Sveriges lantbruksuniversitet
Swedish University of Agricultural Sciences

Department of Plant Breeding

Status of sesame breeding

Mohammed Elsafy

Introductory paper at the Faculty of Landscape Architecture, Horticulture and Crop Production Sciences, 2023:2

Swedish University of Agricultural Sciences

Alnarp, Sweden

February, 2023

Status of sesame breeding

Mohammed Elsafy

Place of publication: Alnarp, Sweden

Year of publication: 2023

Title of series: Introductory paper at the Faculty of Landscape Architecture, Horticulture and Crop Production Science

Number of part of series: 2023:2

Cover pictures: Sesame field.

Cover pictures Source: https://www.unicorningredients.com/news/sesame-pumpkin-survey-2019/

Online publication: https://pub.epsilon.slu.se

Bibliographic reference: Elsafy, M. 2023. Status of sesame breeding. Introductory paper at the Faculty of Landscape Architecture, Horticulture and Crop Production Science, 2023:2

Keywords: *Sesame breeding, Sesame genome project, capsule shattering*

Swedish University of Agricultural Sciences

Faculty of Landscape Architecture, Horticulture and Crop Production Science

Department of Plant Breeding

Plant Product Quality Division

Abstract

Sesame (Sesamum indicum L.), an ancient domesticated oilseed crop, has been utilized for thousands of years, and it contains a high level of oil, protein, and other nutrients, making it an important food and feed crop. According to FAO statistics, the top-producing countries are Sudan, Myanmar, Tanzania, India, Nigeria, and China. The significant breeding orientations in sesame have been tightly linked to human needs: increased seed yield, improved morphological architecture of the plants, tolerance to biotic and abiotic stresses, indehiscent capsules, and improved oil quality. Furthermore, novel advanced breeding tools such as phenomic and genomic markers assisted selection have mapped the sesame genome, revealing a small diploid genome of 350 Mb size. The novel technologies pave the road for a fast-track breeding process for sesame, adapting it to climate change, biofortification, and food security challenges. This study reviews the features and achievements obtained related to opportunities for sesame breeding programs.

Preface

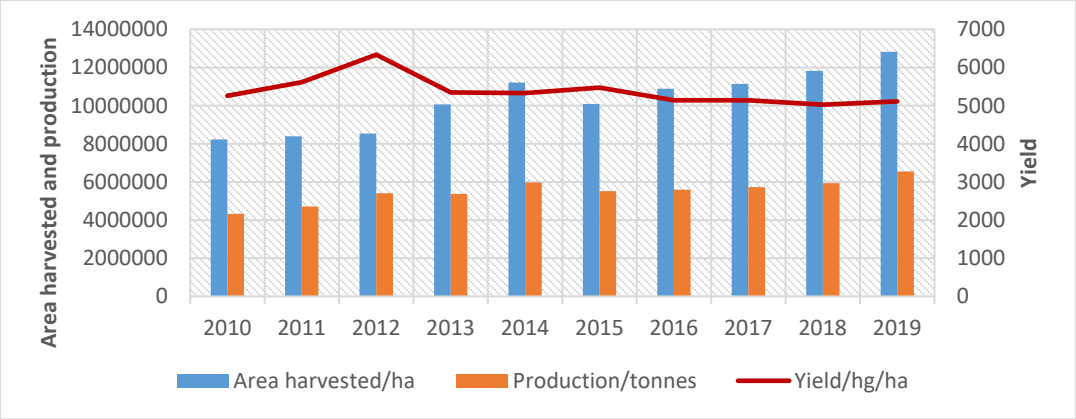
Sesame is an important crop in tropical and semi-topical climate zones, and it is a cash crop for small-scale farmers that help finance the agricultural inputs for their food security crops. However, many producing countries have neglected sesame for research and improvement, resulting in low productivity and production. Using genetic diversity and advanced molecular breeding tools will pave the road toward releasing high-yielding new varieties resilient to climate change and adapted to harsh conditions. If breeding is successful, sesame production will improve the livelihood of vulnerable small-scale farmers.

Contents

Introduction

Sesame (*Sesamum indicum* L.) is a domesticated oilseed crop that has been grown and utilized by humans since ancient times. Sesame originates from Africa, although India is claimed as its first place of domestication. Thereafter, sesame was introduced to Mesopotamia by 2000 BC and then to the Mediterranean region, where it became an essential crop in the early and late bronze age [1]. Sesame belongs to the genus *Sesamum* and the family *Pedaliaceae.* Totally, up to 38 species have been affiliated with the genus, using morphological and cytogenetical characterization. Presence in different geographical zones has also been used to classify the species of sesame [2]. The crop is widely distributed in areas between 40° N to 40° S, although the most intensive cultivation is carried out north of the equator [3]. The branched root system in sesame contributes significantly to its soil improving properties and is the reason for its ability to act as a super drought-tolerant crop. However, sesame is a low yielding crop, which is mainly due to its common problem with capsule shattering [4]. Thus, in 2019, the 12.8 million hectares used for sesame production only resulted in a total of 6.5 million tonnes of sesame produced (Figure 1), which has to be considered a low yield in such a vast area [5]. The top producing countries of sesame are Sudan, Myanmar, India, and China.

Figure 1. Total world production, harvested area and yield of sesame from 2010-2019 according to FAO STAT



Sesame is considered an important crop, with a substantial content of high-quality oil, protein, and other nutrients, thereby contributing substantially to food and feed in areas where it is produced [6]. The sesame seeds contain approximately 35–60% oil, 19–30% protein, 13.5% carbohydrate, 5% ash, and an energy value of 6,355 kcal kg^{-1} has been reported [7-9]. Additionally, sesame contains essential nutritional elements such as copper, magnesium,

manganese, and iron, and it is considered a rich source of vitamins E and B. Sesame oil is more stable against oxidation than most other vegetable oils due to the presence of specific lignans such as sesamin and sesaminol, which contribute to antioxidative activity [10]. In general, sesame has an important economic role as a cash crop in the countries of production [11].

The growth habit of sesame is indeterminate, although it is considered an annual crop related to seed production [12]. Genetically, sesame is a diploid (2n = 2x = 26), with a large genetic variation and a high number of wild relatives. Plant breeding of sesame has focused on several traits, not least on specific needs to solve issues related to biotic and abiotic stresses [13]. Wild relatives of sesame have been used as a potential source to target traits linked to genes on specific species and chromosomes. Thus, tolerance to waterlogging was found encoded on chromosome 26 in *S. malabaricum*, while tolerance to drought was encoded on chromosome 32 in *S. occidentale*. Furthermore, resistance to Fusarium wilt was found encoded on chromosome number 64 in *S. radiatum* [7]. However, there is still a lack of information on one of the most critical traits for grain yield in sesame; an indehiscent capsule has the potential to reduce the harvest loss of the mature seeds and increases the opportunities for adaptation to mechanized harvest [14].

Novel advanced breeding tools such as phenomic and genomic markers assisted selection have resulted in the mapping of the sesame genome, which revealed a small diploid genome of 350 Mb size [15]. Opportunities prevail to develop a fast-track breeding process for sesame, adapting it to climatic change, biofortification, and food security challenges. This review features the achievement obtained and opportunities for sesame breeding programs.

Domestication

Plant domestication is the first step towards breeding and developing high-yielding and high-quality crops securing food for the human population. Early domestication and breeding were based on selecting plants with desirable traits matching humans' needs. Sesame is one of the earliest domesticated crops [16-18], and the crop is still essential, particularly for farmers in Africa and Asia [19]. Several studies have focused on the first place of origin and domestication of sesame, and its wild relatives, taking into account the historical, cultural, genetic, and phytochemical facts. These studies have depicted that the Pedaliaceae family, to which sesame belongs, is found mainly in the tropical part of Africa, although two exclusive sections of the

genus *Sesamum* are shown to belong to India. Thus, Africa as the only place of origin has been debated, and the Indian subcontinent has been suggested as the first place of sesame domestication [20]. Sesame is generally regarded as a multi-use crop, as the seeds and the green leaves are used. Sesame is a rich source of nutrients, especially in times of famine [21]. Sesame leaves contain a rich amount of calcium, iron, protein, carotene, and ascorbic acid. The leaves are also shown to keep a high nutritional value after being dried and powdered for long-term storage [22].

Breeding aspects and genetic resources alert

The primary breeding objectives for sesame, which are tightly linked to human needs, are increasing the seed yield, improving the morphological architecture of the plants, tolerance to biotic and abiotic stresses, indehiscent capsules, and improving oil quality [23]. The recent development of novel cultivars has resulted in genotypes with increased adaptability and resistance to biotic and abiotic stresses [24]. However, the lack of intensive research on sesame continues to be a significant obstacle to increasing crop production [6, 20, 25]. Erosion of the genetic resources of sesame has been ongoing for a long time, resulting in a loss of critical genetic diversity, not least of sesame originating from Africa, and in particular of genotypes from Sudan [26]. For decades, the civil war in Sudan continuously destroyed the Nuba life, including their fields and crops, resulting in losses of masses of unique genetic sesame materials and cultivars [27].

The war elsewhere in Africa has also resulted in the erosion of crop diversity [28]. Thus, several studies suggested immediate efforts to improve germplasm resources, including filling the gab collection, core collections establishment, evaluation, and germplasm documentation [20, 29]. Therefore, some significant efforts were taken at the beginning of the 2000th to establish and strengthen gene banks for the conservation and maintenance of plant genetic resources in the East Africa region through the Eastern African Plant Genetic Resources Network (EAPGRN) [30]. This effort was carried out in collaboration with the Nordic Gene Bank (NordGen) and was funded by the Swedish government agency for development cooperation (Sida). Hence, various genetic resources of agricultural and horticultural crops, including sesame, are currently under maintenance [31].

Improving yield and seed production

The productivity of sesame is generally low, and the main constraints for increased productivity are a narrow genetic base, a low degree of genetic improvement, and cultivation primarily in marginal lands [32]. Thus, the total world production of sesame is relatively low compared to the area cultivated and harvested (Fig.1).

High yield is an essential trait for sesame breeders and farmers; therefore, specific traits associated with high yield are essential, e.g., the number of capsules/plant, seeds/capsules, and the thousand seed weight [33]. However, the most important trait for the yield component is if the capsule is indehiscent (pods do not open to release seeds when ripe; non-shattering) or dehiscent (shattering) [34]. Indehiscent or semi-indehiscent characteristics of the sesame crop have been shown to reduce the harvest loss of mature seeds in sesame [35]. Several traits have been linked to the shattering trait of sesame, e.g., capsule constriction, membrane completeness, capsule opening, capsule split, placenta attachment, capsule membrane attachment, tip roll back, capsule position on stem, and seed blocks [35]. The first 100% shattering resistance capsule was found in 1946 in a natural mutant with curly leaves (c*l*1) [36]. The c*l*1 attribute was found controlled by a single gene pair and contributed to the indehiscent character of the capsule after physical maturity when the plant is dry; the character is present independent of the environment [37]. However, the c*l*1 capsule is hard, and breaking it needs mechanical treatment, making c*l*1 genotype unsuitable for production as the extra force required for breaking the capsule might damage the seed, resulting in fatty acid leakage and eventual rancidity [37]. Continuous breeding efforts in the USA resulted in a non-dehiscent cultivar released in 1997, with a capsule that was not as difficult to open as the capsule of the dehiscent genotypes but simultaneously, this genotype did not shatter. The capsule of this genotype only opened at the tip and could be left in the field for more than 50 days after maturity, and it could also be dried down to 6% seed moisture without shattering [38].

The second most important trait in sesame correlated with yield is the thousand seed weight, which ranged between 0.79g to 4.47g in a worldwide collection [39]. Therefore, in China, the sesame is graded according to seed size based on thousand seed weights, where >3.5 g is considered a large seed [40]. Other traits such as seed length, seed width, capsule length, and size of the seed area have been found to strongly correlate with the thousand seed weight, and

accordingly, these characteristics play an essential role in increasing the yield and productivity of sesame.

Resistance to biotic and abiotic stresses

Similarly, as for other crops, resistance to biotic and abiotic stresses are important to obtain a high yield, and therefore, sesame breeders are continuously evaluating and integrating valuable genes for these characteristics in their breeding material and cultivars [32]. Several abiotic stresses affecting sesame productivity have been identified, e.g., salinity, drought, waterlogging, and chilling. Sesame is sensitive to calcium/sodium chloride ions in soil solutes and chilling (0–15°C) conditions [37]. In addition, sesame has been found to be sensitive to drought, especially in the vegetative stage [23]. Furthermore, several biotic stresses have been shown to contribute to a reduction of the yield in sesame, e.g., Phytophthora blight, Cercospora spot, Alternaria leaf spot, phyllody, leaf curl virus [41].

Resistance to critical diseases and pests

One of the major diseases attacking sesame is phyllody of phytoplasma, which affects the vegetative development of sesame plants, thereby causing significant yield losses [42]. Thus, developing Phyllody tolerance in sesame is one of the main objectives of breeding programs. Moreover, insect pests such as leaf roller and capsule borer are significant problems to sesame production, causing significant yield losses, especially in the area with low rainfall. However, in the rainy season, sucking insects such as leafhoppers, thrips, whitefly, and bugs arrive and act as carriers of various pathogens, causing phyllody and leaf curl [43]. Several resistance genes to biotic and abiotic stresses are available in wild forms of sesame and can potentially be introduced into cultivated sesame through backcrossing or genetic engineering [24]. Pests and disease-resistance genes encode nucleotide-binding and leucine-rich repeat (NLR). Therefore, sesame breeding programs have the potential to benefit from advanced genomics tools, utilizing bioinformatics in combination with genotyping by sequencings (GBS) to search for NLR [44]. Annotator software can then be used to identify the physical position of NLR genes on chromosomes [45].

Improving nutritional and oil quality

Sesame seed is a rich source of several nutritional elements, such as protein, vitamins, minerals, and antioxidants [46]. Also, the presence of lignans such as sesamin and sesaminol improves the oxidative stability and antioxidative activity of sesame oil [10], as described above. On the

negative side, sesame contributes immunoglobulin E (IgE)-mediated food allergy. One of the major allergens in the sesame seed is oleosins. Furthermore, high levels of phytic and oxalic acid encumber the use of sesame protein as food [47, 48]. Advanced technologies have allowed profiling of the change in mRNA coding of sesame oleosin, caleosin, and steroleosin during seed maturation, and a high accumulation was found in the maturing seeds when oil bodies were assembled, followed by a reduction of the content in the mature seed [49]. Thus, the use of genetic engineering in breeding programs to suppress gene expression may result in a decrease in levels of the compounds causing allergies and hard digestibility.

Breeding methods in sesame

Sesame is a crop with a narrow genetic diversity base, resulting in limitations in developing new cultivars. Different traditional breeding methods have been applied to sesame, including space mutation, heterosis application, hybridization, system breeding, and interspecific hybridization [50]

Space mutation

Space mutation is a technique utilized to mutagenize the DNA of seed or seedlings by high-energy ion radiation, space magnetic field, ultra vacuum, microgravity, and other physical stresses in space, which would change inherited traits in the progeny [51].

Chemical Mutation

Several chemical mutagens have been applied to sesame, including EMS, sodium azide, diethyl sulfate, and colchicines [52, 53]. Thus, EMS with concentrations ranging from 0.2 to 2.0 mM has been utilized to evaluate the mutation efficiency on sesame seed germination rate (%). In these studies, a 1.0 mM EMS concentration was found to decrease seed germination by 50% [54]. Optimal EMS concentrations (0.5%/24 h, 1.0%/24 h, 1.0%/12 h, and 1.5%/6 h) were determined for sesame to reach the highest mutation efficiency (0.80% or higher; [53].

Heterosis breeding in sesame

Heterosis is an increase in vigor, fast development, and high fertility of the biomass as compared to parent lines while hybrid breeding is carried out [55]. The first heterosis effect from hybrid breeding was reported in 1945 for sesame, when the yield increase due to hybrid vigor reached 252% in China [50]. The first sesame hybrid variety was released in 1993, which increased the yield by 29.52% [29].

Hybridization and interspecific hybridization in sesame

Since the 1950s, plant breeders have been collecting wild and landrace forms of sesame to utilize these collections for improvements of different traits related to the production [50]. Hybridization breeding using pedigree selection is one effective method that has been utilized for sesame variety improvement. Considerable variations have been found for traits of interest, which can be transferred into new varieties through controlled crosses. Thus, two or more parental lines are used in crosses for a combination of traits [56]. Interspecific hybridization in sesame has been used in resistance breeding, and this methodology has been using wild sesame as a source of genes to deliver resistance to pests, diseases, and severe environments. However, the interspecific hybridization method has some limitations for sesame breeding, as various *Sesamum* species show incompatibility [57].

Molecular marker in sesame

History of Molecular marker in sesame

So far, sesame is considered as a neglected crop when it comes to breeding. Before the discovery of molecular markers, which was followed by advanced next-generation sequencing (NGS), morphological phenotyping and isozymes of isocitrate dehydrogenase (IDH) was used to evaluate the genetic diversity of sesame germplasm [58]. The early molecular genetic research on sesame resulted in universal markers such as Random Amplified Polymorphic DNA (RAPD), Sequence Characterized Amplified Region (SCAR), Inter-Simple Sequence Repeats (ISSR), Amplified Fragment Length Polymorphism (AFLP), Sequence-Related Amplified Polymorphisms (SRAP), and Simple Sequence Repeat (SSR) markers which were gradually integrated for assessing the genetic diversity in sesame accessions [59-63]. However, an instability of polymorphism was claimed for these universal markers. Therefore, effort and research were used to exhibit species-specific markers, including Single Nucleotide Polymorphism (SNP) and Insertion/Deletion (InDel) markers, which were then introduced to the sesame breeding program in the early twenty-first century.

Importance markers in sesame

Microsatellite makers SSR

SSR markers are robust markers that can discriminate the genetic diversity between varieties of the same species. Moreover, SSRs mostly have short tandem (about 1-6 bp length) repeats, codominant in the genome, with high reproducibility, abundance, and variability [64]. In 2005,

10 SSR markers were developed to investigate the genetic diversity in 16 sesame accessions for the first time, and these were shown to be highly polymorphic [65]. In 2008, more efforts were exerted after studying 3,328 sesame EST sequences in NCBI, which led to the development of 50 EST-SSR, and 27 out of the total were found to be highly polymorphic (61.4%) in 34 sesame cultivars [66]. Thereafter, the work of developing SSR markers in sesame has continued [67-70]. Consequently, a genetic linkage map for sesame has been created, utilizing EST-SSRs, AFLP, and RSAMPLs (random selective amplification of microsatellite polymorphic loci) markers [71, 72].

Single Nucleotide Polymorphism (SNP) and InDel markers

SNP is a marker that can differentiate differences at a single location in a DNA sequence of individuals. [73], while InDel polymorphic molecular marker is a PCR-amplified marker based on specific primers designed from both sides of the sequence of insertion/deletion [74]. In sesame, the accomplishment of the reference genome enhanced the aggregation of genomics data allowing the utilization of these markers. Thus, transcriptome analysis based on genome data, utilizing SNP and InDel markers, were used to construct a genetic map in sesame, to analyze the traits of interest. Alignments between 'Rongxian black sesame' (RXBS) and 'Zhongzhi 11 variety detected 10,950 SNPs in 4660 contigs and 590 InDels in 524 contigs, which were then used to design 40 SNP primers [75]. Furthermore, Next Generation Sequencing (NGS) has been used to improve the high-density SNP genetic maps in sesame [76]. Thus, the intensive work on SNP has led to the construction of high and ultra-density SNP genetic maps for sesame [77, 78].

Genome-Wide Association Studies in sesame (GWAS)

GWAS is a technique to test the genetic variation across the genome to detect the genotype-phenotype associations related to individuals [79]. It has been a successful method used widely to provide information on complex traits, e.g., diseases, in humans, animals, and plants. However, despite the success in identifying important genes correlating with specific traits and the biological pathways behind the traits, gaps in information are still present, especially for plants [80].

Quantitative trait locus (QTL) mapping in sesame

QTL mapping is a methodology used to discover the genome-wide relationship between phenotypic traits determined by several minor genes. These traits are also often affected by the interaction between the genotype and the environment [81]. The expression effect for genes of a

QTL-mapped trait may be the result of various interactions of genes, e.g., additive effects or dominance of one gene interacting with other genes [82]. An additive gene effect refers to that two alleles contribute equally to the phenotype of a plant. In sesame, genetic mapping has been used to explore the inheritance of essential agronomic traits, e.g., yield and seed quality, and up to now, 138 QTLs related to 44 agronomic traits have been determined, with a high phenotypic variance explanation (R2) of $\geq 5\%$ [39]. Moreover, QTL of the Male Sterile (MS) trait was determined utilizing 13 SSR markers linked to the ms gene, which resulted in flanking sides of SBM_{298} and GB_{50} with a genetic distance of 0.15 - 0.70 cm, respectively [83]. In addition, several QTLs have been found to be linked to charcoal rot resistance (10 QTLS) and waterlogging (6 QTLS) using Chinese lines [70, 84].

Yield-related traits in sesame

To increase the seed yield of sesame, GWAS was conducted on 705 accessions for 39 seed yield-related traits, including capsule number, capsule size, and seed size. The study revealed 646 loci associated with the 39 yield traits and 547 QTL, including six multi-environment QTL and 76 pleiotropic QTL associated with 2-5 traits (Zhou et al., 2018). Consequently, 48 potential genes with significant functional loci were identified, e.g., *SiLPT3 and SiACS8* were assigned as candidate genes controlling capsule length and capsule number.

Seed coat color in sesame

For a long time, the genetic background of the seed coat color of sesame remained unclear. However, recently, the factors affecting the genetic architecture of seed coat color in sesame were explained by an investigation of 366 sesame germplasm in 12 different environments [85]. In total, 197 single nucleotide polymorphisms (SNP) were detected related to seed coat color in sesame, of which 30 were captured in six different environments, identifying 92 genes linked with sesame seed coat color.

Plant height

The plant height is one of the essential morphological characters in sesame that is directly linked to the yield. For this character, 41 QTL associated with sesame plant height have been located in the 350 and 928-kb spaces on Chromosome 8 and Chromosome 3, respectively, explaining 3–24 % of the phenotypic variation [50]. In addition, it has been found that (*qPH-8.2* and *qPH-3.3*) are the primary loci contributing to 23 and 18 % of the plant height [86]. Recently, a range of

studies (summarized in Table 1) has applied functional QTL to differentiate different traits in sesame.

Table 1. Different QTLs related to morphology and abiotic stress in sesame

Trait	References
Capsule zone length	[87]
Waterlogging tolerance	[88]
Node Number	[86]
Tip Length without capsule	[86]
Height first capsule	[86]
Grain number per capsule	[87]
Internode Length	[86]

Cytogenetic studies on sesame

The first initiative on sesame chromosome research was carried out in 1929, reporting the number of chromosomes of cultivated sesame (*S. indicum*) as 2n = 26 [89]. So far, 36 species of *Sesamum* have been evaluated for their cytogenetic characteristics, e.g., chromosome number, satellite chromosome number, chromosome structure, and karyotype. Based on the somatic chromosome number, *Sesamum* species are currently divided into three categories (Table 2). However, for several of the *Sesamum* species, the chromosome characters are still unknown to a large extent [90].

Table 2. Number of chromosomes in Sesamum species

***Sesamum* species**	**Number of chromosomes**
S. indicum	2*n* = 26
S. alatum	2*n* = 26
S. angolense	2*n* = 32
S. latifolium	2*n* = 32
S. radiatum	2*n* = 64
S. schinizianum	2*n* = 64

The recent discovery of fluorescence in situ hybridization (FISH) and bacterial artificial chromosome (BAC), with the assistance of genome assembly, have led to the differentiation of the 13 chromosome pairs in *S. indicum* and the construct of a high-density cytogenetic map in

sesame [91]. However, it has been reported that the chromosome morphology is highly affected by the specimen preparation [91, 92], which directly influences the visibility of the satellite region due to the residue of pre-preparation. Therefore, a new method of chromosome specimen preparation has been introduced [91, 93], which includes a conventional pressing technique with a modification including hypotonic cell wall degradation and specimen press methods. The application of this new preparation methodology resulted in a clear chromosome separation of high quality, which was suitable for morphological characterization. Accordingly, three pairs of satellite chromosomes were detected in the Chinese cultivar Yuzhi 11. The satellite chromosomes were shown to contain repeat sequences of 45S (18S-5.8S-25S) of ribosomal DNA (rDNA). In addition, six wild species of sesame were characterized using chromosome categories 26, 23, and 64 in the presence of Yuzhi 11 as cultivated sesame. The result showed that the somatic chromosome length varies from 30.597 µm in *S. indicum* to 85.507 µm in *S. radiatum*. Moreover, a cytological map for an accurate physical position of the 13 chromosomes has been developed using 210 BACs of stable hybridization signal pair with the aid of sesame genome. This work resulted in 7 – 40 BAC markers in each chromosome located in a range between 10.7 to 354.6 Kb (Zhang et al., 2021).

Sesame genome

Sesame genome project

The sesame genome project was ongoing between 2010 to 2015, and the aim was to achieve and construct a fine genome map by sequencing the sesame genome, performing genome information analysis, and constructing a functional genome database [50]. Accordingly, the project initially applied Illumina sequencing as a next-generation sequencing (NGS) platform. However, with the development of the assembly techniques, the project was enriched with more information using real-time (SMRT) sequencing, Bionano for optimal mapping, and, HiC sequencing [94-96]. This achievement allowed mapping the scale of the chromosome for the sesame genome. In addition, the knowledge of how to construct the chromosome scale for the wild *Sesamum* species was expanded, which allowed for conducting comparative structure for evolution analysis and applying maker-assisting breeding to the sesame accessions [50].

Updating on sesame genome assemblies

The first draft of the sesame genome reported it to be 293.7 Mb in length using the Solexa platform for the Chinese cultivar Yuzhi 11, with an average gene length of 1.2 kb in total of

23,713 gene models. However, recently- also three wild forms of sesame (Table 1) have been sequenced and reassembled, allowing genomics and comparative genomics analysis [50].

Chloroplast genome mapping of sesame

The chloroplast genome of *S. indicum* has been sequenced utilizing the Yuzhi 11 cultivar and Illumina [50]. The results revealed 153,338 bp and a total of 114 unique genes, thereby matching the numbers obtained for *Platanus occidentalis, Nicotiana tabacum,* and *Vitis vinifera*. In total, 77 functional chloroplast genes with the deletion of *ycf1* were found. Furthermore, a deletion of 1,179 bp length was detected in the *ycf2* gene (5,721 bp). Additionally, the sesame chloroplast genome exhibited five unique sequence repeats (R10, R12, R13, R14, and R17) besides contraction/expansion in some inverted repeats in the chloroplast genome [97].

Functional markers in sesame

Oil and protein content

In sesame seed, oil and protein content are the most important quality traits, and it has been found that the oil and protein content range between 27.89%–58.73% and 16.72%–27.79%, respectively. The oil and protein content are known to be controlled by major genes [98]. In total, 19 oil-content-associated and 24 protein-relevant SSR markers have been described. Of the 19 markers associated with oil content, 17 are located near lipid pathway genes, and 2 are close to the fatty acid elongation gene. [99].

Dominant male sterility

Strong hybrid vigor is frequently observed in sesame, explained by male sterility (GMS). The development of advanced RNA-seq-based transcriptome profiling led to the investigation of near-isogenic breeding lines with a dominant GMS (DGMS) to differentiate genes associated with male sterility. A total of 1502 significantly expressed genes were detected, of which 751 were upregulated genes, and the other 751 were downregulated in sterile flower buds. Implying the predicted role in identifying the development of tapetal fate assigned to homologous genes resulted in the encoded transcription factors bHLH089, MYB99, and AMS [100].

Branching habit

The methods of cloning genes based on mapping, assembling genome sequences, and specific length amplified fragment sequencing (SLAF-seq) were used to create a high-density genetic linkage map in sesame [101]. Accordingly, 13 linkage groups containing 9378 SLAF markers

were constructed, and the basal branching habit (*SiBH*) and flowers per leaf axil (*SiFA*) genes were mapped to linkage groups 5 and 11 [102].

Functional genes in sesame

In the last ten years, the investigation of functional genes in sesame has increased dramatically, as summarized in Table 3.

Response to drought and salinity stresses

A recent study approved that the genes regulating plant development, growth, and response to different stresses are associated with the transcription family of the homeodomain-leucine zipper (HD-Zip) gene group, which is related to drought and salinity stresses in sesame [103]. However, it was found that 75% HD-Zip genes have different responses to drought and salinity, although the HD-ZipI and HD-ZipII genes were found to play a significant role in stress response in sesame [104].

Oil Content

The two lignan compounds in sesame that benefit human health are sesamin and sesamolin, which are strongly associated with the gene of oil content [105]. However, the strongest signal of association missense SNP (from C to A) was detected in the *SiNST1,* which modifies T to K at the 82 amino acid position in the oil metabolic pathway that includes two genes encoding lipases (*CXE17*, SIN_1003248, and GDSL-like lipase, SIN_1013005) and two encoding lipid transfer proteins (SIN_1019167 and SIN_1009923) [106].

Resistance of Macrophomina Phaseoli

Genes involved in pathogenesis have been identified through a transcriptomic study comparing resistant and susceptible genotypes to Charcoal rot caused by *Macrophomina phaseolina*. The analysis cataloged the genes involved in the synthesis of pathogenesis-related (PR) proteins as MYB, WRKY, leucine zipper protein, bHLH, bZIP, and NAC transcription factors, ABC transporters (B, C, and G subfamily), glutathione metabolism, secondary metabolites, fatty acid biosynthesis and phytohormones like auxin, abscisic acid, ethylene, and gibberellic acid [107].

Table 3. Collection of functional genes associated with traits in sesame

Trait	Predicted function of gene	Reference
Plant Height	IAA-leucine resistant 1 (ILR1)	[106]
Full Flowering Date	GIGANTEA (GI)	[106]
Seed Color	polyphenol oxidase (PPO)	[106]
TAG biosynthesis	PDAT1	[108]
Life Cycle Period	early flowering 9 (ELF9)	[106]
Susceptibility of Phyllody Disease	leucine-rich repeat (LRR) protein kinase family protein	[106]

References

1. Lim, T., *Sesamum indicum*, in *Edible Medicinal And Non-Medicinal Plants*. 2012, Springer. p. 187-219.
2. Kobayashi, T.J.C.e.i.p.g., breeding, evolution. Part B., *Cytogenetics of sesame (Sesamum).* 1991: p. 581-592.
3. Yol, E. and B.J.C.s. Uzun, *Geographical patterns of sesame accessions grown under Mediterranean environmental conditions, and establishment of a core collection.* 2012. **52**(5): p. 2206-2214.
4. Uzun*, B., et al., *Heterosis for agronomic traits in sesame hybrids of cultivars× closed capsule mutants.* 2004. **54**(2): p. 108-112.
5. Stat, F., *Food and Agriculture Organisation of the UN (FAO) statistics database: production, trade, supply*. 2019.
6. Najeeb, U., et al., *Sesame*, in *Technological Innovations in Major World Oil Crops, Volume 1*. 2012, Springer. p. 131-145.
7. Nimmakayala, P., et al., *Sesamum*, in *Wild Crop Relatives: Genomic and Breeding Resources*. 2011, Springer. p. 261-273.
8. Elleuch, M., et al., *Quality characteristics of sesame seeds and by-products.* 2007. **103**(2): p. 641-650.
9. Tunde-Akintunde, T. and B.J.B.E. Akintunde, *Some physical properties of sesame seed.* 2004. **88**(1): p. 127-129.
10. Wu, W.-H.J.F.c., *The contents of lignans in commercial sesame oils of Taiwan and their changes during heating.* 2007. **104**(1): p. 341-344.
11. Myint, D., et al., *Sustainable sesame (Sesamum indicum L.) production through improved technology: An overview of production, challenges, and opportunities in Myanmar.* Sustainability, 2020. **12**(9): p. 3515.
12. Dutta, D., et al., *Validation of determinate (dt) gene-based DNA marker in inter-specific hybrid sesame and in-silico analysis of the predicted dt protein structures.* Physiology and Molecular Biology of Plants, 2022. **28**(1): p. 139-152.
13. Teklu, D.H., H. Shimelis, and S. Abady, *Genetic Improvement in Sesame (Sesamum indicum L.): Progress and Outlook: A Review.* Agronomy, 2022. **12**(9): p. 2144.
14. Zhang, H., H. Miao, and M. Ju, *Potential for adaptation to climate change through genomic breeding in sesame*, in *Genomic designing of climate-smart oilseed crops*. 2019, Springer. p. 371-440.

15. Wei, X., et al., *Identification of sesame genomic variations from genome comparison of landrace and variety.* 2016. **7**: p. 1169.
16. Joshi, A.B., E. Narayanan, and R.J.S. Vasudeva, *Sesamum.* 1961.
17. Mabberley, D.J., *The plant-book: a portable dictionary of the vascular plants*. 1997: Cambridge university press.
18. Weiss, E.J.O.s.c.L., London., *Oilseed crops.,(Longman: London).* 1983: p. -.
19. Orsi, L., et al., *The role of collective action in leveraging farmers' performances: Lessons from sesame seed farmers' collaboration in eastern Chad.* Journal of Rural Studies, 2017. **51**: p. 93-104.
20. Bedigian, D., *Evolution of sesame revisited: domestication, diversity and prospects.* Genetic resources and crop evolution, 2003. **50**: p. 779-787.
21. Latham, M.J.H.N.i.T.A.A.T.f.H.W.w.s.r.t.C.H.P.i.E.A., *Human Nutrition in Tropical Africa. A Textbook for Health Workers with special reference to Community Health Problems in East Africa.* 1965.
22. Bennett, M., *Sesame seed.* Handbook for Farmers and Investors, 1998.
23. Islam, F., et al., *Sesame*, in *Breeding oilseed crops for sustainable production*. 2016, Elsevier. p. 135-147.
24. Lakhanpaul, S., et al., *Sesame: overcoming the abiotic stresses in the queen of oilseed crops.* Improving crop resistance to abiotic stress, 2012: p. 1251-1283.
25. Ashri, A., *Sesame.* 1989.
26. Robinson, J., *Desertification and disarray: the threats to plant genetic resources of southern Darfur, western Sudan.* Plant Genetic Resources, 2005. **3**(1): p. 3-11.
27. Bedigian, D. and J.R.J.E.B. Harlan, *Nuba agriculture and ethnobotany, with particular reference to sesame and sorghum.* 1983. **37**(4): p. 384-395.
28. Richards, P. and G. Ruivenkamp, *Seeds and survival: Crop genetic resources in war and reconstruction in Africa*. 1997: Bioversity International.
29. Ashri, A.J.P.b.r., *Sesame breeding.* 1998. **16**: p. 179-228.
30. Wambugu, P. and Z. Muthamia, *The state of plant genetic resources for food and agriculture in Kenya.* Submitted to FAO Commission on Plant Genetic Resources for Food and Agriculture, 2009.
31. Demissie, A.J.H., *Regional strategy for the ex situ conservation of plant genetic resources: Eastern Africa. Eastern Africa Plant Genetic Resources Network (EAPGRN), Entebbe, Uganda, July 2006. Abebe Demissie & Bjornstad, A. 1996. Phenotypic diversity of Ethiopian barleys in relation to geographical regions, altitudinal range and agroecological zones: as an aid to germplasm collection and conservation strategy.* 2006. **124**: p. 17-29.
32. Tripathy, S.K., J. Kar, and D. Sahu, *Advances in sesame (Sesamum indicum L.) breeding*, in *Advances in plant breeding strategies: industrial and food crops*. 2019, Springer. p. 577-635.
33. Kalaiyarasi, R., et al., *Correlation and Path Analysis for Yield and Yield Traits in Sesame (Sesamum indicum L.) Genotypes.* International Journal of Current Microbiology and Applied Sciences, 2019. **8**(11): p. 1251-1257.
34. Arriel, N.H.C., et al., *Genetic divergence in sesame based on morphological and agronomic traits.* Crop Breeding and Applied Biotechnology, 2007: p. 253-261.
35. Langham, D., *Shatter resistance in sesame.* 2001.
36. Miao, H., D. Langham, and H. Zhang, *Botanical Descriptions of Sesame*, in *The Sesame Genome*. 2021, Springer. p. 19-57.
37. Zhang, H., et al., *Identification of a SiCL1 gene controlling leaf curling and capsule indehiscence in sesame via cross-population association mapping and genomic variants screening.* 2018. **18**(1): p. 1-12.

38. Couch, A., et al., *Non-dehiscent sesame (Sesamum indicum L.): its unique production potential and expansion into the southeastern USA.* 2017. **31**(2): p. 101-172.
39. Duan, Y., et al., *The Sesame Genome for Gene Discovery in Sesame*, in *The Sesame Genome*. 2021, Springer. p. 283-290.
40. Miao, H., H. Zhang, and C. Kole, *The Sesame Genome*. 2021: Springer.
41. Pathak, N., et al., *Sesame crop: an underexploited oilseed holds tremendous potential for enhanced food value.* Agricultural Sciences, 2014. **2014**.
42. Mohanty, T.A., et al., *Study of genetic variability, heritability and genetic advance in sesame (Sesamum indicum L.) genotypes.* International Journal of Current Microbiology and Applied Sciences, 2020. **9**(2): p. 347-356.
43. Panday, A., R.B. Dwarka, and S.J.I.P.M. Jain, *Major Insect Pests of Sesame and Their Management.* 2021: p. 188.
44. Barragan, A.C. and D. Weigel, *Plant NLR diversity: the known unknowns of pan-NLRomes.* The Plant Cell, 2021. **33**(4): p. 814-831.
45. Steuernagel, B., et al., *The NLR-Annotator Tool Enables Annotation of the Intracellular Immune Receptor Repertoire1 [OPEN].* Plant Physiology, 2020. **183**(2): p. 468-482.
46. Pathak, K., et al., *Sesame (Sesamum indicum L.), an underexploited oil seed crop: Current status, features and importance-A review.* Agricultural Reviews, 2017. **38**(3).
47. Wolff, N., et al., *Allergy to sesame in humans is associated primarily with IgE antibody to a 14 kDa 2S albumin precursor.* 2003. **41**(8): p. 1165-1174.
48. Johnson, L., T. Suleiman, and E.J.J.o.t.A.O.C.S. Lusas, *Sesame protein: A review and prospectus.* 1979. **56**(3Part3): p. 463-468.
49. Frandsen, G.I., J. Mundy, and J.T.J.P.p. Tzen, *Oil bodies and their associated proteins, oleosin and caleosin.* 2001. **112**(3): p. 301-307.
50. Zhang, H., et al., *Traditional Breeding in Sesame*, in *The Sesame Genome*. 2021, Springer. p. 145-158.
51. Liu, L., et al., *Research progress in mutational effects of aerospace on crop and ground simulation on aerospace environment factors.* 2004. **18**(4): p. 247-251.
52. Shi, S.J.C.J.O.C.S., *Application of mutagenesis technique in the improvement of sesame varieties.* 1991. **2**: p. 93-96.
53. Wang, H., et al., *Optimization of EMS mutagenesis condition and screening of mutants in sesame.* 2017. **46**(1): p. 36-41.
54. Anbarasan, K., et al., *Studies on the mutagenic effect of EMS on seed germination and seedling characters of Sesame (Sesamum indicum L.) Var. T MV3.* 2013. **3**(1): p. 68-70.
55. Stuber, C.W. and J. Janick, *Heterosis in plant breeding.* Plant breeding reviews, 2010. **12**: p. 227-251.
56. Zhao, Y., et al., *Characterization and genetic mapping of a novel recessive genic male sterile gene in sesame (Sesamum indicum L.).* 2013. **32**(4): p. 901-908.
57. Yang, M., et al., *Production and identification of F1 interspecific hybrid between Sesamum indicum and wild relative S. indicatum.* 2017. **50**(10): p. 1763-1771.
58. Isshiki, S. and T.J.E. Umezaki, *Genetic variations of isozymes in cultivated sesame (Sesamum indicum L.).* 1997. **93**(3): p. 375-377.
59. Bhat, K.V., P.P. Babrekar, and S.J.E. Lakhanpaul, *Study of genetic diversity in Indian and exotic sesame (Sesamum indicum L.) germplasm using random amplified polymorphic DNA (RAPD) markers.* 1999. **110**(1): p. 21-34.
60. Ercan, A.G., et al., *Analysis of genetic diversity in Turkish sesame (Sesamum indicum L.) populations using RAPD markers⋆.* 2004. **51**(6): p. 599-607.

61. Kim, D., et al., *Genetic relationships of sesame germplasm collection as revealed by inter-simple sequence repeats.* 2002. **121**(3): p. 259-262.
62. Zhang, Y.-x., et al., *Analysis of genetic diversity among indigenous landraces from sesame (Sesamum indicum L.) core collection in China as revealed by SRAP and SSR markers.* 2010. **32**(3): p. 207-215.
63. Laurentin, H.E. and P.J.B.g. Karlovsky, *Genetic relationship and diversity in a sesame (Sesamum indicum L.) germplasm collection using amplified fragment length polymorphism (AFLP).* 2006. **7**(1): p. 1-10.
64. Powell, W., et al., *The comparison of RFLP, RAPD, AFLP and SSR (microsatellite) markers for germplasm analysis.* 1996. **2**(3): p. 225-238.
65. Dixit, A., et al., *Development of polymorphic microsatellite markers in sesame (Sesamum indicum L.).* 2005. **5**(4): p. 736-738.
66. Li-Bin, W., et al., *Developing EST-derived microsatellites in sesame (Sesamum indicum L.).* 2008. **34**(12): p. 2077-2084.
67. Spandana, B., et al., *Development and characterization of microsatellite markers (SSR) in Sesamum (Sesamum indicum L.) species.* 2012. **168**(6): p. 1594-1607.
68. Badri, J., et al., *Development of microsatellite markers in sesame (Sesamum indicum L.).* 2014. **38**(5): p. 603-614.
69. Uncu, A.Ö., et al., *Genomic simple sequence repeat markers reveal patterns of genetic relatedness and diversity in sesame.* 2015.
70. Wang, L., et al., *Development of an SSR-based genetic map in sesame and identification of quantitative trait loci associated with charcoal rot resistance.* 2017. **7**(1): p. 1-8.
71. Wei, L.-B., et al., *A genetic linkage map construction for sesame (Sesamum indicum L.).* 2009. **31**(2): p. 199-208.
72. Zhang, Y., et al., *Construction of a high-density genetic map for sesame based on large scale marker development by specific length amplified fragment (SLAF) sequencing.* 2013. **13**(1): p. 1-12.
73. Syvänen, A.-C., *Toward genome-wide SNP genotyping.* Nature genetics, 2005. **37**(6): p. S5-S10.
74. Riahi, L., et al., *Single nucleotide polymorphism and haplotype diversity of the gene NAC4 in grapevine.* 2013. **43**: p. 718-724.
75. Wei, L., et al., *Development of SNP and InDel markers via de novo transcriptome assembly in Sesamum indicum L.* 2014. **34**(4): p. 2205-2217.
76. Zhao, X., et al., *Loci and candidate gene identification for resistance to Sclerotinia sclerotiorum in soybean (Glycine max L. Merr.) via association and linkage maps.* 2015. **82**(2): p. 245-255.
77. Du, H., et al., *A high-density genetic map constructed using specific length amplified fragment (SLAF) sequencing and QTL mapping of seed-related traits in sesame (Sesamum indicum L.).* 2019. **19**(1): p. 1-20.
78. Liang, J., et al., *Construction of a High Density Genetic Map and QTL Mapping of PEG-Induced Drought Tolerance at Seedling Stage in Sesame Using Whole Genome Re-Sequencing.* 2020.
79. Korte, A. and A. Farlow, *The advantages and limitations of trait analysis with GWAS: a review.* Plant methods, 2013. **9**(1): p. 1-9.
80. Tam, V., et al., *Benefits and limitations of genome-wide association studies.* Nature Reviews Genetics, 2019. **20**(8): p. 467-484.
81. Williams, C.G., *QTL mapping in outbred pedigrees.* Molecular dissection of complex traits, 2019: p. 81-94.
82. Caballero, A., *Quantitative genetics*. 2020: Cambridge University Press.
83. Liu, H., et al., *Inheritance and molecular mapping of a novel dominant genic male-sterile gene in Sesamum indicum L.* 2015. **35**(1): p. 1-14.

84. Zhang, Y., et al., *Mapping of sesame waterlogging tolerance QTL and identification of excellent waterlogging tolerant germplasm.* 2014. **47**: p. 422-430.
85. Cui, C., et al., *Genome-wide association study of seed coat color in sesame (Sesamum indicum L.).* Plos one, 2021. **16**(5): p. e0251526.
86. Wang, L., et al., *Updated sesame genome assembly and fine mapping of plant height and seed coat color QTLs using a new high-density genetic map.* BMC genomics, 2016. **17**(1): p. 1-13.
87. Wu, K., et al., *High-density genetic map construction and QTLs analysis of grain yield-related traits in Sesame (Sesamum indicum L.) based on RAD-Seq techonology.* BMC plant biology, 2014. **14**(1): p. 1-14.
88. Zhang, Y., et al., *Mapping of sesame waterlogging tolerance QTL and identification of excellent waterlogging tolerant germplasm.* Sci. Agric. Sin, 2014. **47**: p. 422-430.
89. Morinaga, T., et al., *Chromosome numbers of cultivated plants II.* Shokubutsugaku Zasshi, 1929. **43**(515): p. 589-594.
90. Bedigian, D., *Systematics and evolution in Sesamum L.(Pedaliaceae), part 1: Evidence regarding the origin of sesame and its closest relatives.* Webbia, 2015. **70**(1): p. 1-42.
91. Zhao, R., et al., *Identification of sesame (Sesamum indicum L.) chromosomes using the BAC-FISH system.* Plant Biology, 2018. **20**(1): p. 85-92.
92. Tran, T.D., et al., *Chromosome identification for the carnivorous plant Genlisea margaretae.* Chromosoma, 2017. **126**(3): p. 389-397.
93. Liu, Y., et al., *Development and applications of a set of chromosome-specific DNA markers in sesame.* Research on Crops, 2014. **15**(2): p. 481-486.
94. Rhoads, A. and K.F. Au, *PacBio sequencing and its applications.* Genomics, proteomics & bioinformatics, 2015. **13**(5): p. 278-289.
95. Shelton, J.M., et al., *Tools and pipelines for BioNano data: molecule assembly pipeline and FASTA super scaffolding tool.* BMC genomics, 2015. **16**(1): p. 1-16.
96. Servant, N., et al., *HiC-Pro: an optimized and flexible pipeline for Hi-C data processing.* Genome biology, 2015. **16**(1): p. 1-11.
97. Zhang, H., et al., *Insights from the complete chloroplast genome into the evolution of Sesamum indicum L.* PloS one, 2013. **8**(11): p. e80508.
98. Wei, X., et al., *Genetic discovery for oil production and quality in sesame.* Nature communications, 2015. **6**(1): p. 8609.
99. Li, C., et al., *Association mapping of seed oil and protein content in Sesamum indicum L. using SSR markers.* PLoS One, 2014. **9**(8): p. e105757.
100. Liu, H., et al., *Comparative transcriptome profiling of the fertile and sterile flower buds of a dominant genic male sterile line in sesame (Sesamum indicum L.).* BMC plant biology, 2016. **16**(1): p. 1-13.
101. Hu, X., et al., *High-density genetic map construction and identification of QTLs controlling oleic and linoleic acid in peanut using SLAF-seq and SSRs.* Scientific reports, 2018. **8**(1): p. 1-10.
102. Mei, H., et al., *High-density genetic map construction and gene mapping of basal branching habit and flowers per leaf axil in sesame.* Frontiers in plant science, 2017. **8**: p. 636.
103. You, J., et al., *Transcriptomic and metabolomic profiling of drought-tolerant and susceptible sesame genotypes in response to drought stress.* BMC plant biology, 2019. **19**(1): p. 1-16.
104. Wei, M., et al., *Genome-wide characterization and expression analysis of the HD-Zip gene family in response to drought and salinity stresses in sesame.* BMC genomics, 2019. **20**(1): p. 1-13.
105. Andargie, M., et al., *Lignans of sesame (Sesamum indicum L.): a comprehensive review.* Molecules, 2021. **26**(4): p. 883.
106. Wei, X., et al., *Genetic discovery for oil production and quality in sesame.* Nature communications, 2015. **6**(1): p. 1-10.

107. Radadiya, N., et al., *Transcriptome analysis of sesame-Macrophomina phaseolina interactions revealing the distinct genetic components for early defense responses.* Physiology and Molecular Biology of Plants, 2021. **27**(8): p. 1675-1693.
108. Wang, L., et al., *Genome sequencing of the high oil crop sesame provides insight into oil biosynthesis.* Genome biology, 2014. **15**(2): p. 1-13.