from Korea and 27 from China)	Variability among the panel was low as there were only 2.8 alleles per marker locus; some markers were discriminative with PIC values in the range of 0.24 and 0.77 with an average of 0.51. Markers were found to be potentially useful in deciphering genetic variability in sesame	Park et al. (2014)
15	SSR (8); morphological characters (38)	60 genotypes of sesame including exotic collections, cultivars, and indigenous collections	Microsatellite marker loci showed 27 alleles with an average of 3.37 alleles per locus which ranged from 2 to 6. Based on morphological and molecular variability, dendrogram grouped the accessions into two major groups where accessions from the same geographical area were grouped into different clusters	Pandey et al. (2015)
16	SSR (10)	23 accessions	Four of the 10 marker loci had 14 alleles which were averaged to 3.5 alleles per locus. Polymorphic information continent values ranged between 0.28 and 0.78 and had an average of 0.53. Pairwise similarity coefficient values were in the range of 0.2 and 0.7, with an average of 0.45	Kiranmayi et al. (2016)
17	SSR (68); 19 morphological traits	41 lines comprising varieties and advanced breeding lines	Plant height was the most variable trait. Microsatellites revealed 29% polymorphism with an average PIC value of 0.409 and 2.8 alleles per locus, suggesting the presence of moderate diversity	Ramprasad et al. (2017)
18	SSR (50)	33 Indian genotypes	Twenty-seven of the 50 markers were polymorphic with 49 of the 78 alleles showing polymorphism with an average of 2.89 alleles per locus in the range of 1–5 alleles. Similarity coefficients were in the range of 0.931 and 0.591 with mean of 0.754	Gogoi et al. (2018)
19	SSR (32); morphological traits (12)	30 sesame genotypes	Marker-based and morphological trait-based dendrogram revealed that genotypes from same geographical area were grouped into different clusters; PIC value for the discriminative markers ranged from 0.07 to 0.87	Bhattacharjee et al. (2019)
20	ISSR (4); morphological qualitative traits (5)	10 Ethiopian genotypes	Molecular markers revealed 56.25–100% polymorphism; five sesame genotypes formed one group, while three other grouped to their own clusters	Kahsay et al. (2020)

11.4 Sesame Improvement in the Post-genomics Era

11.4.1 Sesame Genome Modification

Suppose a set of tools and techniques are used for the modification or manipulation of the genome of an organism that does not occur in nature. In that case, such a modification is called genome modification, genetic manipulation, or genetic engineering. Genetic manipulation helps mobilize gene resources across the taxonomic barriers, making it possible to create a myriad of variability by using varied combinations of genes from a wide array of biodiversity to achieve the target biological process(es) and/or product(s) to serve the humankind. Genome editing or engineering helps introduce new traits and knock out already existing undesirable ones. Advanced tools such as CRISPR/Cas9-based genome editing have allowed for achieving required genome modification and functional genomic analyses in crop plants, including sesame (You et al. 2022).

Genome editing requires prior knowledge of functional genomics of the trait to be modified. Aside from this, it involves tedious steps of vital procedural importance such as the development of gene construct having validated *cis*-regulatory elements including terminator and promoter sequences, repeatable in vitro culture and genetic transformation procedures, selection markers, and methods for hardening and acclimatization of transformed plants up to the stage of obtaining T_0 generation seeds. Stable integration of transgene is another crucial feature of successful transgenic technology, and therefore, it is needed to be confirmed through empirical molecular analyses. In addition, genomic location and genetic background influence the transgene's desired biological effect(s). Therefore. The technical advantage of genome editing approaches needs to be explored for functional analysis of gene (s) and their modification for commercial benefits.

11.4.1.1 Fundamental Prerequisites for Genome Engineering

As discussed herein before, genetic manipulation strategy involves validation and confirmation of suitable gene(s) to be modified, *cis*-regulatory or enhancer sequences including promoters and terminators to be employed, gene expression pattern and pathways involved, etc. The other key procedural requirements are strategy and protocols for transgene construct delivery for achieving stable integration into the target organism's genome, selection of transformants, and acclimatization for life cycle completion to obtain transgenic seeds. In the following subsections, we briefly discuss these requirements with special reference to sesame.

11.4.1.2 In Vitro Culturing of Sesame

Developing transgenic genotypes in sesame, as in any plant species, necessitates repeatable in vitro regeneration and transgene delivery methods. These procedural requirements are critical to the efficiency of transgene integration and realization of transgene product(s) or effect(s). Optimization of parameters, namely, nutrient media, growth condition, hormonal regime, frequency of subculturing, and plant

parts to be deployed as explants, is important for the successful in vitro culturing of sesame.

The effectiveness and the efficiency of regeneration and, therefore, that of transformation depend on the nature of the selection marker and the kind of antibiotics deployed during the selection of transformed cells against the non-transformants (Zhang et al. 2000; Kumaraswamy 2000; Penna et al. 2002). Transformed cells selectively grow on the culture media containing herbicides such as glyphosate or antibiotics such as hygromycin, phosphinothricin, and kanamycin, as transformed cells alone can neutralize the effect of these selection chemicals with the help of corresponding degrading enzymes produced by the deployed selectable marker genes "*gox*," "*hpt*," "*bar*," and "*nptII*." Thus, even in the chimeric tissue (e.g., callus), the selection agents coupled with the products of selectable marker genes integrated with the transgene in the recombinant construct assist the selective survival, growth, development, and regeneration of only transformed cells, while non-transformed cells get killed at the initial stage of selection cycle itself (Zhang et al. 2000). Besides, deployment of the selection markers helps overcoming the inherent problems associated with low efficiency of transformation (Jones 2003).

Cell, tissue, and organ culture in sesame provides a critical tool for sesame genetic improvement not only by providing means for genetic transformation and genome editing but also for embryo rescue of distant hybridization (Yang et al. 2017) and doubled haploid production through anther/ovary culture. However, highly reproducible protocols for efficient regeneration up to R_0 seed production are yet to be developed. Reported sesame tissue culture and plant regeneration works are reviewed in Miao et al. (2021). Culture-time contamination is one of the serious problems in realizing successful tissue-cultured plants. Shashidhara et al. (2011) reported that while Alternaria, Rhizopus, and Trichoderma are the major endogenous contaminants, Bacteria, Aspergillus, and Penicillium were the exogenous contaminants. Such factors must be considered while carrying out routine protocols such as disinfecting seed material and glass wares.

Different variants of protocols work for different genotypes. For instance, genotype "Darak" was used by Seo et al. (2007); Wadeyar and Lokesha (2011) used genotypes such as "DS-1," "E-8," and "W-II"; genotype "RT-54" (Kushwaha and Khan 2011) and "SVPR-1" (Raja and Jayabalan 2011) were also used in tissue culture experiments. The type and age of explants play another important role in the successful in vitro culturing of sesame in terms of developmental pathways. While culturing of de-embryonated cotyledons could give rise to multiple shoot production (Seo et al. 2007), hypocotyl leads to callus-mediated regeneration (Kushwaha and Khan 2011; Wadeyar and Lokesha 2011), and nodal explants and shoot tips resulted in shoot regeneration and flower bud formation (Raja and Jayabalan 2011).

Seo et al. (2007) reported high-efficiency sesame in vitro regeneration protocol where they used Murashige and Skoog (MS) basal medium supplemented with 5.7 μM indole-3-acetic acid (IAA) along with 22.2 μM 6-benzylaminopurin (BA) to obtain adventitious shoots. They reported that AgNO3 (29.4 μM) and abscisic acid (3.8 μM ABA) enhanced the efficiency. When cotyledon explants were cultured for 2 weeks on media containing 6–9% sucrose before exposing

them to a low sucrose concentration of 3%, an elevated frequency of adventitious shoot formation was recorded. The deployment of high sucrose concentration (6–9%) for 2-week-long pre-culturing of cotyledon explants followed by exposure to 3% sucrose resulted in further efficiency enhancement. Root induction was exhibited by 2.7 μM of α-naphthalene acetic acid (NAA). Wadeyar and Lokesha (2011) used the hypocotyl to induce callus. They sub-cultured it for 2 weeks on high sucrose (6–9%), followed by culturing it on MS media with 3% sucrose and then to MS supplemented with 20 μM silver nitrate (AgNO3), 3.5 mg/L BAP, and 2.5 mg/L NAA.

Raja and Jayabalan (2011) could get 91.8% of explants responding to shoot regeneration at an average of 25.9 shoots when shoot tips were used as explants to culture on Murashige and Skoog media carrying 0.3 mg/L NAA and 2.0 mg/L BAP. Further, they could observe rooting and in vitro flowering on MS media supplemented with 0.03 mg/L BAP and 1.5 mg/L NAA. They could successfully acclimatize plantlets under protected conditions. Kushwaha and Khan (2011) could achieve callus induction when in vitro seedling-derived hypocotyl segments of sesame cultivar RT-54 were cultured on MS basal media with a hormonal regime of 3.0 mg/L 2,4-dichloro phenoxy acetic acid. They could get shoot regeneration (85%) with 6.0 mg/L BAP and 2.0 mg/L NAA from 40-day-old callus, and shoot elongation was achieved with 6 mg/L BAP combined with 20% coconut water or a combination of 8.0 mg/L and 05. Mg/L NAA. Rooting (85–90%) was caused by 2.0 mg/L IBA, and 80–85% of seedlings survived in the natural field condition upon acclimatization.

11.4.1.3 Genetic Transformation Studies in Sesame

Globally there is limited work on sesame genetic transformation. Yadav et al. (2010) attempted to standardize agrobacterium-mediated genetic transformation protocol using a reporter β-glucuronidase (GUS) gene (*uidA*) and a selection marker gene neomycin phosphotransferase gene (*nptII*) jointly cloned but separated by an intron in a binary vector pCAMBIA2301. Cotyledons were used as explants for agroinfection with the vector, and transformants were allowed to produce green shoots on MS media carrying selection pressure of 25.0 mg/L kanamycin and 400.0 mg/L cefotaxime and supplemented with 25.0 μM BA and were further rooted with 2.0 uM IBA and 5.0 mg/L kanamycin. Transformants (T_0) were confirmed using GUS assay, Southern blotting, and polymerase chain reaction with gene-specific primers.

Jin et al. (2001) studied the effect of the SeFAD2 gene encoding a microsomal ω-6 desaturase on linoleic acid levels in sesame (*Sesamum indicum* L.) seeds and based on the phylogenetic analysis. It was found that the SeFAD2 gene might have diverged as a different member of a family. Driven by a seed-specific promoter, the SeFAD2 gene expresses 18–27 days post-bloom. They observed that levels of linoleic acid were concomitant with that of SeFAD2 transcript, changing the hitherto assumption that linoleic acid played a role in the synthesis of stored linoleic acid in sesame seed.

The seed-specific expression of the gene of stearoyl-acyl carrier protein desaturase (SACPD) was characterized by Yukawa et al. (1996) by cloning its cDNA. Interestingly, they could isolate and clone two cDNAs of the gene: CDES01 and CDES04; these differed with respect or expression pattern. While the messenger RNA of CDES01 was found at low in young levels, its products accumulated along with that of CDES04 only in developing seeds 21 days post anthesis. The existence of a distinct regulatory pattern suggests that at least two isozymes of ASCPD exist in sesame.

11.4.2 Potentials of Genome Editing in Sesame

With the help of a genome editing tool, it is possible to design tailor-made crop plants. Already witnessed soybean (Bao et al. 2020) and maize (Young et al. 2019) will create a wave of impact on crop breeding due to which it will be the most used genetic modification tool in the twenty-first century. The following four types of genetic engineering tools can be used for making an edited genome:

- Clustered regularly interspaced short palindromic repeats/CRISPR-associated protein (CRISPR/Cas, Barrangou et al. 2007; Jansen et al. 2002; Zhang et al. 2016)
- Zinc finger nucleases (ZFNs, Urnov et al. 2005; Baltes et al. 2014)
- Base editing system where nucleotide deaminase is fused with a Cas9-D10A nickase (nCas9, Chen et al. 2017; Li et al. 2017; Qin et al. 2020; Zong et al. 2017)
- Transcription activator-like effector nucleases (TALENs, Christian et al. 2010; Haun et al. 2014)

Global literature search suggested that no genome editing work has been reported in sesame. However, the first report of successful deployment of CRISPR/Cas9 tool to accomplish targeted editing of the sesame genome has most recently been made by You et al. (2022). In their investigation, they designed two single guide RNAs (sgRNAs) to target *CYP81Q1* and *CYP92B14* gene sequences for functional validation of their vital role in sesamin and sesamolin biosynthesis, respectively. Disruption of sesamin and sesamolin synthesis in transgenic tissue (hairy roots) proved the critical role of the genes in their biosynthesis. The targeted insertion-deletion (InDel) mutations were achieved to the efficiency of 93.33% and 90.63% in *CYP92B14* and *CYP81Q1*, respectively. It is imperative to note that despite mismatches, *CYP81Q1*-sg RNA did not show any off-target consequences. Their findings demonstrate that sesame functional genomics is empowered with CRISPR/Cas9 tool aided by hairy-root method of delivering sg-RNA-harboring gene construct into plant cell interior (You et al. 2022).

With the successful demonstration of CRISPR/Cas9-mediated genome editing (You et al. 2022) and the availability of tissue culture (Kushwaha and Khan 2011; Raja and Jayabalan 2011; Wadeyar and Lokesha 2011) and non-tissue culture (Ellison et al. 2020; Maher et al. 2020) modes of DNA delivery in sesame, concerted

and coordinated research efforts are required to be directed towards genome editing of sesame for functional genomics, metabolic engineering, and sesame crop improvement. Further, the possibility needs to be explored in sesame for developing sesame genotype resistance or tolerance to biotic and or abiotic stresses as well as meeting other breeding objectives.

11.5 Biotic Stress Tolerance in Sesame

11.5.1 Biotic Stress

11.5.1.1 Insect Pests

Several pests and diseases in sesame have emerged as serious problems. Antigastra, caused by *Antigastra catalaunalis* Dup. (Pyralidae), is one of the devastating pest problems in sesame cultivation. Leaf webber-infested sesame plant is depicted in Fig. 11.3. Mukherji (1947) reported that the food preference of the larvae depends on the total soluble salts of cell sap contents. Therefore, he created a synthetic hybrid of *S. orientale* and *S. prostratum* and demonstrated their resistance to the larva.

11.5.1.2 Diseases

A fungal species *Macrophomina phaseolina* causes charcoal rot in sesame. Yang et al. (2017) developed inter-specific crosses between wild sesame *S. indicatum*, a cultivar Zhongzhi 14, and an autotetraploid of Zhongzhi 14 (Yang et al. 2017). They confirmed the hybrid nature of the progenies using cytological and molecular marker

Fig. 11.3 Leaf webber-infested sesame under field condition

techniques. The degree of the disease resistance was assessed using the artificial inoculation method. The inter-specific hybrid of the cross: *S. indicatum* X Zhongzhi 14 exhibited the maximum degree of charcoal rot resistance (measured by infection lesion length of 6.65 cm) compared to those of other combinations of the crosses. However, it was of intermediate degree compared to that of *S. indicatum* (4.80 cm), diploid Zhongzhi 14 (14.30 cm), and autotetraploid Zhongzhi 14 (11.46 cm). Phyllody, Macrophomina, and Fusarium wilt are the other serious diseases in sesame, and concerted efforts are required to develop resistant or tolerant sources of sesame genotypes. In addition, pre- and post-emergence herbicides are required to be developed to reduce the cost of sesame cultivation.

11.5.2 Abiotic Stress Tolerance in Sesame

Drought tolerance, waterlogging tolerance, salt tolerance, and heavy metal tolerance studies in sesame are limited. Waterlogging is among the most significant factors constraining sesame production (Van Rheenen 1973; Khidir 1997; Osman 1985; Islam et al. 2016; Li et al. 2017). Changing climate poses the risk of heavy and continuous rainfall, resulting in waterlogging-induced damage to sensitive crop plants, particularly sesame. The loss of sesame seed yields due to waterlogging ranges from 30 to 100% worldwide (Wang et al. 2012b, 2016; Li et al. 2017) and 15 to 80% in India (Athul 2016; Sangeeta et al. 2019; Sreepriya and Girija 2020), depending on the duration of waterlogging, the growth stage of the crop, and type of soil (Sarkar et al. 2016). In the last 2 years, excess rainfall caused 75% of crop loss in Gujarat and the Saurashtra region in India (Faldu 2019; Sanghavi and Lashmi-Patel 2021).

Sesame is a crop of choice for small and marginal farmers who cultivate it on soil with poor and marginal fertility (Kumaraswamy et al. 2015). On soil with poor soil aeration, waterlogging due to excess rainfall further negatively impacts plant growth (Boru et al. 2001) due to oxygen deficiency (Kozolwski 1984). Sesame is more sensitive to waterlogging at the seedling establishment stage (Sarkar et al. 2016). Since waterlogging is a complex mechanism, a holistic and comprehensive understanding of the underlying mechanism is a prerequisite for initiating sesame breeding programs for waterlogging tolerance in sesame.

11.6 Applications of Genomics and Post-genomic Approaches in Sesame

11.6.1 Seed and Seed Oil Quality Engineering in Sesame

Unfortunately, in nature, nutrient factors mostly go hand in hand with antinutritional factors in the seeds of crop species, including sesame, which requires biotechnological intervention to separate them. Aside from this, desirable nutritional traits are needed to be included as value addition to enhance the nutritional gain of sesame

oils. This necessitates the modification of nutritional aspects of seeds and seed oils in sesame. For instance, genome editing tools CRISPR/Cas9 offer technological empowerment for seed and seed oil quality engineering in sesame. For example, modification of oil biosynthetic pathway to achieve enhanced levels of unsaturated fatty acids and reduced levels of saturated fatty acids is vital for securing nutrition through engineered sesame seed and seed oil.

There are different ways of modifying fatty acid quality: physico-chemical methods, including partial fractionation and hydrogenation of oils (Thimm et al. 2004). However, these methods are costlier and result in unwanted components in the final products. Therefore, genetic modification of sesame for nutritionally enhanced oil quality is a viable option, not only from the nutritional security point of view but also for the economic profitability of the sesame farmers, for it may help them fetch premium market prices. Efforts are being made to alter bioactive compounds, including antioxidants, namely, sesamolin and sesamin, in sesame by employing conventional breeding (reviewed in Kumaraswamy et al. 2015) as well as genome editing (You et al. 2022). While the breeding approaches are limited to naturally available variability within the sesame species, genetic engineering helps appropriation of gene wealth from other taxonomic units, and genome editing offers the creation of targeted and desirable variabilities that are naturally not present in sesame.

The current global trends suggest that the increasing demand for vegetable oils with nutritional value addition will be on an accelerated trajectory. This warrants that concerted global research efforts must be directed towards functional genomics focused on investigating the individual role of gene sets and metabolic engineering, particularly for oil quality and value addition, using advanced genome editing tools and accelerated breeding approaches.

The biotechnological method of quality oil engineering provides efficiency and ecological and economic advantages against physico-chemical methods (Hosur et al. 2020). For specific modification of fatty acid composition, genetic modification strategies need to be so oriented that unintended or adverse effect(s) and off-targets remain unaltered. However, unforeseen favorable effect(s) rather contribute(s) to extra value addition. In sesame seed oil, for instance, elevated tocopherol and lignan levels may cause favorable effects of enhanced oil quality, ultimately resulting in better keeping quality of the oil.

Using molecular marker-assisted back-cross breeding approach, nutritionally vital traits, including high antioxidant quality, must be transferred from wild relatives to popular cultivars. Sesame seed oil comprising 45–50% of the total mass of the seed contains numerous bioactive compounds that add health and nutritional values to the product. A detailed investigation into the metabolic network leading to the biosynthesis of different kinds of bioactive compounds needs to be undertaken before venturing into metabolic engineering for oil quality (Pathak et al. 2014; Kumaraswamy et al. 2015).

Sesame seed is naturally endowed with health-benefiting compounds with wide spectrum of applications (Pathak et al. 2014), including health foods (Cheng et al. 2006). In addition, oil extracted from sesame seeds also contains various beneficial

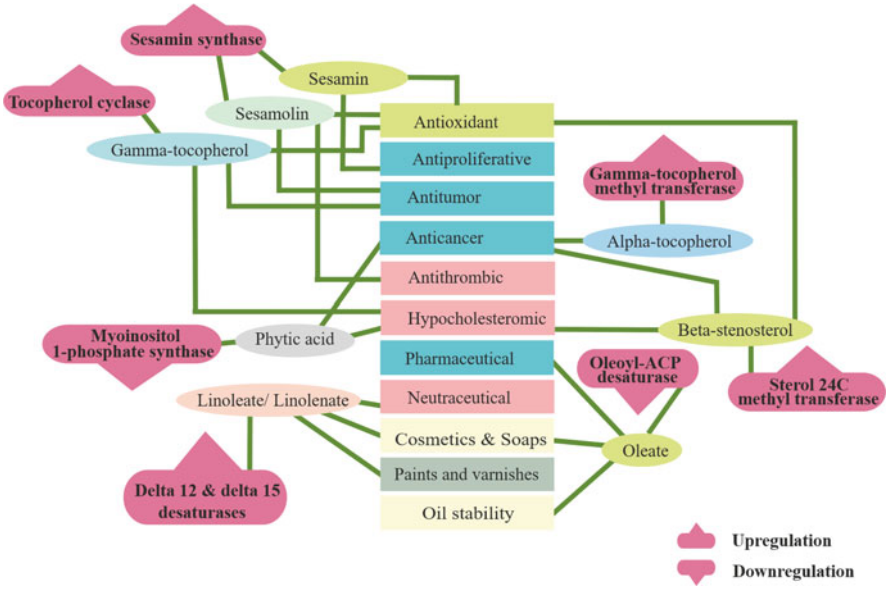

Fig. 11.4 Strategies for oil quality engineering in sesame. Industrial applications (represented by rectangular shapes) of bioactive compounds (represented by oval shapes) are given in the central column, and respective enzymes to be upregulated or downregulated to produce corresponding compounds are represented by upward and downward callout shapes, respectively

compounds such as sesamin, sesamolin, gamma-tocopherol, alpha-tocopherol, oleate, linoleate (linolenate), beta-sinosterol, and phytic acid. Through upregulation or downregulation of rate-limiting enzymes taking part in the biochemical pathways leading to production of respective enzymes, it is possible to enhance required compound and diminish undesired components in engineered sesame oil (Pathak et al. 2014; Kumaraswamy et al. 2015), and overview of the strategy is illustrated in Fig. 11.4.

11.6.2 Utilization of Sesame Oilcake/Meal

The by-product obtained after oil extraction from oleaginous material is called oil cake/meal. It is economically important as it is rich in minerals, protein, and other nutrients (Table 11.2). Sesame cake is rich in dietary fiber, essential amino acids, antioxidants, and health enhancers such as glucosides of triglucosides of sesaminol and sesamolinol (Sarkis et al. 2014; Shu et al. 2019).

Valorizing sesame cake is a viable option to utilize lipids and proteins from the sesame seed. By this method, what is otherwise waste can be efficiently as well as effectively used in the food chain (Nunes et al. 2018; Hosur et al. 2020; Melo et al. 2021).

Table 11.2 Nutrient components of sesame seed (reviewed by Pathak et al. 2014)

Constituent	Composition %
Moisture	6–7
Proteins	20–28
Oil	48–55
Sugars	14–16
Fiber content	6–8
Minerals	5–7

11.7 Conclusions

Even though sesame is an important oilseed crop from nutritional, industrial, and pharmaceutical viewpoints, the benefit of advancement in molecular biology and biotechnology is yet to be harnessed in sesame crop improvement. Development of high-density linkage map, consensus linkage maps, marker-trait association studies, and deployment of genome editing is required to be focused as high-priority area of research at the global level, and concerted efforts are needed worldwide to develop plant idiotypes suitable for mechanical harvesting, high-density planting, plant types with engineered quality seeds oil, value addition with bioactive compounds, and sesame genotype resistance or tolerance to abiotic as well as biotic stresses.

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