

REVIEW



A review on yield improvement of the important oilseed sesame (*Sesamum indicum* L.) using biotechnology

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Received: 28 October 2024 / Revised: 6 May 2025 / Accepted: 28 August 2025 / Published online: 5 September 2025
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Abstract

The worldwide steep rise of vegetable oil consumption creates an urgency to improve oilseed crop yield. Sesame (*Sesamum indicum* L.) is called the “Queen of Oilseeds” due to the voluminous presence of several vitamins, minerals, antioxidants, and beneficial fatty acids; the oil is considered safe for consumption. It is widely cultivated in the tropical and subtropical regions throughout the world. However, compared to other oilseed crops, the meagre yield of sesame largely hampers its successful commercialisation. The major problems associated with this crop are early pod shattering and susceptibility to various abiotic and biotic stresses. Biotechnology-mediated crop improvement is a good alternative to slow, labour-intensive, and cumbersome conventional breeding methods. Worldwide efforts can be observed to improve targeted traits of this crop using modern biotechnological tools. However, the lack of a well-accepted regeneration and transformation protocol is the major burden in implementing biotechnological yield improvement methods in sesame, especially transgenesis-mediated gene manipulation techniques. In this review, we discussed the growth and cultivation scenario of sesame. We also depicted the important problems associated with low crop yield. Next, we represented the current progress of regeneration and associated transgenesis-mediated gene manipulation research in sesame. We also briefed on the importance of sesame whole-genome sequencing. Finally, we presented a concise discussion on the available potential genes, regulatory elements, DNA markers, and QTLs that can be used in gene manipulative and marker-assisted selection-based yield improvement programmes. Information presented in this review article could potentially be utilised for yield improvement research in sesame.

Keywords Biotechnology · Gene manipulation · Plant stress tolerance · QTL · Sesame · Yield improvement

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Abbreviations

2,4-D	2,4-Dichlorophenoxyacetic acid
ABA	Absciscic acid
AFLP	Amplified fragment length polymorphism
BAP	6-Benzylaminopurine
CAPS	Cleaved amplified polymorphic sequences
CIM	Composite interval mapping
EST-SSR	Expressed sequence tag-simple sequence repeat
GWAS	Genome-wide association study
IAA	Indole-3-acetic acid
InDel	Insertion–deletion marker
ISSR	Inter-simple sequence repeat
KASP	Kompetitive allele-specific PCR
MAB	Marker-assisted breeding
MCIM	Mixed composite interval mapping
miRNA	MicroRNA
NAA	Naphthaleneacetic acid
QTL	Quantitative trait locus
RAPD	Random amplified polymorphic DNA
SAAT	Sonication-assisted <i>Agrobacterium</i> -mediated transformation
SCAR	Sequence-characterised amplified region
SGWG	Sesame genome working group
SLAF	Specific length amplified fragment sequencing
SNP	Single-nucleotide polymorphism
SRAP	Sequence-related amplified polymorphism
SSR	Simple sequence repeat
TF	Transcription factors

Introduction

The current vegetable oil consumption in the World and India is 224 million tonnes (MT) and 25 MT, respectively. By 2030, the consumption is expected to reach 247 MT and 34 MT in the World and India, respectively (Chauhan et al. 2021; OECD/FAO 2021; USDA 2024b). Moreover, a 60% uprise in agricultural yield by 2050 is necessary to complement the simultaneous rapid rise of the human population and several farming constraints (United Nations 2009; Da Silva 2012). The urgent situation critically demands a production increase in oilseed crops in the upcoming years. Sesame (*Sesamum indicum* L., Pedaliaceae family) is the “Queen of Oilseeds” due to its excellent oil quality (Table S1). The abundance of vitamins, minerals, antioxidants, and beneficial fatty acids in sesame oil makes it safe for consumption (Wu 2007; Debnath et al. 2018; Kim et al. 2020; Andargie et al. 2021; USDA 2024a). However, the production of sesame is very inadequate compared to other oilseed crops (Table S2) (Popa et al. 2012; Tunde-Akintunde et al. 2012; Jnanadevan 2017; FAOSTAT 2024; DOING 2024; NCDEX 2024). The lower yield restricts its use as

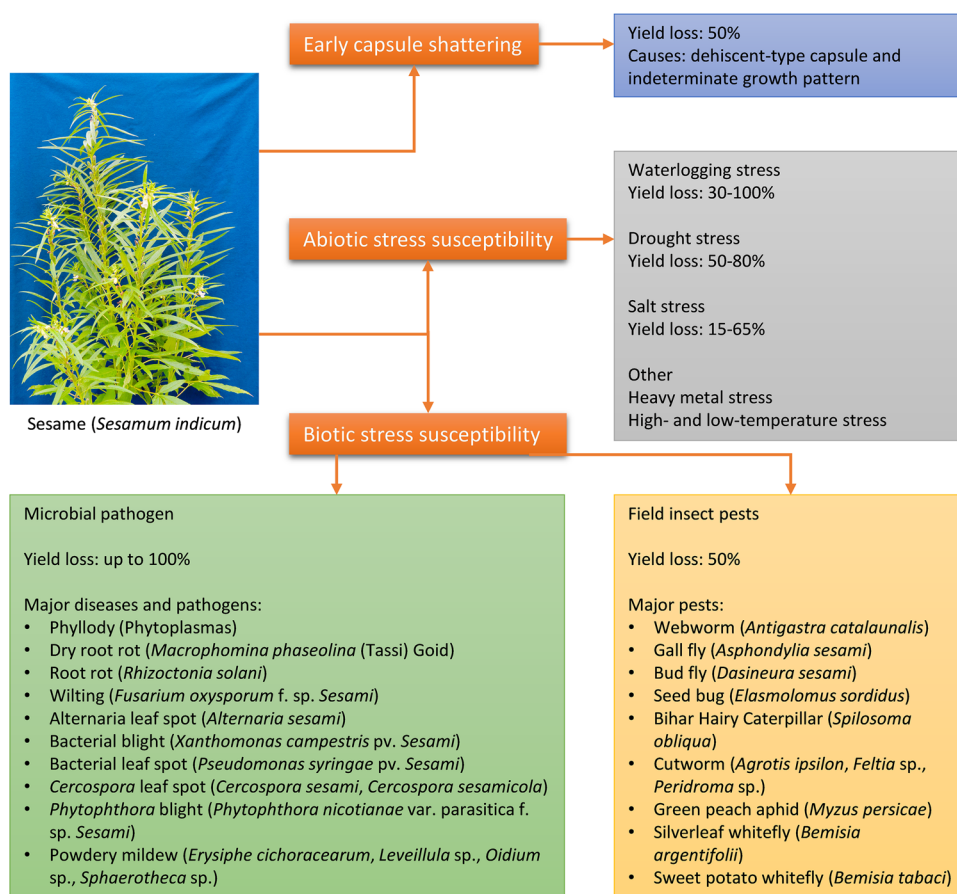
an everyday farmer’s crop and hinders the successful commercialisation of this crop.

Conventional breeding has been used to improve plant traits since the era of crop domestication (Patel et al. 2023). However, limited breeding efforts have been applied for sesame improvement (Qureshi et al. 2022). Moreover, the conventional breeding method has several drawbacks—(1) traits governed by multiple or recessive alleles are difficult to select using this technique; (2) since this technique does not focus on the genome, the environmental influence on a trait expression often introduces errors in the outcome; (3) sexually incompatible plants cannot be used in breeding programmes; (4) desired traits are not always available in cultivated lines of sesame; and (5) the need for multiple field trials before releasing a variety makes the process prolonged, labour-intensive, and cumbersome. As an alternative, biotechnological methods can overcome the setbacks of conventional breeding technology and are potentially useful for expressing a desired trait (Debnath et al. 2014; Lamichhane and Thapa 2022). Plant biotechnologies that help in trait development, including yield improvement, are plant tissue culture, transgenesis, and molecular-genomic breeding (Pathirana and Carimi 2024). We will start the review with a briefing on sesame production and yield. Then, we will discuss three major issues of sesame that contribute to its meagre yield—early pod shattering, abiotic stress, and biotic stress (Fig. 1) (Ashri 1987; Rao and Vaidyanath 2003; Seo et al. 2007; Tiwari et al. 2011; Samadder and Arumugam 2023). After that, we will focus on the biotechnological aspects used to date for improving sesame yield (Fig. 2).

Sesame is primarily cultivated in the tropics

Sesame is a tropical and Subtropical crop, cultivated primarily in the developing countries of Asia and Africa and a few regions of North and South America, mostly located from 40° N to 40° S latitude (IPGRI and NBPGR 2004). Primary producers are Sudan, India, the United Republic of Tanzania, and other countries. Worldwide sesame production was 6,741,479.41 tonnes in 12,836,776 hectares in 2022. India was the second largest producer (788,740 tonnes) of sesame after Sudan (12,31,701.39 tonnes) in 2022 (Fig. 3). In 2022, sesame seeds were cultivated in 16,27,040 hectares of the field in India (FAOSTAT 2024). West Bengal, Madhya Pradesh, Gujarat, Rajasthan, Uttar Pradesh, Tamil Nadu, Karnataka, Andhra Pradesh, and Telangana are the primary producing states of India. Sesame production was highest in West Bengal (230,486 tonnes) in the country in 2019–20. In West Bengal, in the year 2019–20, Paschim Medinipur district produced the maximum quantity of sesame (13,734 tonnes), whereas North and South 24 Parganas ranked ninth (3,520 tonnes) and tenth (1,271 tonnes), respectively, in this

Fig. 1 Major problems associated with the low yield of sesame. Sesame yield is primarily affected by early capsule-shattering problem, abiotic stress Susceptibility, and biotic stress Susceptibility. The dehiscent-type capsule phenotype and indeterminate growth pattern cause around 50% yield loss of sesame. Waterlogging, drought, salinity, heavy metals, and high- and low-temperature are the Major abiotic stress factors of sesame affecting up to 100% yield loss. Several microbial pathogens and field insect pests cause biotic stress and reduce up to 100% sesame yield



regard. Besides these districts, sesame is also cultivated in Nadia, Hooghly, Bankura, Bardhaman (Purba and Paschim), Murshidabad, Jhargram, Birbhum, Coochbehar, Jalpaiguri, Howrah, etc. in West Bengal (APS 2024).

Three major issues reduce sesame yield

Early capsule-shattering problem

Capsule shattering/dehiscence in wild plants is an essential reproductive process but is undesirable for farmers because of yield loss (Dong and Wang 2015). The growth pattern of sesame is indeterminate, and 99% of global cultivars are capsule dehiscent type (Teklu et al. 2022). Due to such growth characteristics, sesame grows and flowers continuously until resources are available. Lower capsules dry and shatter as flowering continues (Qureshi et al. 2022). Such pre-harvest capsule shattering reduces around 50% yield and is the greatest cause of yield loss in sesame (Kadkol et al. 1989; Gebremichael 2017; Phumichai et al. 2017). So far, traditional and molecular breeding programmes have achieved limited success in producing sesame varieties with

indehiscent capsules and determinant growth (Kotcha 2012; Qureshi et al. 2022).

Abiotic stress susceptibility

Sesame is often cultivated in marginal to submarginal lands facing some environmental extremities such as high heat and low water supply. Therefore, environmental factors cause significant production losses due to abiotic stresses in this crop. Approaches for assessing and developing abiotic stress-resistant sesame cultivars have achieved limited success (Islam et al. 2016; Singh et al. 2022).

Sesame is primarily cultivated in rainfed regions; heavy rainfall, poor drainage systems, and improper irrigation cause waterlogging in Such cultivation systems. Waterlogging is the most damaging stress of sesame, leading to yield loss of 30–100% and 15–80% in the World and India, respectively (Zhang et al. 2022a, b; Kumaraswamy et al. 2023). The reproductive stage of sesame is most sensitive to waterlogging (Saha et al. 2010). Waterlogging primarily causes hypoxia in sesame, leading to yield reduction via various stress-responsive physiological, biochemical, and metabolic changes (Shah et al. 2024). The growth and yield arrest can

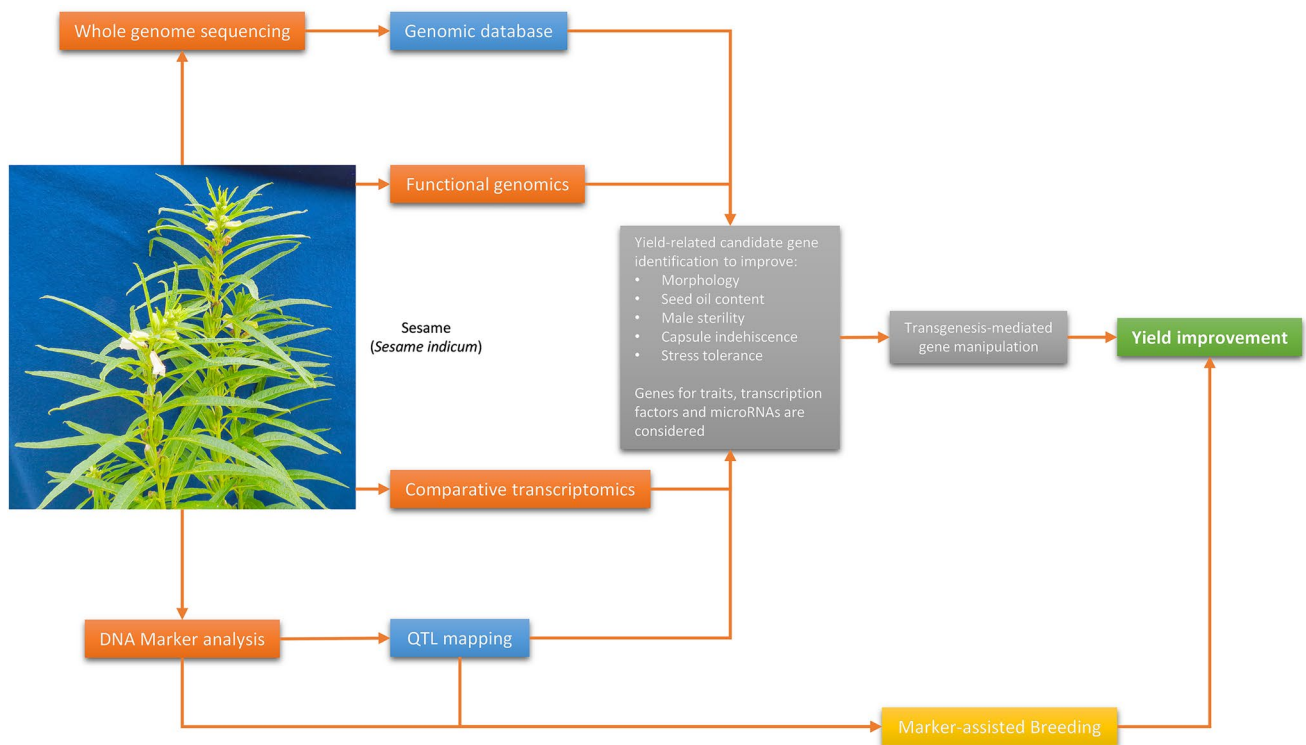


Fig. 2 Provision of biotechnology for sesame yield improvement. Various approaches of whole-genome sequencing in sesame created several genomic databases consisting of a vast array of genome information that can be utilised to identify potential yield-improving genes. Several functional genomic and comparative transcriptomic studies have revealed useful genes for sesame yield improvement. DNA-marker-derived QTL analysis also identified candidate genes for yield. Such genes regulate important yield-related traits such as

morphology, seed oil content, male sterility, capsule indehiscence, and abiotic and biotic stress tolerances. Candidate genes controlling regulatory elements such as transcription factors and microRNAs have also been identified. All these genes can be deployed in transgenesis-based gene manipulation systems to achieve improved yield. In a separate strategy, DNA markers and QTLs can be utilised in marker-assisted breeding to improve the yield of sesame. *QTL* quantitative trait locus

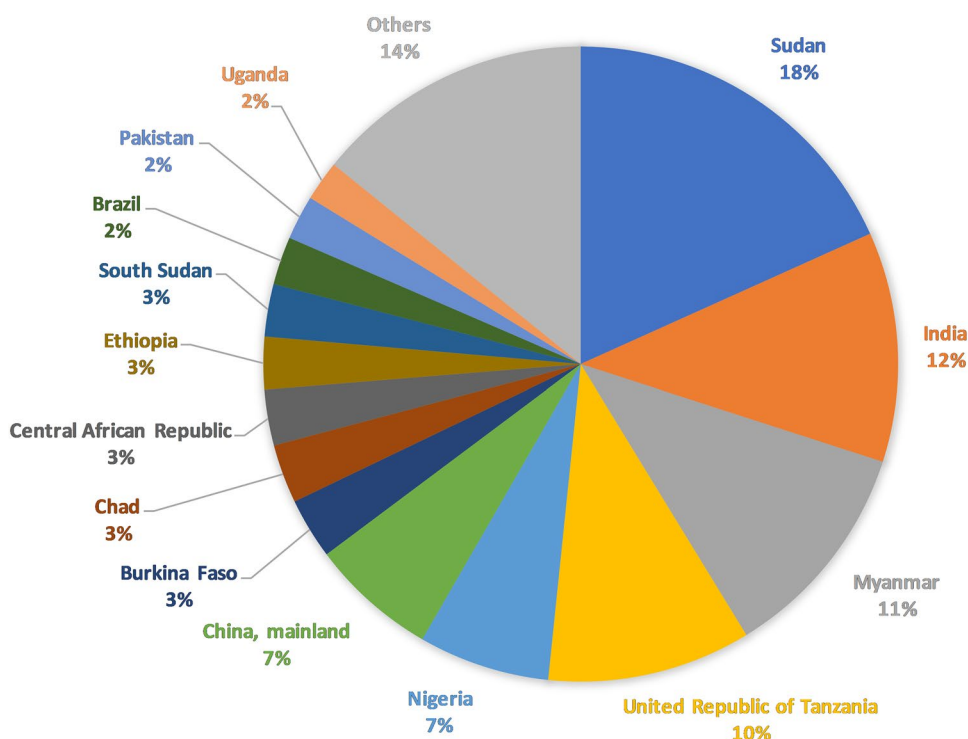
happen within 2–3 days of waterlogging in sesame (Islam et al. 2016).

The extensively deep taproot system of sesame provides drought tolerance to some degree. At equivalent osmotic potential, the inhibitory effect of salt stress is lesser on seedling germination and growth than drought stress (El Harfi et al. 2016; Bahrami et al. 2012). In addition, sesame resistance to drought stress is genotype-dependent. The yield of a high-yielding genotype may decline under water-deficit conditions (Sun et al. 2010; Ghotbzade Kermani et al. 2019). However, drought affects sesame's vegetative stage and causes 50–80% yield loss (Singh et al. 2022; Zhang et al. 2022a, b). Drought stress also decreases chlorophyll content, unsaturated fatty acids, and seed yield up to 25.4% (Mahdavi Khorami et al. 2020). Moreover, drought stress causes a significant reduction in endogenous salicylic acid or kinetin in sesame. Drought significantly increased levels of total soluble protein, polypeptide bands and proline in sesame (Hussein et al. 2015). Similarly, drought stress also causes micronutrient deficiency in sesame (Movahhedi Dehnavi et al. 2017).

Sesame is a moderately salt-tolerant species. Primarily, NaCl , CaCl_2 , Na_2CO_3 , Na_2SO_4 , NaNO_3 , and NaHCO_3 cause salinity stress to this plant (Singh et al. 2022; Zhang et al. 2022a, b). The sensitivity of sesame to different salts is not the same. While at an osmotic pressure of 0.10 MPa, CaCl_2 reduced the yield of sesame shoots and pods by up to 65%, Na_2SO_4 by 33%, NaCl by 26%, and NaNO_3 by only 15%. At an osmotic pressure of 0.20 MPa, $\text{Ca}(\text{NO}_3)_2$ was the most damaging (Nassery et al. 1979). NaCl stress response in sesame is genotype-dependent. The salinity-derived antioxidant response is better in the genotype Cumhuriyet than in Orhangazi (Koca et al. 2007; Bahrami and Razmjoo 2012).

Cadmium (Cd) and lead (Pb) are the major critically contaminating heavy metals in the ecosystem (Mehmood et al. 2018). In sesame, Cd reduces root and shoot growth and photosynthetic pigment content. In addition, it increases the contents of hydrogen peroxide, malondialdehyde, soluble sugar, diacylglycerol, and sterol esters (Abd_Allah et al. 2017). Moreover, seed germination and seedling growth are significantly affected by Cd, Co, Cu, Ni, and Zn (Pires et al. 2016; Abirami and Vikrant 2023).

Fig. 3 Worldwide contribution to sesame production of different countries in 2022. Sudan's contribution to sesame production was the highest (18.27%). India (11.7%), Myanmar (11.29%), and the United Republic of Tanzania (10.38%) were the second, third, and fourth highest sesame producers, respectively



The cardinal temperature range of sesame is 15.7–44.6 °C, with 27.3 °C the optimum for growth (Baath et al. 2021). Cultivating sesame below 20 °C considerably affects its growth, stress defence mechanism, and oil quality and promotes senescence (Oplinger et al. 1990; Islam et al. 2016). Sesame seeds do not germinate and grow below 10 °C. Moreover, it needs 90–120 frost-free days during the reproductive stage for optimal yield (Oplinger et al. 1990). High-temperature stress could reduce 40–50% of the sesame yield in India. Rani and Kiranbabu (2017) reported genotype-dependent yield loss among 442 sesame genotypes when cultivated above 40 °C. On a molecular basis, genotype-dependent differential antioxidant regulation contributes to the variability of heat-stress tolerance in different sesame cultivars (Su et al. 2022b). A prolonged vegetative phase during high-temperature stress could be a reason for such yield reduction (Firmansyah et al. 2012).

Biotic stress susceptibility

Bacteria, fungi, and viruses cause major diseases in sesame (Teklu et al. 2022). Among them, phyllody caused by phloem-limiting phytoplasmas is the most devastating disease, causing 34–100% sesame yield loss. The phytoplasma vector *Orosius albicinctus* (jassid) spreads the disease during the flowering stage of sesame. Phytoplasmas spread all over the infected plant through phloem, causing the primary symptom of phylloid structures where floral parts are converted into leafy structures and flowers lose fertility (Gupta

et al. 2022; Yadav et al. 2022). The disease is most prevalent in tropical countries of Asia and Africa, including India (Win et al. 2010). Dry root rot is another common and detrimental disease that affects sesame, caused by the Deuteromycetes soil fungus *Macrophomina phaseolina* (Tassi) Goid (Islam et al. 2016). The disease mostly occurs in tropical and Subtropical countries having semi-arid climates, causing 50–100% yield loss (Yan et al. 2021). Root rot caused by *Rhizoctonia solani* reduces massive yield in Egypt (Teklu et al. 2022). Furthermore, wilting caused by *Fusarium oxysporum* f. sp. *sesami* is one of the most economically damaging soil-borne diseases, causing a global 15–30% yield loss of sesame (Li et al. 2012; Wei et al. 2016a). Besides these, *Alternaria* leaf spot (*Alternaria sesami*), bacterial blight (*Xanthomonas campestris* pv. *Sesami*), bacterial leaf spot (*Pseudomonas syringae* pv. *Sesami*), *Cercospora* leaf spot (*Cercospora sesami* and *Cercospora sesamicola*), *Phytophthora* blight (*Phytophthora nicotianae* var. *parasitica* f. sp. *Sesami*), powdery mildew (*Erysiphe cichoracearum*, *Leveillula* sp., *Oidium* sp., and *Sphaerotheca* sp.), and stem anthracnose (*Colletotrichum* sp.) cause major yield loss in sesame (DOD 2021; Teklu et al. 2022).

Besides microbial pathogens, field insect pests reduce 50% of sesame yield worldwide (Weiss 2000). More than 299 insect species of sesame pest are known to date (Langham 2019). Among them, major insect pests of sesame are webworm (*Antigastra catalaunalis*), gall fly (*Asphondylia sesami*), bud fly (*Dasineura sesami*), and seed bug (*Elasmolomus sordidus*) (Gebregergis et al. 2016). Sesame webworm

larvae feed on the topmost leaves and primary meristem of the plant, resulting in leaf webbing, growth retardation, and plant mortality. The larvae also bore the capsules, penetrate them, and eat the developing seed, causing 50% yield loss (Gebregergis et al. 2016; Simoglou et al. 2017; Yadav et al. 2022). Gall fly and bud fly also bore the capsule to penetrate, create gall-like structures in the penetrated capsules, and feed on the seeds. Seed bugs cause 50% yield loss by attacking capsules during plant drying after harvest and in storage conditions (Ahirwar and Gupta 2010; Teklu et al. 2022). Other important sesame pests that affect yield are Bihar hairy caterpillar (*Spilosoma obliqua*), cutworm (*Agrotis ipsilon*, *Feltia* sp., and *Peridroma* sp.), green peach aphid (*Myzus persicae*), leafhoppers (*Orosius orientalis*, *O. albicinctus*, *O. argentatus*, *O. cellulosus*, *Empoasca lybica*, *Circulifer haematiceps*, *Hishimonus phycitis*, and *Deltoccephalus* sp.), moths (*Acherontia styx*, *Agrius* sp., *Coenotes* sp., *Erinnyis* sp., *Hippotion* sp., *Manduca* sp., *Psilogramma* sp.), silverleaf whitefly (*Bemisia argentifolii*), stink bug (*Nezara viridula*, *Acrosternum* sp., *Euschistus* sp., *Halyomorpha* sp., *Loxa* sp., *Piezodorus* sp., and *Thyantha* sp.), sweet potato whitefly (*Bemisia tabaci*), and warehouse pests (*Carpophilus obsoletus*, *Corcyra cephalonica*, *Ephestia cautella*, *Tribolium castaneum*, *Tribolium confusum*, *Trogoderma granarium*, *Cryptolestes pusillus*, and *Oryzaephilus mercator*) (Langham 2019; DOD 2021).

Well-established regeneration and transformation systems are prerequisites for sesame gene manipulation

Plant gene manipulation involving transgenesis requires the following steps—(1) suitable explant selection, (2) transformation of the explant with the gene of interest, (3) selection of the transformants, (4) regeneration of the transformants into full-grown plants, (5) confirmation of the transgene integration in the transgenic lines, and (6) analysis of the transgene. The first four steps in this process are mediated by plant tissue culture. Therefore, a well-responsive regeneration and transformation protocol facilitates the gene manipulation workflow (Wędzony et al. 2014).

Regeneration of sesame

The idea of plant tissue culture was first proposed by Haberlandt (1902). Since then, this technique has been used in many sectors of plant science. Presently, the establishment of a highly efficient regeneration and a suitable subsequent transformation protocol is a prerequisite task for crop improvement. Possibly, Lee et al. (1985) published the first report of tissue culture in sesame. The authors tested various combinations of plant growth regulators (NAA, IAA,

2,4-D, BAP, and Kinetin) to establish micropropagation using shoot tip explants. They induced whole plant induction using 2.69 μ M NAA, while 9.29 μ M kinetin induced the highest shoot differentiation. Since then, efforts have been made over the past 4 decades to regenerate sesame using direct organogenesis via adventitious shoot regeneration, indirect adventitious organogenesis, somatic embryogenesis, thin cell layer culture, and protoplast culture. Some authors also reported micropropagation.

Direct organogenesis via adventitious shoot regeneration is one of the quickest plant regeneration methods, where regenerated shoots appear directly on the cultured explants, without involving any callus induction phase. Due to the ease and speed of the process, this method is often preferred to regenerate transformants in transgenesis studies (Wędzony et al. 2014). Adventitious shoot regeneration in sesame has been achieved from hypocotyl and cotyledon (Taskin and Turgut 1997; Younghee 2001; Were et al. 2006; Seo et al. 2007; Yadav et al. 2010; Al-Shafeay et al. 2011; Rao and Honnale 2011; Loksha et al. 2012; Pratik et al. 2016; Zimik and Arumugam 2017; Anandan et al. 2018a; Debnath et al. 2018; Weldemichael et al. 2020; Rajput et al. 2022) by direct organogenesis (Table 1, S3). The first available report in this regard was published by Taskin and Turgut (1997). They achieved 4.5% adventitious shoots from de-embryonated cotyledon explants obtained from 7-day-old seedlings by culturing them in MS medium (Murashige and Skoog 1962) supplemented with various concentrations of BAP and NAA. After about a decade, Were et al. (2006) reported a breakthrough regeneration rate of 63% from de-embryonated cotyledons having 4.4 shoots per regenerating explant. They used basal N₆ medium supplemented with 20 μ M TDZ + 2.5 μ M IAA. In the next year, Seo et al. (2007) pointed out the importance of explant pre-culture in ABA and high carbohydrate sources, along with cytokinin and auxin for sesame regeneration. Among their tested hormone combinations, MS medium supplemented with 22.2 μ M BAP and 5.7 μ M IAA was best for direct adventitious shoot formation. Further supplementation of 3.8 μ M ABA and 29.4 μ M AgNO₃ enhanced the adventitious shoot formation frequency. They also found that a 2-week pre-culture of cotyledon explants on regeneration medium supplemented with 9% sucrose enhanced the frequency of adventitious shoot induction up to 50%. Yadav et al. (2010) reported enhanced adventitious shoot regeneration (88%) from 2-day-old de-embryonated cotyledons using MS medium supplemented with 25 μ M of BAP. After 8 years of this report, Debnath et al. (2018) achieved the maximum adventitious shoot regeneration frequency of 94.81% with 5.4 shoots per explant by experimenting with the effect of explant orientation in culture medium. They found that 4-day-old cotyledon explants provide the maximum regeneration frequency when cultured in a vertical orientation in MS medium

Table 1 A summary of the reports of regeneration in sesame

Method	Explant	Regeneration frequency (%)	References
Direct organogenesis via adventitious shoot regeneration	Cotyledon [#]	94.81 (5.40)*	Debnath et al. 2018
	Cotyledon [#]	83.30 (5.90)*	Rajput et al. 2022
	Cotyledon [#]	88.00 (9.30)*	Yadav et al. 2010
	Cotyledon [#]	74.00 (4.50)*	Anandan et al. 2018a
	Cotyledon [#]	73.30 (7.07)*	Lokesha et al. 2012
Indirect adventitious organogenesis	Hypocotyl	100.00	Wadeyer and Lokesha 2011
	Hypocotyl	90.80	Asad et al. 2019
	Leaf	90.80	Raja and Jayabalan 2010
	Hypocotyl	85.00	Singh and Shagufta 2011
	Hypocotyl	83.30	Wadeyar et al. 2013
Somatic embryogenesis	Zygotic embryo	50.00–100.00	Ram et al. 1990
	Hypocotyl	62.30	Mary and Jayabalan 1997
	Hypocotyl	51.00	Xu et al. 1997
Micropropagation	Apical shoot tip	100.00 (3.70)*	Abdellatef et al. 2010
	Apical shoot tip	100.00 (2.70)*	Ahmed et al. 2008
	Plumule tip	94.44 (15.96)*	Gayatri and Basu 2020
	Cotyledonary node	90.66 (23.36)*	Elayaraja et al. 2019
	Apical shoot tip	80.00 (18.00)*	Baskaran and Jayabalan 2006
Thin cell layer culture	Intermodal transverse thin layer	29.80 (15.00)*	Chattopadhyaya et al. 2010
Protoplast	Callus	0.24 ^a	Debnath et al. 2024

[#]All the studies used de-embryonated cotyledon explants

*The numbers inside the first brackets indicate the number of regenerated shoots per explant

^aCallus-derived protoplasts regenerated up to the micro-callus stage

Supplemented with 33 μM BAP + 2.85 μM IAA + 3.78 μM ABA + 29.43 μM AgNO₃ for 14 days and Subcultured in MS medium Supplemented with 33 μM BAP + 2.85 μM IAA + 29.43 μM AgNO₃.

Indirect adventitious organogenesis involves an intermediate callus induction phase, and the induced calluses differentiate into regenerated shoots. This regeneration method is often chosen in transformation programmes of such species where the de-differentiated meristem cells of callus are preferred to transform (Wędzony et al. 2014). In sesame, such protocols were established from hypocotyl (Kwon et al. 1993; Yonghua et al. 1997; Saravana and Nadarajan 2005; Singh and Shagufta 2011; Wadeyer and Lokesha 2011; Wadeyar et al. 2013; Savitha et al. 2016; Asad et al. 2019), leaf-derived callus (Raja and Jayabalan 2010), anther (Yifter et al. 2013), and de-embryonated cotyledon-derived callus explants (Anandan et al. 2018b) (Table 1, S4). All these reports are unique because the authors have employed diverse strategies of indirect organogenesis. The regeneration frequencies also varied from 6.18% to 100%. Wadeyer and Lokesha (2011) cultured 15–17-day-old hypocotyl-derived calluses in MS Supplemented with 2.15 μM NAA, 15.55 μM BAP and 20 μM AgNO₃ for 55–65 days and reported 100% shoot induction frequency. Raja and Jayabalan (2010)

cultured leaf explants from 12-day-old seedlings in MS salts + B5 vitamins (Gamborg et al. 1968) fortified with 13.56 μM 2,4-D and 2.66 μM BAP medium to induce callus. They cultured these calluses in the medium containing MS salts + B5 vitamins Supplemented with 2.15 μM NAA + 8.88 μM BAP and reported 90.8% organogenesis. Asad et al. (2019) cultured 8-day-old hypocotyl explants in MS medium Supplemented with 13.56 μM 2,4-D and 2.66 μM BAP to achieve 85.8% green friable organogenic callus induction frequency. They inoculated these calluses to MS medium Supplemented with 6.66 μM BAP + 2.15 μM NAA and reported 90.8% indirect shoot induction. Wadeyar et al. (2013) induced callus from hypocotyl explants of the Dharwad Selection-1 (DS-1) sesame variety in two steps. At first, they cultured Surface-sterilised sesame seeds in MS medium Supplemented with 2.69 μM of NAA + 6.66 μM of BAP + 6.99 μM of KIN. After 45 days of culture, they obtained Light green, healthy, and moderately compact callus with a 100% induction rate. They cultured these calluses in MS medium Supplemented with 25 μM TDZ and 3 μM IAA for 55–65 days and reported 83.3% shoot regeneration with two shoots per callus.

Somatic embryogenesis initiates from a single or a small group of plant cells. Therefore, the somatic embryogenesis

of a transformed cell is not likely to develop into a chimeric plant (Bautista-Montes et al. 2022). Somatic embryogenesis in sesame has been obtained from cotyledon- and hypocotyl-derived calluses (Ram et al. 1990; Mary and Jayabalan 1997; Xu et al. 1997) (Table 1, S5). The rate of somatic embryo induction varied from 50 to 100%. Achieving an optimised embryogenesis protocol is often considered a difficult plant tissue culture technique because it is time-consuming, labourious, and involves complex processes (Hesami et al. 2020). Possibly, this is the reason for the minuscule availability of somatic embryogenesis reports for sesame.

Micropropagation can generate a large-scale clonally propagated plant population in a short period. This regeneration method can potentially save time in a transformation experiment if transformants are regenerated using this method (Bautista-Montes et al. 2022). Micropropagation has been achieved from shoot tip, node, and plumule tip explants (Lee et al. 1985; George et al. 1987; Gangopadhyay et al. 1998; Baskaran and Jayabalan 2006; Dasharath et al. 2007; Ahmed et al. 2008; Abdellatif et al. 2010; Chakraborti and Ghosh 2010; Chamandoosti 2016; Elayaraja et al. 2019; Asad et al. 2020; Gayatri and Basu 2020) (Table 1, S6). Most authors used apical shoot tip explants and obtained up to 100% shoot multiplication rates; however, the micropropagated shoot numbers varied extensively (2.7–23.36). The shoot multiplication rate and number of propagated shoots per explant were > 90% and > 15, respectively, when cotyledonary node and plumule tip explants were used (Elayaraja et al. 2019; Gayatri and Basu 2020).

The thin cell layer culture system can develop a high density of regenerated organs or embryos on a small explant tissue. This process can improve the yield of transformants in a transformation study. Chattopadhyaya et al. (2010) used 0.5–1.0 mm-thick intermodal transverse thin layer sections from 4- to 6-week-old sesame seedlings as explants. The Maximum reported regeneration rate was 29.8% with 15 shoots per explant (Table 1).

Protoplasts are plant cells without cell walls. They are an excellent biotechnological tool for studying plants. A single protoplast can regenerate to develop a whole plant. Therefore, protoplast transformation systems are useful for producing chimera-free transgenic plants. Dhingra and Batra (1990) isolated protoplasts from sesame hypocotyls. Shoji et al. (1988) and Bapat et al. (1989) regenerated hypocotyl-derived protoplasts of sesame up to the micro-colony stage. Recently, Debnath et al. (2024) optimised protoplast isolation protocols from hypocotyl, internode, leaf, and hypocotyl-derived callus explants. They obtained micro-callus from the callus-derived protoplasts (Table 1). However, reports of protoplast regeneration to develop full-grown sesame plants do not exist to date.

The authors used different genotypes in most of the sesame regeneration studies. Despite using various regeneration

strategies in these multi-decade-long efforts, the reported regeneration frequencies are still inconsistent, ranging from 2.7 to 100%. It supports the well-accepted fact of genotype dependency of sesame regeneration. Some authors pointed out this fact experimentally. For example, among the ten tested varieties of sesame (TMV3, TMV4, TMV5, TMV6, VRI1, AKT64, TC25, RT127, Rajeshwari, and UMA), Zimik and Arumugam (2017) found that the UMA variety is better suited for adventitious plant regeneration. Moreover, Debnath et al. (2018) showed that although their optimised regeneration protocol works best for the genotype JK-1, variable regeneration frequency was found using other genotypes such as JT-7, PADMA, RT-103, PHULE TIL-1, and TAPI-A. The establishment of a well-suited universal regeneration is still a challenging task for sesame.

However, an interesting point is revealed after reviewing the regeneration reports. Seo et al. (2007), Debnath et al. (2018), and Rajput et al. (2022) used a similar regeneration protocol. They all used young de-embryonated cotyledon explants and cultured them on MS medium supplemented with BAP + IAA + AgNO₃ in two steps. In the first step of culture, they used ABA supplementation, which was removed in the next step. The concentrations of the hormone supplements were also in a similar range in these reports. Despite using different genotypes, the authors achieved a good regeneration frequency. Especially, the reported frequencies of Debnath et al. (2018) and Rajput et al. (2022) are very close, 94.81% and 83.3%, respectively. They also obtained a similar number of regenerated shoots per explant, 5.4 and 5.9, respectively. Possibly, this phenomenon indicates that the applied methodologies by these three authors may also become suitable for other genotypes. However, more positive reports of sesame regeneration with different cultivars using methods like the abovementioned facts are needed to answer the question. Therefore, could this methodology pave the way to establish a universal protocol for sesame regeneration is now a matter of debate, and the answer remains in the future only.

Transformation of sesame

Genetic engineering-mediated biotechnological improvement of plants involves the introduction of foreign gene(s) to express a new trait, deregulation of genomic expression to control the expression of an existing trait, or knockout of gene(s) to silence a specific trait. An efficient transformation protocol is a prerequisite for deploying genetic engineering in plants. However, only a few reports on transformation optimisation are available in sesame (Table 2). Since their invention in the 1980s, conventional *Agrobacterium*-mediated transformation and biolistic-mediated transformation have become two major tools to introduce alien genes into plants. Conventional

Table 2 Reports of transformation protocol standardisation in sesame

Explant	Transformation method	Transformation frequency	Transformed gene	Gene function	References
Cotyledon	Biolistic-mediated transformation	1.46%	<i>BAR</i>	Herbicide-resistant reporter	Chen et al. 1996
Cotyledon	Conventional <i>Agrobacterium</i> -mediated transformation	–	<i>GUS</i>	Reporter	Taskin et al. 1999
Unpollinated mature flower	In planta <i>Agrobacterium</i> -mediated floral transformation	49.8%	<i>EGFP</i>	Reporter	Were 2006
Cotyledon (de-embryonated)	Conventional <i>Agrobacterium</i> -mediated transformation	1.01%	<i>GUS</i>	Reporter	Yadav et al. 2010
Cotyledon	Conventional <i>Agrobacterium</i> -mediated transformation	1.67%	<i>GUS</i>	Reporter	Al-Shafeay et al. 2011
Cotyledon (de-embryonated)	Sonication-assisted <i>Agrobacterium</i> -mediated transformation	85.56%	<i>GUS</i>	Reporter	Debnath et al. 2014
Cotyledon (de-embryonated)	Conventional <i>Agrobacterium</i> -mediated transformation	42.66%	<i>GUS</i>	Reporter	Chowdhury et al. 2014
Shoot apical meristem	Biolistic-mediated transformation	15.86%	<i>BAR</i>	Herbicide-resistant reporter	Bhattacharyya et al. 2015
Plumule tip	Conventional <i>Agrobacterium</i> -mediated transformation	1.33%	<i>GFP</i>	Reporter	Gayatri and Basu 2020
Seed (de-coated)	Conventional <i>Agrobacterium</i> -mediated transformation	6.1%	<i>BAR</i>	Herbicide-resistant reporter	Sultan and Tawfik 2023

“–” indicates that no information is available

Agrobacterium-mediated transformation is widely used in many plant species to create transgenics due to its simplicity and low cost. This method can introduce stable and low-copy-number transgenes with high efficiency of transformation (Tiwari and Rajam 2024).

Taskin et al. (1999) first reported transgenic calli through conventional *Agrobacterium*-mediated transformation but failed to recover transgenic shoots. Yadav et al. (2010) reported the first successful sesame transformation and plant recovery using conventional *Agrobacterium*-mediated transformation. Al-Shafeay et al. (2011) and Gayatri and Basu (2020) also reported conventional *Agrobacterium*-mediated transformation in sesame. In a recent interesting report, Sultan and Tawfik (2023) transformed sesame seeds using the conventional *Agrobacterium*-mediated transformation technique and bypassed the troublesome regeneration-related tissue culture phase by directly germinating the transformed seeds to obtain putative transgenic plants. To date, Chowdhury et al. (2014) found the conventional *Agrobacterium*-mediated transformation-derived maximum transformation efficiency (42.66%).

Studies on the conventional *Agrobacterium*-mediated transformation in sesame reflect a wide distribution of reported transformation efficiency ranging from 1.01% (Yadav et al. 2010) to 42.66% (Chowdhury et al. 2014). Moreover, the authors have used different explants such as cotyledon, plumule tip, and seed to achieve optimum transformation frequency. Such phenomena suggested that the efficiency of sesame transformation is dependent on sesame genotype and explant, which is also reported in other plants. Biolistic-mediated transformation can overcome these limitations (Su et al. 2023). Chen et al. (1996) and Bhattacharyya et al. (2015) reported biolistic-mediated transformation, and a Maximum transformation rate of 15.86% has been achieved.

A few alternative transformation methods are also standardised in sesame. Were et al. (2006) used in planta *Agrobacterium*-mediated floral transformation to transform unpollinated Mature flowers by the floral dip method and achieved transformed seed at the rate of 49.8%. This straightforward transformation method bypasses the tissue culture step and can generate a large population of transgenic

plants with minimal effort. Debnath et al. (2014) attempted a less-known transformation technique known as “Sonication Assisted *Agrobacterium*-mediated Transformation” (SAAT). It was the first SAAT report in sesame. In SAAT, the target plant tissue is placed in the *Agrobacterium* infection solution, and a high-frequency sound wave (sonication) is applied. Sonication creates micro-wounding in the target tissue. It increases the release of phenolics, facilitating the *Agrobacterium* infection and transformation process. The authors used a 40 kHz sound wave to achieve 85.56% transient expression of GUS after 48 h of SAAT application. Such a transient expression system is useful in rapid recombinant protein production, protein localisation and trafficking studies, and the development of various functional genomics assays.

Despite various efforts by researchers exploring different paths of sesame transformation, the outcome is still inconsistent from a practical point of view of crop improvement. The success of conventional *Agrobacterium*-mediated transformation is primarily dependent on the choice of explant and genotype. Biolistic-mediated transformation can disrupt the target tissue structure, introduce a high copy number of the transgene, and cause undesired chromosomal rearrangement. On the one hand, addressing these limitations could lead to a widely accepted and optimised gene manipulation protocol for sesame using these two most popular transformation techniques. On the other hand, exploration of alternate transformation methodologies such as electroporation, microinjection, pollen tube-mediated gene insertion, and silicon carbide whisker-mediated transformation could open multiple possibilities for obtaining another potential sesame transformation protocol. Contemporary transformation technologies involving nanoparticles and peptides could potentially deliver genes with less explant and genotype specificity and minimal target tissue damage (Su et al. 2023). Such methodologies also need to be deployed in sesame. Molecular genetic improvement of a crop by precise gene transfer-derived targeted trait improvement is mostly dependent on a high-throughput plant regeneration and transformation system. A well-responsive regeneration and transformation protocol remains a major bottleneck for sesame yield improvement (Debnath et al. 2014; Zimik and Arumugam 2017).

Sesame whole-genome sequencing provides a platform to choose genes to manipulate

Whole-genome sequencing is a prerequisite resource for understanding a species fully. A high-quality reference gene sequence is like a complete gene catalogue of an organism, containing the regulatory elements that control their function and a framework to study genomic variation. This valuable

resource can give fundamental insight into the role of the different genes in various processes of the organism. The information can be used to take genome-based approaches to improve the organism, including plants. Using the cultivar Zhongzhi No.13, a Chinese research group has provided high-quality draft genome data of 27,148 genes using the Illumina Hiseq2000 platform (Wang et al. 2014). In parallel research, the Sesame Genome Working Group (SGWG) also sequenced the whole nuclear genome of sesame using the cultivar Yuwhi 11 (Zhang et al. 2013a). So far, they have sequenced 335.19 Mb (94.7%) of the estimated 354 Mb sesame genome. The Subsequent gene ontology analysis identified 31,462 genes that are grouped into three categories: biological process (28,415 genes), molecular function (10,004 genes), and cellular component (8,400 genes) (Zhang et al. 2019). Besides that, Wei et al. (2016b) have released the genome sequence of two sesame landraces Baizhima and Mishuozhima. In addition, a group from the National Bureau of Plant Genetic Resources, India, sequenced the genome of the Indian variety Swetha (Dossa et al. 2017a). Moreover, the re-sequencing of several sesame accessions provided much more genomic insight into this plant (Zhang et al. 2013a, 2016; Wang et al. 2014, 2016b; Uncu et al. 2015, 2016; Wei et al. 2015). Findings about sesame genomes are compiled in several databases (Table S7). These databases contain a generous amount of information on the sesame genome, which is useful in various aspects of sesame research, including yield improvement.

Potential genes are available for sesame yield improvement

Current agricultural practice for yield improvement relies mostly on fertiliser and pesticide applications. However, overuse of fertilisers and pesticides affects the environment and the health of end-users. Genetic engineering is a better alternative solution than conventional breeding for crop improvement. Crop yield is a complex trait contributed by numerous genes that control various aspects of plant morphology and stress resistance (Gao et al. 2023). Therefore, understanding these genetic factors can facilitate biotechnological crop improvement in further research.

Morphology-related genes

Various reports of the last decade discussed morphology-related key target genes for sesame yield improvement (Table 3). Plant architecture plays a critical role in the yield (Wang et al. 2016b). Since the sesame stems tend to lodge at the ripening stage, short-height cultivars are desired to minimise yield loss (Wei et al. 2016b). Whole-genome sequencing studies identified sesame *DWARF IN LIGHT 1 (DFL1)*,

Table 3 Morphology-related key target genes useful for sesame yield improvement

Gene	Trait	References
<i>SiACS8</i> (SIN_1006338)	Capsule number per axil	Wei et al. 2015
<i>SiKNAT4</i> (SIN_1007270), <i>SiCOL5</i> (SIN_1011796), <i>SiABI5</i> (SIN_1013020), <i>SiGIGANTEA</i> (SIN_1015799), <i>SiGF14</i> (SIN_1017003), <i>SiARF</i> (SIN_1017183), <i>SiIAA14</i> (SIN_1021838), <i>SiDOG1</i> (SIN_1022538), and <i>SiIAA33</i> (SIN_1023837)	Flowering time	Wei et al. 2015
<i>SiDFL1</i> (SIN_1014512), and <i>SiILR1</i> (SIN_1018135)	Plant height	Wei et al. 2015
<i>SiGA20ox1</i>	Plant height	Wei et al. 2016b
<i>SiDt</i>	Growth determinacy	Zhang et al. 2016
<i>SiBH</i>	Plant branching	Mei et al. 2017a
<i>SiFA</i>	Flower number per axil	Mei et al. 2017a
<i>SiLPT3</i> , and <i>SiACS8</i>	Capsule length and number	Zhou et al. 2018a, b
<i>SiDWF1</i>	Internode length-derived plant height	Miao et al. 2020
<i>SiARGOS</i> (SIN_1015854), <i>SiHMG1</i> (SIN_1015831), and <i>SiRHF2A</i> (SIN_1015130)	Seed size and shape	Mei et al. 2023
<i>SiOFP1</i>	Length of capsule	Wang et al. 2023a, b
<i>SiPT1</i>	Plant branching	Miao et al. 2024
<i>SiDT1</i>	Inflorescence determination	Miao et al. 2024

IAA-LEUCINE RESISTANT 1 (ILR1), and *GIBBERELLIN 20 OXIDASE 1 (GA20ox1)* genes that control plant height. The *DFL1* is a negative regulator of shoot elongation. *ILR1* and *GA20ox1* contribute to plant height by modulating the auxin and gibberellin metabolic processes, respectively (Wei et al. 2015, 2016b). The *SiDWF1* gene was identified by morpho-genomic analysis of a dwarf sesame line. *SiDWF1* encodes a gibberellin receptor GID1B-like protein and influences plant height by controlling the internode length in sesame (Miao et al. 2020). Capsule length and number per axil, flower number per axil, and plant branching are important morphological parameters of sesame that positively contribute to the yield. Sesame whole-genome sequencing analysis and genome-wide association studies revealed that *LIPID TRANSFER PROTEIN 3 (SiLTP3)* and *1-AMINO-CYCLOPROPANE-1-CARBOXYLATE SYNTHASE 8 (SiACS8)* control the capsule length and number per axil (Wei et al. 2015; Zhou et al. 2018a, b). Capsule length is also controlled by *SiOFP1* (Wang et al. 2023a, b). Mei et al. (2017a) analysed specific length amplified fragment sequencing (SLAF-seq)-derived high-density genetic linkage map and identified two candidate genes—*FLOWERS PER LEAF AXIL (SiFA)* and *BASAL BRANCHING HABIT (SiBH)* that impact the plant branching and flower number per axil, respectively. Recently, using a genome-wide association study (GWAS), Miao et al. (2024) found that *SiPT1* also controls the branching of sesame. The characteristic indeterminate growth pattern of sesame causes asynchronous capsule ripening. Coupled with the capsule-shattering problem, the situation leads to difficulties in mechanical harvesting and affects yield. To solve this problem, Zhang et al. (2016) constructed an ultra-dense SNP genetic map of sesame and identified a candidate gene, *SiDt*, that controls the growth determinacy. In a later

genome-wide association study (GWAS), Miao et al. (2024) identified that *SiDT1* subfamily genes also control sesame growth determinacy.

Seed size and shape have a positive impact on sesame yield. In a recent study, Mei et al. (2023) identified three candidate genes controlling seed size and shape by quantitative trait locus analysis. Among the identified genes, *AUXIN-REGULATED GENE INVOLVED IN ORGAN SIZE (ARGOS)* increases plant organ size; *HMG1* is a 3-hydroxy-3-methylglutaryl coenzyme A reductase that impacts seed morphology by regulating sterol biosynthesis; *RHF2A* encodes an E3 ubiquitin-protein ligase and contributes to gametogenesis and seed development.

Oil content-related genes

Sesame seeds contain 44–58% oil (Table S2). Enhancement of seed oil content can contribute to an increase in production. Several authors have identified candidate genes for seed oil content using whole-genome sequencing (Wang et al. 2014a; Wei et al. 2015, 2016b), comparative transcriptomics (Wang et al. 2019; Dutta et al. 2022), and genome-wide sequence analysis (Song et al. 2021) studies. Such pinpointed candidate genes are *LIPID TRANSFER PROTEIN (LTP)*, *3-KETOACYL-ACYL CARRIER PROTEIN SYNTHASE II (KASII)*, *GDSL-LIKE LIPASE*, *NAC SECONDARY WALL THICKENING PROMOTING FACTOR1 (NST1)*, *ACONITASE A (ACNA)*, *LIPOXYGENASE 2 (LOX2)*, *ACETYL-COA CARBOXYLASE*, *GLYCEROL-3-PHOSPHATE ACYL-TRANSFERASE*, and *CARBOXYLESTERASE* to name a few (Table 4). These genes primarily regulate fatty acid biosynthesis and lipid transfer pathways, leading to oil

Table 4 Seed oil content- and seed coat colour-related key target genes useful for sesame yield improvement

Gene	References
Seed oil content	
<i>SiLTP1</i>	Wang et al. 2014
<i>SiCXE17</i> (SIN_1003248), <i>SiLTP</i> (SIN_1007213), <i>SiKASII</i> (SIN_1007554), <i>SiLTP</i> (SIN_1010931), <i>GDSL-like lipase</i> (SIN_1013005), <i>SiSTART</i> (SIN_1009923), <i>SiLTP4</i> (SIN_1019167), and <i>SiNST1</i> (SIN_1005755)	Wei et al. 2015
<i>SiLTP</i> , <i>SiACNA</i> , and <i>SiLOX2</i>	Wei et al. 2016b
<i>SiLTP</i> (SIN_1010009), <i>SiLTP</i> (SIN_1019172), and <i>SiLTP</i> (SIN_1019175)	Wang et al. 2019
<i>SiLTPI.23</i> and <i>SiLTPI.28</i>	Song et al. 2021
<i>Acetyl-CoA carboxylase</i> , <i>glycerol-3-phosphate acyltransferase</i> , <i>choline phosphotransferase</i> , <i>GDSL esterase or lipase</i> , <i>lipid transfer protein</i> , and <i>carboxylesterase</i>	Dutta et al. 2022
<i>SiPPO</i>	Miao et al. 2024
Seed coat colour	
<i>SiPPO</i> (SIN_1016759)	Wei et al. 2015, 2016b; Wang 2016b
<i>Polyphenol oxidases</i> , <i>NAC domain-containing protein 43</i> , and <i>pentatricopeptide repeat-containing proteins</i>	Dutta et al. 2022

synthesis and transfer to sesame seeds. Therefore, these genes can serve as valuable targets to manipulate the oil quantity in sesame seeds.

Seed coat colour-related genes

The seed coat colour is a vital agronomic character associated with sesame yield. White sesame seeds are superior in oil content (Wang et al. 2012a). Several studies identified *POLYPHENOL OXIDASE* (*SiPPO*), *NAC DOMAIN-CONTAINING PROTEIN 43*, and *PENTATRICOPEPTIDE REPEAT-CONTAINING PROTEINS* controlling the seed coat colour-mediated oil content (Table 4) (Wei et al. 2015, 2016b; Wang 2016b; Dutta et al. 2022; Miao et al. 2024). Another genome-wide association study (GWAS) reported 92 potential genes associated with sesame seed colour (Cui et al. 2021).

Male sterility-related genes

Molecular heterosis breeding is a great alternative to conventional breeding (Debnath et al. 2014). A prerequisite of this approach is a male sterile line, which is still unavailable and is the primary constraint affecting the applicability of this technology on sesame. Until now, a few sesame genes have been identified that could be manipulated to induce male sterility (Table 5). Earlier studies with mutant male sterile sesame lines identified two male sterility-associated genes—*MALE STERILE 1* (*SiMs1*) and *MALE STERILE 2* (*SiMs2*) (Lichuan et al. 1995; Zhao et al. 2013). Later, Liu et al. (2018) investigated a recessive genic male sterile sesame line (D248A) and identified a few male sterility-related genes. Their identified SIN_1013909 gene encodes the UDP-glucuronosyl/UDP-glucosyltransferase that contributes to pollen development. The SIN_1013911 gene-encoded GTP-binding protein interacts with the *Ms2* gene and contributes to male sterility. Parveen et al. (2018) identified and characterised a tapetum-specific sesame promoter (*SiBGproplus*, also called

Table 5 Male sterility- and capsule indehiscence-related key target genes useful for sesame yield improvement

Gene	Trait	References
Male sterility		
<i>SiMs2</i>	Male sterility. Heterosis-mediated yield improvement	Lichuan et al. 1995
<i>SiMs1</i>	Male sterility. Heterosis-mediated yield improvement	Zhao et al. 2013
SIN_1013909 and SIN_1013911,	Male sterility. Heterosis-mediated yield improvement	Liu et al. 2018
<i>SiBGproplus</i>	Tapetum-specific promoter. Male sterility. Heterosis-mediated yield improvement	Parveen et al. 2018
Capsule indehiscence		
<i>SiCLI</i>	Non-shattering capsule, curly leaf	Zhang et al. 2018a
<i>SiKANI</i>	Non-shattering capsule, curly leaf	Yol et al. 2021

GN13) through the functional genomic approach. Recently, Debnath et al. (2025) showed the GN13-driven tapetum-specific expression of GUS in transgenic sesame. In future research, the GN13 promoter can be utilised to express cytotoxicity in anther tissue to manifest male sterility in sesame. Utilising these reported genes, genetically induced male sterile lines-mediated heterosis exploitation could increase sesame yield in future research.

Capsule indehiscence-related genes

Early capsule shattering is a major hindrance to sesame yield. Langham (1946) identified a homozygous recessive mutant sesame genotype (*id/id*) conferring capsule indehiscence. However, he failed to recognise the causative gene. In two parallel studies, Zhang et al. (2018a) and Yol et al. (2021) identified *SiCLI/SiKANI* as the single candidate gene for the capsule indehiscence trait in sesame (Table 5). *SiCLI* is the sesame homolog of the *Arabidopsis* transcription repressor *KANADII* (*KANI*). Zhang et al. (2018a) crossed between the curly leaf mutant *cll* and the wild type of sesame, developed 130 F2 progenies, sequenced them, and performed cross-population association mapping and genome variants screening to identify a single recessive gene *SiCLI*, which controls sesame capsule indehiscence and curly leaf traits. Yol et al. (2021) crossed between a capsule-shattering and non-shattering mutant sesame genotype, produced an F2 population, and sequenced the F2 lines by ddRAD-Seq. They analysed the sequenced data and found *SiKANI* associated with capsule shattering and curly leaf traits. *SiCLI/SiKANI* regulates abaxial parenchyma cell development to control the polarity and curling of leaves. Loss of function in *SiCLI/SiKANI* can cause capsule indehiscence and curly leaf traits. It is still unclear whether the capsule indehiscent trait of the mutant sesame genotype (*id/id*) that Langham (1946) found was due to the mutation of *SiCLI/SiKANI*. However, research progress establishes *SiCLI/SiKANI* as a potential candidate that can solve the early capsule-shattering problem by genetic engineering in future.

Abiotic stress-related genes

Several abiotic stress factors cause a significant yield decrease in sesame. Various gene expression studies have identified a set of genes for abiotic stress tolerance (Table 6). Wang et al. (2012b) compared the gene expression profile before and after waterlogging stress in root tissues of a waterlogging sesame genotype. They found waterlogging stress-mediated 13,307 deregulated genes (DEG) related to energy metabolism and signal transduction. They also found DEG of flavone, flavonol, phenylpropanoid and steroid biosynthesis, cysteine, methionine and glutathione metabolism,

photosynthesis, spliceosome, and circadian rhythm. In another study, Wang et al. (2016a) compared the transcriptomes of waterlogging-tolerant and -susceptible genotypes and pinpointed 66 candidate genes for waterlogging tolerance. These genes are related to chitinase activity, chitin catabolism, and chitin binding to cell walls. They hypothesised that chitin-mediated mechanical endurance of cell walls could facilitate waterlogging tolerance. Recently, Shah et al. (2024) conducted a comprehensive morphological, biochemical, genomic, and microscopic study to compare the response between waterlogging stress-tolerant and -susceptible sesame genotypes. Their study revealed the importance of carbohydrate metabolism genes *SUCROSE SYNTHASE 2* (*SiSuSy2*) and *STARCH SYNTHASE 1* (*SiStSy1*), antioxidant gene *PEROXIDASE* (*SiPOD*), and ethylene synthesis gene *1-AMINOCYCLOPROPANE 1-CARBOXYLIC ACID* (*SiACC*) in sustaining waterlogging stress. In addition, they identified two morphological genes, *RESPIRATORY BURST OXIDASE HOMOLOG C* (*SiRBOH-C*) and *PHOSPHATE STARVATION 1* (*SiPSRI*), that help in sustaining root morphology under waterlogging stress.

Dossa et al. (2017b) compared drought stress-mediated gene expression analysis between drought-tolerant and -sensitive varieties to divulge 61 candidate genes for drought tolerance in sesame. These genes encode alpha-L-fucosidase, cytochrome P450, HSP20 family protein, HSP70 family protein, indole-3-acetate O-methyltransferase, interleukin receptor-associated kinase 4, NADH dehydrogenase, pectinesterase, peroxidases, solute carrier family 15, etc. They also denoted the importance of ABA- and ethylene-mediated hormonal regulation, enzymatic antioxidants, and osmoprotectants for drought tolerance in sesame. In a GWAS analysis involving 490 sesame worldwide accessions, seven candidate genes solely responsible for drought tolerance in sesame were identified. Among these genes, *CAROTENOID CLEAVAGE DIOXYGENASE 8* (*SiCCD8*) promotes plant growth under drought stress, and *12-OXOPHYTODIENOATE-REDUCTASE 3* (*SiOPR3*) is a jasmonic acid biosynthesis gene that regulates abscisic acid-mediated drought tolerance in plant roots (Li et al. 2018). Parveen et al. (2018) identified the promoter region (*SiBGproplus*) of the drought-inducible tapetum-specific sesame gene *β-1,3-glucanase* using a functional genomics-coupled transgenic analysis. This tapetum-specific promoter gene could be a potential candidate for expressing drought-inducible Male fertility genes in anthers to enhance Male gametogenesis and yield under drought stress. Another GWAS study in 400 sesame accessions revealed a few known and novel candidate genes for drought tolerance. They identified sesame *S-ADENOSYLMETHIONINE SYNTHETASE* (*SiSAM*), an *Arabidopsis* homolog of *AtSAM* that encodes *S-adenosylmethionine* (SAM). SAM is a biosynthetic precursor of ethylene and polyamines that multi-dynamically regulates drought

Table 6 Abiotic and biotic stress-related key target genes useful for sesame yield improvement

Gene	Trait	References
Abiotic stress tolerance		
<i>SiGRV2</i> (SIN_1001572), <i>SiRABA1D</i> (SIN_1019660), <i>SiCCD8</i> (SIN_1021558), <i>SiEMF1</i> (SIN_1021566), and <i>SiOPR3</i> (SIN_1024693)	Drought tolerance	Li et al. 2018
<i>SiG6PD1</i> (SIN_1003799), <i>SiLSD1</i> (SIN_1006753), <i>SiUDG</i> (SIN_1008463), SIN_1013032, <i>SiHSFA1</i> (SIN_1015378), <i>SiDUF538</i> (SIN_1017475), <i>SiCC-NBS-LRR</i> (SIN_1018894), <i>SiPOD</i> (SIN_1021322), <i>SiPOD</i> (SIN_1021323), <i>SiPOD</i> (SIN_1021324), <i>SiPOD</i> (SIN_1021325), <i>SiPOD</i> (SIN_1021326), <i>SiPOD</i> (SIN_1021327), <i>SiANTH</i> (SIN_1021330), <i>SiMLP31</i> (SIN_1021337), <i>SiLHCB6</i> (SIN_1021624), <i>SiXTH15</i> (SIN_1022410), <i>SiCP24</i> (SIN_1026087), and <i>SiXXT5</i> (SIN_1026318)	Salt tolerance	Li et al. 2018
<i>SiHKT1</i> (SIN_1007698), <i>SiAGL37</i> (SIN_1007708), <i>SiGPAT3</i> (SIN_1007701), <i>SiGDH2</i> (SIN_1008841), and <i>SiCYP76C7</i> (SIN_1008842)	Drought and salt tolerances	Li et al. 2018
<i>SiBGproplus</i>	Drought-induced tapetum-specific promoter	Parveen et al. 2018
<i>SiGolS</i> and <i>SiRS</i>	Drought, salt, waterlogging, and cold stress tolerances	You et al. 2018
SIN_1004716, SIN_1004723, <i>SiPOD3</i> (SIN_1005662), <i>SiTTM3</i> (SIN_1012134), <i>SiP450</i> (SIN_1015691), SIN_1015693, <i>SiGOLS1</i> (SIN_1022774), <i>SiNIMIN1</i> (SIN_1022782), and <i>SiSAM</i> (SIN_1022789)	Drought tolerance	Dossa et al. 2019a
<i>SiSRO2b</i>	Salt and osmotic tolerances	Liu et al. 2021
<i>SiF3H</i> , <i>Si2-OGD AOP1</i> , and <i>SiCASP</i>	Drought tolerance	Baghery et al. 2022
<i>SiPUB</i>	Drought tolerance	Cao et al. 2023
<i>SiTPS</i>	Drought, salt, waterlogging, and osmotic tolerances	Zhou et al. 2023
<i>SiACC</i> , <i>SiPOD</i> , <i>SiPSRG</i> , <i>SiRBOH-C</i> , <i>SiSuSy2</i> , and <i>SiStSy1</i>	Waterlogging tolerance	Shah et al. 2024
<i>SiPRX</i>	Drought tolerance	Vishwakarma et al. 2024
Biotic stress tolerance		
<i>SiLRR</i> (SIN_1009480), <i>SiDUF538</i> (SIN_1010897), <i>SiG-STF9</i> (SIN_1017036), <i>SiLRR</i> (SIN_1023555), and <i>SiLRR</i> (SIN_1024378)	Phyllody tolerance	Wei et al. 2015
<i>SiLRR</i> (SIN_1017074)	Charcoal rot tolerance	Wei et al. 2015
<i>SiPAL</i> and <i>SiPOD</i>	Fusarium wilt tolerance	Wei et al. 2016a
SIN_1019016	Phytophthora blight tolerance	Asekova et al. 2021
<i>SiLRR-RLK</i>	Charcoal rot tolerance	Yan et al. 2021
<i>SiRLK1</i>	Fusarium wilt tolerance	Duan et al. 2024
<i>SiDIR</i>	Fusarium wilt tolerance	Miao et al. 2024

stress response by hormonal crosstalk, ROS homeostasis, and activation of other stress-responsive genes. A few novel genes that played significant roles in drought tolerance are a pathogen defence responsive gene *NIM1-interacting 1* (*SiNIMIN1*), a negative regulator of root development *TRIPHOSPHATE TUNNEL METALLOENZYME 3* (*SiTTM3*), and a wax biosynthesis gene *SIN_1004716* (Dossa et al. 2019a). Another study identified three novel candidates of sesame drought-tolerant genes, *FLAVONOID 3'-MONOOXYGENASE-LIKE*, also known as *FLAVONOID 3'-HYDROXYLASE* (*SiF3H*), *2-OXOGLUTARATE-DEPENDENT DIOXYGENASE AOP1* (*Si2-OGD AOP1*), and *CASPARIAN STRIP MEMBRANE PROTEIN* (*SiCASP*). The *F3H* is a key

flavonoid biosynthetic gene that confers drought tolerance by improving secondary metabolite synthesis. The *2-OGD AOP1* biosynthesises glucosinolates that control stomatal closure during drought stress. The *CASP* genes upregulate Casparian strip formation by increased lignin deposition; it decreases water loss during drought conditions (Baghery et al. 2022). Members of the plant U-Box (PUB) proteins have diverse roles in plant growth, development, and stress response. A genome-wide analysis study identified 56 drought-responsive, candidate *SiPUB* genes (Cao et al. 2023). The peroxidase (PRX) enzyme family is an important enzymatic antioxidant component of the drought stress mitigation system. Recently, genome-wide analysis of the *SiPRX*

family identified 45 non-redundant members, and their role in drought stress tolerance has been elucidated in sesame (Vishwakarma et al. 2024).

Using GWAS, Li et al. (2018) identified 21 candidate genes that exclusively control salt stress response in sesame. Among these genes, *MLP-LIKE PROTEIN 31* (*SiMLP31*) is a salicylic acid biosynthesis gene that facilitates seed germination and seedling vigour under saline conditions, *SIANTH* is a phosphatidic acid-binding protein that is transported to the cell membrane as a salt stress response, and *PEROXIDASE* (*SiPOD*) is an antioxidant encoder useful in salinity mitigation. They have also found six genes commonly associated with drought and salt stress mitigation. Among these, the *HIGH-AFFINITY PHOSPHORIC TRANSPORTER* (*SiHKT*) is a sodium–potassium transporter that plays a crucial role in salt stress mitigation by interfering with cellular ion homeostasis. However, their function in drought stress tolerance is unknown. Raffinose family oligosaccharides (RFOs) play significant roles in abiotic stress mitigation by acting as osmoprotectants and ROS scavengers. Galactinol synthase (GolS) and raffinose synthase (RS) are two of the key RFO biosynthetic enzymes in plants (Seki et al. 2007; ElSayed et al. 2014). A genome-wide analysis revealed 7 *SiGolS* and 15 *SiRS* genes of sesame. These genes were simultaneously responsive under drought, salt, and cold stresses but differentially regulated in these conditions (You et al. 2018). Another genome-wide analysis identified four sesame *SIMILAR TO RCD-ONE* (*SiSRO*) genes that regulate multiple abiotic stress responses by controlling stress-responsive hormonal pathways and transcription factors. *SiSROs*, especially *SiSRO2b*, showed improved tolerance to salt and osmotic stresses in transgenic yeast models (Liu et al. 2021). Trehalose is an important osmolyte that protects cells from multiple abiotic stress-induced damages. In plants, trehalose is biosynthesised by trehalose-6-phosphate synthase (TPS). Overexpression of the *TPS* gene improved abiotic stress tolerance in many plants (Chary et al. 2008; Zhou et al. 2023). Ten sesame *TREHALOSE-6-PHOSPHATE SYNTHASE* (*SiTPS*) genes were identified by genome-wide analysis and categorised into two groups. Expression analysis depicted that the group II *SiTPS* (*SiTPS4–SiTPS10*), particularly *SiTPS10*, was significantly upregulated during drought, salt, waterlogging, and osmotic stresses (Zhou et al. 2023).

Biotic stress-related genes

Yield loss due to various diseases is a serious concern in sesame cultivation. A handful of reports depict sesame biotic stress-tolerant genes (Table 6). Phyllody disease is the most serious concern for sesame growth and yield reduction. Wang et al. (2015) reported that sesame *LEUCINE-RICH REPEAT* (*SiLRR*), *DOMAIN OF UNKNOWN FUNCTION*

358 (*SiDUF538*), and *GLUTATHIONE S-TRANSFERASE CLASS PHI* (*SiGSTF9*) genes show defence response against phyllody. Primarily, these genes activate antioxidant defence in response to biotic stress. They also reported *SiLRR* was associated with charcoal rot defence response in sesame. Yan et al. (2021) compared charcoal rot susceptible and tolerant sesame varieties and reported that *LEUCINE-RICH REPEAT RECEPTOR-LIKE KINASE* (*SiLRR-RLK*) is the most important gene for charcoal rot tolerance. A recent study emphasised the roles of cell wall-related genes (*SiCS13* and *SiLXR3*), phenylpropanoid pathway genes (*SiCCR*, *SiCAD5*, and *SiCOMT*), and hydrolases (*SiBX4*) in sesame charcoal rot tolerance. These genes can strengthen the cell walls of sesame to improve the physical barrier against the rot-causing fungus. In addition, the phenylpropanoid pathway-synthesised secondary metabolites provide antioxidant resistance to the fungus (Najar and Gangopadhyay 2024). Other comparative transcriptomic analyses between susceptible and tolerant sesame *Fusarium* wilt varieties uncovered the importance of *PHENYLALANINE AMMONIA LYASE* (*SiPAL*), *DIRIGENT* (*SiDIR*), *PEROXIDASE* (*SiPOD*), and *RECEPTOR-LIKE KINASE1* (*SiRLK1*) genes in disease resistance. *SiPAL* and *SiDIR* genes encode rate-determining enzymes of the phenylpropanoid pathway leading to the biosynthesis of non-enzymatic antioxidants such as lignin and lignan. *SiPOD*-encoded peroxidases are antioxidants and important components of plant biotic defence systems. *SiRLK1* encodes a lectin/receptor-like protein kinase that plays diverse roles in plant physiological processes and immunity against biotic stresses (Wei et al. 2016a; Duan et al. 2024). Asekova et al. (2021) identified a phytophthora blight-resistant NBS-LRR protein-coding sesame gene, *SIN_1019016*.

Gene regulatory elements of sesame have a wide impact on yield improvement

Transcription factors (TFs) and microRNAs (miRNAs) are central regulators of multiple fundamental biological processes. Since TFs often regulate more than one gene, modulation of TF-encoding genes could have a widespread effect. Therefore, TFs are good candidates for genetic engineering, and manipulation of TF gene expression has been reported to improve desired traits in many crop species (Baillo et al. 2019). The miRNAs are transcription regulators that can impact the gene expression of various traits, TFs, and other miRNAs. TFs and miRNAs control multiple sets of densely interconnected genes, resulting in a wider impact on the global gene expression pool (Agarwal et al. 2014). Researchers have identified a few candidate TFs and miRNAs in the last decade whose gene manipulation could profoundly improve sesame yield.

Morphology-related TFs

A few sesame TFs have been detected to be responsible for improved morphology-mediated yield increase (Table 7). The whole-genome sequencing of sesame uncovered the association of *WRINKLED1* (*SiWRI1*) TF with oil content (Wei et al. 2016b). The *WRI1* TF is known for lipid biosynthesis and transfer to seeds; it can regulate seed oil content (Deng et al. 2019). The *SQUAMOSA PROMOTER BINDING PROTEINS* (*SBPs*) are plant-specific TFs that control multiple growth and developmental pathways (Zhou et al. 2018a, b). In sesame, two *SiSBP* TFs (SIN_1013913 and SIN_1013914) have been identified, which control male sterility-related genes (Liu et al. 2018). Dutta et al. (2022) identified *GATA 18-LIKE90*, *ZINC FINGER PROTEIN*, *WRKY*, *PIF1*, and *ASIL2* TFs to control seed coat colour linked to oil content and yield. The *HECATE* (*HEC*) TF belongs to the VIIIb subfamily of the bHLH transcription factor family. *HEC* controls female reproductive organ development in plants. However, *SiHEC3* was found to be associated with the capsule-shattering trait of sesame (Ju et al. 2024).

Abiotic stress-related TFs

Several recently identified sesame TFs regulate different morpho-physiological responses, including abiotic stress tolerance (Table 7). Using genome-wide analysis, Dossa et al. (2016a) identified 40 *HEAT SHOCK TRANSCRIPTION FACTOR* (*SiHsf*) genes in sesame that play pivotal roles in drought tolerance. The *APETALA2/ETHYLENE RESPONSIVE FACTOR* (*AP2/ERF*) is one of the largest TF superfamilies. Under abiotic stress conditions, *AP2/ERF* activate stress-responsive genes and are involved in hormone-mediated abiotic stress responses (Ma et al. 2024). In a comparative genomic study between sesame, *Arabidopsis*, potato, and tomato, three drought-responsive (*SiAP2/ERF*) TF genes were identified in sesame (Dossa et al. 2016b). The *AP2/ERF* superfamily consists of *APETALA2* (*AP2*), *DEHYDRATION-RESPONSIVE-ELEMENT-BINDING* (*DREB*), *RELATED TO ABI3/VP* (*RAV*), *ETHYLENE-RESPONSIVE-ELEMENT-BINDING-FACTOR* (*ERF*), and other proteins (Soloist) subfamilies (Dossa et al. 2016d). Later studies identified three members of the *AP2/ERF* superfamily, *SiAP2si16*, *SiDREB-A1*, and *SiDREB-A6*, as candidate genes for drought tolerance in sesame (Dossa et al. 2016c). The seed-specific *ABSCISIC ACID-INSENSITIVE 4* (*SiABI4*) TF is an *Arabidopsis* homolog of *AtABI4* and is known to be involved in ABA signalling under drought conditions (Dossa et al. 2019a). Li et al. (2018) found that *SiDREB* TFs were associated with drought and salt stress response. The *SiERF* TFs, especially *SiERF5* and *SiERF RAP 2–7*, respond to drought, waterlogging, and osmotic stresses in sesame (Dossa 2019b; Wang et al. 2021; Su et al.

2022a; Shah et al. 2024). The *WRKY*, *MYB*, and *NAC* family TFs are well known for their diverse functions in plants. They also respond under various abiotic stress conditions in many crop species (Li et al. 2017; Mmadi et al. 2017). Two separate genome-wide analyses revealed 71 and 287 *SiWRKY* and *SiMYB* genes in sesame, respectively. Drought and waterlogging stresses deregulated the mostly identified *SiWRKY* and *SiMYB* TFs (Li et al. 2017; Mmadi et al. 2017). In a separate study, two *WRKY* family members, *SiWRKY69* and *SiWRKY14*, were identified as drought- and salt-stress-responsive TFs, respectively (Li et al. 2018). Dossa et al. (2020) reported *SiMYB75* as a drought- and salt-responsive TF. The *SiNAC* TFs, particularly *SiNAC43* and *SiNAC104*, were found to be associated with drought, salt, waterlogging, osmotic, and cold stress tolerances (Li et al. 2018; Zhang et al. 2018b; Dossa et al. 2019b). The *GROWTH-REGULATING FACTOR* (*GRF*) is a plant-specific multigene TF family that plays important roles in growth and development by regulating hormone signalling and metabolism. Li et al. (2018) reported that *SiGRF5* is associated with drought stress response in sesame. The bZIP TFs play crucial roles in various plant morpho-physiological processes and stress responses. By genome-wide analysis, Wang et al. (2018) identified 63 *SibZIP* genes in sesame; most of them were drought, salt, waterlogging, osmotic, and cold stress-responsive. The *HOMEODOMAIN-LEUCINE ZIPPER* (*HD-ZIP*), *TRIHILIX* (*TH*), and *SHI-RELATED SEQUENCE* (*SRS*) are well-characterised plant-specific TF families that regulate various plant growth, development, and stress response genes. The *HD-ZIP* TFs also influence other stress-responsive TF gene expressions. Genome-wide analyses revealed many abiotic stress-responsive candidate *SiHD-ZIP*, *SiTH*, and *SiSRS* TF genes in sesame. Among the 61 identified *SiHD-ZIP* genes, gene expression analysis depicted the significant association of *SiHZ7* and *SiHZ35* with drought stress response (Mehmood et al. 2022). A total of 34 *SiTH* genes were identified so far, and among them, significant deregulations in *SiTH4*, *SiTH34*, *SiTH17*, and *SiTH21* genes were reported under drought, salt, and cold stresses (Zhao et al. 2023). In a recent study, five *SiSRS* genes were identified in sesame; they responded well under drought and salinity stresses (Susmi et al. 2024).

Biotic stress-related TFs

Recent investigations on susceptible and resistant varieties using comparative transcriptomics divulged a few biotic stress-responsive TFs in sesame (Table 7). Jia et al. (2024) identified candidate *NAC* (*LOC105159455*, *LOC105159980*, *LOC105167649*, *LOC105175173*) and *WRKY* (*LOC105167193*, *LOC105175676*, *LOC105176853*, *LOC105177346*) TFs that confer tolerance to *Corynespora* leaf spot disease. *SibHLH*, *SibZIP*, *SiMYB*, *SiNAC*, and

Table 7 Potential sesame transcription factors (TFs) and microRNAs related to sesame yield that control genes for morphological traits, capsule indehiscence, and (a)biotic stress tolerance

Gene	Trait	References
Morphology TFs		
<i>SiWRI1</i>	Oil content	Wei et al. 2016b
SIN_1013913 and SIN_1013914	Male sterility. Heterosis-mediated yield improvement	Liu et al. 2018
<i>GATA 18-like90</i> , <i>Zinc finger protein</i> , <i>WRKY</i> , <i>PIF1</i> , and <i>ASIL2</i>	Seed coat colour-related oil content	Dutta et al. 2022
<i>SiNAC1</i>	Oil content	Miao et al. 2024
Capsule indehiscence TFs		
<i>SiHEC3</i>	Shattering resistance	Ju et al. 2024
Abiotic stress tolerance TFs		
<i>SiHsf</i>	Drought tolerance	Dossa et al. 2016a
<i>SiAP2/ERF</i>	Drought tolerance	Dossa et al. 2016b
<i>SiAP2si16</i>	Drought tolerance	Dossa et al. 2016c
<i>SiDREB-A1</i> and <i>SiDREB-A6</i>	Drought tolerance	Dossa et al. 2016c
<i>SiWRKY</i>	Drought and waterlogging tolerances	Li et al. 2017
<i>SiMYB</i>	Drought and waterlogging tolerances	Mmadi et al. 2017
<i>SiWRKY69</i> (SIN_1019661) and <i>SiGRF5</i> (SIN_1024695)	Drought tolerance	Li et al. 2018
<i>SiWRKY14</i> (SIN_1006749) and <i>SiNAC43</i> (SIN_1018616)	Salt tolerance	Li et al. 2018
<i>SiDREB</i> (SIN_1009337)	Drought and salt tolerances	Li et al. 2018
<i>SibZIP</i>	Drought, salt, waterlogging, osmotic, and cold tolerances	Wang et al. 2018
<i>SiNAC</i>	Drought, salt, waterlogging, osmotic, and cold tolerances	Zhang et al. 2018b
<i>SiABI4</i> (SIN_1012139)	Drought tolerance	Dossa et al. 2019a
<i>SiERF5</i> (SIN_1005239) and <i>SiNAC104</i> (SIN_1026079)	Drought, waterlogging, and osmotic tolerances	Dossa et al. 2019b
<i>SiMYB75</i> (SIN_1015311)	Drought and salt tolerances	Dossa et al. 2020
<i>SiERF</i> and <i>SiWRKY</i>	Waterlogging tolerance	Wang et al. 2021
<i>SiHZ7</i> and <i>SiHZ35</i>	Drought tolerance	Mehmood et al. 2022
<i>SiERF</i>	Drought and waterlogging tolerances	Su et al. 2022a
<i>SiTH</i>	Drought, salt, and cold tolerances	Zhao et al. 2023
<i>SiERF RAP 2–7</i>	Waterlogging tolerance	Shah et al. 2024
<i>SiSRS</i>	Drought and salt tolerances	Susmi et al. 2024
Biotic stress tolerance TFs		
<i>SibHLH</i> , <i>SibZIP</i> , <i>SiMYB</i> , <i>SiNAC</i> , and <i>SiWRKY</i>	Charcoal rot tolerance	Radadiya et al. 2021; Yan et al. 2021
<i>LOC105159455</i> , <i>LOC105159980</i> , <i>LOC105167193</i> , <i>LOC105167649</i> , <i>LOC105175173</i> , <i>LOC105175676</i> , <i>LOC105176853</i> , and <i>LOC105177346</i>	<i>Corynespora</i> leaf spot tolerance	Jia et al. 2024
MicroRNAs		
miR156, miR157, miR396, miR529, miR5658, miR8030, and miR8138	Morphology and (a)biotic stress response	Joshi and Mandavia 2018
miR447 and miR8140	Morphology and (a)biotic stress response	Marakli 2018
miR156, miR159, miR164, miR166, miR319, miR395, miR396, miR408, novel_32, novel_53, and novel_62	Salt tolerance	Zhang et al. 2020
miR171, miR319, and miR530	Drought tolerance	Bagheri et al. 2022

SiWRKY were found to be associated with charcoal rot resistance in sesame (Radadiya et al. 2021; Yan et al. 2021).

Yield improving miRNAs

Very few yield-related miRNAs have been identified in sesame so far (Table 7). In an in-silico analysis of sesame 44,905 expressed sequence tags (ESTs), Joshi and Mandavia (2018) predicted 12 members of miR156, miR157, miR396, miR529, miR5658, miR8030, and miR8138 miRNA families. Targets of these miRNAs encompass expressions of cationic amino acid transporter, argonaute protein, F-box protein, heat shock proteins, nucleotide binding site leucine-rich repeat (NBS-LRR) proteins, and TPX2 micro-tubule binding protein genes and *bHLH*, *bZIP*, *HD-ZIP*, *SBP*, and *WRKY* TFs. These genes and TFs regulate several biological processes and stress adaptation of sesame. Marakli (2018) identified two novel miRNAs of sesame, miR447 and miR8140, by BLAST search of the sesame EST database. These miRNAs regulate genes of the (a)biotic stress response, cell division, organ growth and development (particularly leaf development), protein and lipid transporters, hormone signalling, and TFs of sesame. Zhang et al. (2020) compared two accessions of sesame with contrasting salinity tolerance and identified known salinity stress-responsive members of miRNA families such as miR156, miR159, miR164, miR166, miR319, miR395, miR396, and miR408 along with some novel miRNAs such as novel_32, novel_53, and novel_62. Another study compared two sesame varieties with contrasting drought tolerance and identified three drought-responsive miRNAs, miR171, miR319, and miR530. MiR319 decreases leaf senescence by downregulating *NAC29L* TF. MiR171 regulates *NAC29L* and *SUC2L* TFs to regulate sucrose transport and accumulation. MiR530 regulates two TFs, *TGA1* and *CER1*, that synthesise cuticular wax. These three cumulative factors contribute to drought tolerance in sesame (Bagheri et al. 2022).

Molecular-genomic breeding technology has the potential for sesame yield improvement

Sesame yield improvement-related QTLs can help in marker-assisted breeding

DNA markers and QTL mapping are indispensable tools in marker-assisted breeding (MAB). DNA markers often define useful traits in the genome of an organism. They are used in marker-assisted selection where germplasms bearing desired traits are identified and used in subsequent breeding programmes. A quantitative trait locus (QTL) is a region of the genome harbouring genes for a particular quantitative

trait. QTL mapping that involves a genomic linkage map construction with the DNA markers associated with a trait and subsequent statistical analysis of the map can precisely identify QTLs linked with the trait of interest. Further analysis of QTLs can reveal candidate genes for the trait. MAB has several advantages over conventional breeding techniques—(1) marker analysis can pinpoint desired traits at the seedling stage, (2) polygenic traits are easily selected through QTLs, (3) traits linked with recessive alleles can be selected, (4) since MAB relies on genomic screening, environmental impact on a trait is excluded in the screening process, and (5) techniques used in MAB are time- and effort-saving (Lamichhane and Thapa 2022). Before sesame whole-genome sequencing, molecular marker-derived quantitative trait loci (QTLs) identification was a feasible way to improve this crop. These markers and QTLs can be promisingly used in MAB programmes for sesame yield improvement. Recent progress in sesame molecular marker analysis-related studies identified various QTLs advancing this crop improvement methodology further.

Morphology-related QTLs

In a comprehensive study, Wu et al. (2014) performed restriction-site associated DNA sequencing (RAD-seq) of a recombinant inbred line (RIL) population to construct a simple sequence repeat (SSR), expressed sequence tag-simple sequence repeat (EST-SSR), insertion–deletion (InDel), and single-nucleotide polymorphism (SNP) marker-derived linkage map and identified QTLs linked to several morphologic traits. Among their identified QTLs, *Qph-12*, *Qcl-12*, *Qcal-9*, and *Qfch-12* explained the variations in the plant height (9.1%), length of capsule (75.6%), length of capsule axis (9.2%), and height of the first capsule (11.5%), respectively. In a similar study, Mei et al. (2017b) found that *qFCT9.1*, *qFCL11.1*, *qFCW9.1*, *qMCL13.1*, and *qMCW9.1* QTLs are linked with capsule size. Further studies depicted that the *Qcn-11* and *Hs345* loci are linked with the variation of capsule number per plant; *Qgn-6* and *Hs635* loci explain seed number per capsule variation phenotype (Wu et al. 2014; Wang et al. 2024). Specific length amplified fragment sequencing (SLAF-seq)-mediated high-density genetic map analysis revealed that *qsp11* and *qSL-LG3-2* explain 13.97% and 13.52% variation of seed size and shape, respectively (Du et al. 2019; Mei et al. 2023). Moreover, *qtsw12* and *Qtgw-11* explain 19.53% and 12.3% variations of thousand seed weight, respectively (Table 8) (Wu et al. 2014; Du et al. 2019).

Oil content-related QTLs

Zhang et al. (2013b) used amplified fragment length polymorphism (AFLP), simple sequence repeat (SSR), and

Table 8 Potential sesame quantitative trait loci (QTLs) related to sesame yield that control genes for morphological traits

QTL	Trait	Marker	References
Qcal-5, and Qcal-9	Length of capsule axis	EST-SSR, InDel, SNP, SSR	Wu et al. 2014
Qcl-3, Qcl-4, Qcl-7, Qcl-8, and Qcl-12	Length of capsule	EST-SSR, InDel, SNP, SSR	Wu et al. 2014
Qcn-11	Capsule number per plant	EST-SSR, InDel, SNP, SSR	Wu et al. 2014
Qfch-4, Qfch-11, and Qfch-12	Height of the first capsule	EST-SSR, InDel, SNP, SSR	Wu et al. 2014
Qgn-1, Qgn-6, and Qgn-12	Seed number per capsule	EST-SSR, InDel, SNP, SSR	Wu et al. 2014
Qph-6, and Qph-12	Plant height	EST-SSR, InDel, SNP, SSR	Wu et al. 2014
Qtgw-11	Thousand seed weight	EST-SSR, InDel, SNP, SSR	Wu et al. 2014
qPH-8.2, and qPH-3.3	Plant height	SNP	Wang et al. 2016b
qFCT9.1, qFCL11.1, qFCW9.1, qMCL13.1, qMCW9.1,	Capsule size	CIM	Mei et al. 2017b
ql/w1, qsa1, qsa11, qsc2, qsd5, qsd11, qsl11, qsp11, qsw1, qsw5, and qsw11	Seed size	SLAF	Du et al. 2019
qtsw4, qtsw9, and qtsw12	Thousand seed weight		Du et al. 2019
qSL-LG3-2, qSL-LG5, and qSL-LG6-2	Seed size and shape	SLAF	Mei et al. 2023
Hs345	Capsule number per plant	SSR	Wang et al. 2024
Hs618	Initial flowering stage	SSR	Wang et al. 2024
Hs635	Seed number per capsule	SSR	Wang et al. 2024

CIM Composite interval mapping, *EST-SSR* expressed sequence tag-simple sequence repeat, *InDel* insertion–deletion marker, *SLAF* specific length amplified fragment sequencing, *SNP* single-nucleotide polymorphism, *SSR* simple sequence repeat

random selective amplification of microsatellite polymorphic loci (RSAMPL) markers to create a high-density linkage map of sesame and, for the first time, identified QTLs linked to seed coat colour. Their identified QTLs, QTL1-1, QTL11-1, QTL11-2, and QTL13-1 explain respective 39.95%, 20.61%, 24.02%, and 30.56% phenotypic variations for the trait. Wang et al. (2016b) used RAD-seq to generate a SNP-mediated genetic Map of sesame using 430 RILs and their two parental lines. They identified qSCa-8.2 and qSCb-4.1 as two Major QTLs with their 46% and 39% respective contributions to seed coat colour. Du et al. (2019) used SLAF-seq to generate a high-density genetic Map and identified 14 QTLs spanning seven regions of three linkage groups (LGs). Among the identified QTLs, qscY9, qscZ9, and qscb*4 explained the maximum contributions (33.25%, 32.88%, and 23.10%, respectively) to the trait. AFLP, sequence-related amplified polymorphism (SRAP), and SSR marker-driven association mapping analysis unearthed sesame oil content-influencing QTLs, among which both Hs345 and Hs4381 have the highest (29%) contribution to the trait (Wei et al. 2013; Li et al. 2014). Another study identified five oil content-specific QTLs by multiple interval mapping (MIM) and reported that Qoc-1 and Qoc-9 explained the phenotypic variation most (10.1% and 8.6%, respectively) (Table 9) (Kun et al. 2017).

Capsule indehiscence-related QTLs

Uzun et al. (2003) identified one 258-nucleotide AFLP marker associated with the *closed capsule* mutation trait.

The *closed capsule* mutation develops the capsule indehiscent trait. This marker can detect capsule indehiscent-type sesame genotypes using a simple PCR-mediated approach. Further study revealed two inter-simple sequence repeat (ISSR) markers of the sesame *dt* gene contributing to the determinate growth phenotype (Uzun and Çağırgan 2009). In another study, a sequence-characterised amplified region (SCAR) marker Si-SR-32-19 was developed using bulk segregant analysis and AFLP, which could discriminate between shattering-susceptible and shattering-resistant phenotypes (Phumichai et al. 2017). Genomic mapping of sesame revealed capsule shattering-related SNP/InDel marker S8_5062843 and cleaved amplified polymorphic sequence (CAPS) marker S8_4476867 (Yol et al. 2021). More efforts are needed in marker analysis to identify QTLs linked with capsule indehiscence.

Abiotic and biotic stress-related QTLs

Yan-xin et al. (2014) analysed a RIL population created with waterlogging-sensitive Zhongzhi No.13 and waterlogging-sensitive Yiyangbai varieties of sesame to create a linkage map using AFLP, EST-SSR, SRAP, and SSR markers. They identified six QTLs linked to waterlogging tolerance, among which qWH10CHL09 explained 17.19% phenotypic variation with this trait. They also reported that the ZM428 is a potential SSR marker for marker-assisted breeding of waterlogging tolerance. Liang et al. (2021) re-sequenced the members of a RIL population obtained from two sesame cultivars, Jinhuangma and Zhushanbai, having contrasting

Table 9 Potential sesame quantitative trait loci (QTLs) related to sesame yield that control genes for seed oil content, abiotic, and biotic stress tolerance

QTL	Trait	Marker	References
Oil content			
QTL1-1, QTL11-1, QTL11-2, and QTL13-1	Seed coat colour-related oil content	AFLP, SSR, RSAMPL	Zhang et al. 2013b
E6M9-4, M4E17-7, M9E8-2, M14E2-19, M14E7-2, and M17E10-7	Oil content	AFLP, SRAP, SSR	Wei et al. 2013
Hs02, Hs205, Hs345, Hs376, Hs377, Hs393, Hs485, Hs586, Hs618, Hs635, Hs672, Hs1036, Hs1638, Hs1956, Hs4061, Hs4082, Hs4209, Hs4381, and Y2129	Oil content	SSR	Li et al. 2014
Qoc-1, Qoc-2, Qoc-5, Qoc-9, and Qoc-16	Oil content	MIM	Kun et al. 2017
qscca*4, qscca4-1, qscca4-2, qscca*9, qsccb*4, qsccb4, qsccL*4, qsccL4, qsccX4, qsccY4, qsccY9, qsccZ9, and qsccZ12	Seed coat colour-related oil content	SLAF	Du et al. 2019
Abiotic stress tolerance			
qEZ09ZCL13, qWH09CHL15, qEZ10ZCL07, qWH10ZCL09, qEZ10CHL07, and qWH10CHL09	Waterlogging tolerance	AFLP, EST-SSR, SRAP, SSR	Yan-xin et al. 2014
qRSL1-2, qRRL1, qRRL7, qRRL12, and qRLP12	Drought tolerance	InDel, SNP	Liang et al. 2021
qLignan1-1, qLignan6-1, and qLignan11-1	Salt tolerance	CAPS, InDel, KASP, SNP	Kim et al. 2023
Biotic stress tolerance			
qCRR3.1, qCRR3.2, qCRR3.3, qCRR3.4, qCRR5.1, qCRR8.1, qCRR8.2, qCRR8.3, qCRR9.1, qCRR12.1, qCRR12.2, qCRR12.3, qCRR13.1, qCRR13.2	Charcoal rot tolerance	SSR	Wang et al. 2017

AFLP Amplified fragment length polymorphism, *CAPS* cleaved amplified polymorphic sequences, *EST-SSR* expressed sequence tag-simple sequence repeat, *InDel* insertion–deletion marker, *KASP* kompetitive allele-specific PCR, *MIM* multiple interval mapping, *RSAMPL* random selective amplification of microsatellite polymorphic loci, *SLAF* specific length amplified fragment sequencing, *SNP* single-nucleotide polymorphism, *SRAP* sequence-related amplified polymorphism, *SSR* simple sequence repeat

drought tolerances, performed linkage mapping with SNP/InDel Markers, and identified 13 QTLs that are linked with drought-responsive phenotypes. Among them, qRSL1-2 explained a 9.48% variation in relative shoot length, and qRRL1, qRRL7, qRRL12, and qRLP12 explained respective 6.56%, 10.26%, and 11.85% variations in relative root length under drought stress. Kim et al. (2023) performed genetic analyses of F7 RIL populations deduced from Goenbaek and Gomazou as respective low and high lignan content variants. Using QTL-seq, they identified three QTLs (qLignan1-1, qLignan6-1, and qLignan11-1) associated with lignan biosynthesis. Ražná et al. (2021) depicted the role of lignans in salt stress mitigation. Therefore, these lignan-related QTLs could be useful for sesame salt tolerance. Wang et al. (2017) used a RIL population of 548 lines generated from ZZM2748 (charcoal rot susceptible) and Zhongzhi No. 13 (charcoal rot tolerant) to construct an SSR Marker-based Linkage Map and identified 14 QTLs linked with charcoal rot tolerance using SSR markers. Among the identified QTLs, qCRR12.2 had the highest (14.16%) contribution to the trait (Table 9). A comparative transcriptomic analysis between cultivated and wild (*Sesamum malayanum*) revealed 26,880 SSR, 90,181 SNP, and 25,063 InDel Markers and 22,494 SSR primer pairs related to charcoal rot tolerance

(Dutta et al. 2020). RAPD primers A05, C07, and O16 can potentially differentiate sesame varieties resistant to *Macrophomina phaseolina* infection (Omara et al. 2020). Two ISSR and five RAPD primers were developed to differentiate varieties with high yield and resistance to Fusarium wilt (Anter and Ghada 2021).

High-throughput genomic marker analysis has the potential to identify desired yield improvement-related QTLs. Wild sesame relatives are reservoirs of several key agronomic traits, including yield improvement (Yadav et al. 2022). Therefore, genomic marker and QTL analyses can identify potential sesame germplasms that can be utilised in subsequent breeding programmes. Moreover, QTL analysis can reveal candidate genes for a desired trait. Such identified yield-related genes could improve sesame yield by manipulative approaches. Therefore, marker and QTL analyses are necessary for sesame yield improvement programmes.

Molecular heterosis is a novel approach for sesame yield improvement

Crop improvement is possible by integrating conventional breeding programmes with biotechnological methods, especially gene manipulation approaches to express

a desired trait (Debnath et al. 2014; Teklu et al. 2022). Molecular markers can identify valuable agronomic traits of sesame germplasms, benefiting the breeding programme. However, limited breeding efforts have been applied to improve this useful crop (Qureshi et al. 2022). Moreover, conventional breeding is a slow process, and the desired traits are not always available in cultivated sesame lines (Debnath et al. 2014). As an alternative approach, heterosis breeding has been applied for years to improve the plant species, including sesame. Several reports on sesame show positive heterosis for plant height, number of branches, number of pods per plant, number of pods in the main stem, number of pods in branches, and number of seeds per capsule (Ragiba and Reddy 2000; Mothilal and Ganesan 2005; Yadav et al. 2005; Khan et al. 2009; Prajapati et al. 2009; Shobha Rani et al. 2015; Virani et al. 2017; Ismail et al. 2020; Kumar et al. 2022). Heterosis exploitation for commercial purposes is challenging in sesame because hand emasculation and pollination techniques are labour-intensive (Yermanos and Osman 1981; Prabakaran 1998). Male sterile and restorer lines can be used in breeding techniques to resolve this issue since *Sesamum indicum* is predominantly a self-pollinating crop (Mariani et al. 1990; Carlsson et al. 2008). Male sterility in sesame was first reported by Roy (1931). A wild variety of sesame, *S. malabaricum*, is believed to be involved in the transfer of male sterility in *S. indicum* during heterosis (Prabakaran et al. 1995; Kavitha and Ramalingam et al. 1999). However, the primary constraint is the availability of male sterile, restorer, and maintainer lines, essential for the hybrid vigour exploitation (Mariani et al. 1990). Silencing the anther-specific gene(s) that inhibit pollen production could be an alternative approach to achieving genetically induced male sterility (Nawaz-ul-Rehman et al. 2008). This approach of “molecular heterosis” involving gene-manipulated male sterile lines has been widely used to develop transgenic male sterile lines in *Brassica*, *Arabidopsis*, tobacco, rice, maize, and wheat as well as in various other plants (Kultunow et al. 1990; Mariani et al. 1990; Hernould et al. 1993; Rong et al. 1996; Burgess et al. 2002; Tehseen et al. 2010; Jing et al. 2012; Rao et al. 2017; Wan et al. 2019; Singh et al. 2021). However, there is no report to induce male sterility through genetic engineering in sesame to date. Manipulation of sesame recessive genic male sterility genes *SiMs1* and *SiMs2* could induce male sterility (Lichuan et al. 1995; Zhao et al. 2013). Liu et al. (2018) also identified 16 sesame recessive genic male sterility genes. The tapetum-specific promoter gene *SiBGproplus* could be utilised to express cytotoxicity in anther tissue. This approach will selectively inactivate the sesame androecium, leading to male sterility (Parveen et al. 2018; Debnath et al. 2025). However, many efforts are needed to identify more potential genes related to male

sterility and subsequent successful induction of genetic male sterility using gene manipulation tools in sesame.

Gene manipulation studies in sesame to date are not adequate for yield improvement

Sesame yield improvement is crucial on the verge of the United Nations-predicted upcoming food scarcity (United Nations 2009; Da Silva 2012). Due to the impracticality of the conventional breeding technology, biotechnological methods involving transgenesis-mediated gene manipulative approaches to express a desired trait are critically important in this demanding situation (Debnath et al. 2014; Teklu et al. 2022). Manipulation of yield-related genes can directly improve the production of sesame. Improvements in abiotic and biotic stress defence by gene manipulation can make a plant healthy, extend its life, and improve its yield. Therefore, defence gene manipulation in sesame can also improve production. Except for transformation protocol standardisation, only a handful of gene manipulation reports are available in sesame (Table 10). Among them, the study of Mitsuma et al. (2004) was the first of this kind. They introduced the calmodulin gene that contributes to the sesame defence response. Raja (2012) transformed sesame with *Theobroma cacao* Class I *CHITINASE* gene (*Chi I*) that encodes a cell wall-hydrolysing enzyme chitinase. Transgenic sesame plants harbouring *Chi I* showed resistance against the *Cercospora sesami* leaf spot disease. Overexpression of *OSMOTIN-LIKE PROTEIN (OLP)* in the transgenic sesame line enhanced the expression of several defence response genes, conferring multiple stress tolerance against *Macrophomina phaseolina* infection, salinity, and drought conditions (Chowdhury et al. 2017). Parveen et al. (2018) identified the promoter region (GN13) of the sesame β -1,3-glucanase gene. Using transgenesis, Debnath et al. (2025) demonstrated sesame tapetum-specific expression of GN13 and TA29, a well-known tobacco tapetum-specific promoter (Mariani et al. 1990). This finding can be utilised to create anther-specific cytotoxicity leading to a male sterile sesame line to be used in heterosis-derived yield improvement programmes. Fatty acid synthesis-related gene manipulation could also improve sesame oil yield (Muthulakshmi et al. 2021). In a recent report, Shetty et al. (2023) carried out the heterologous expression of a *Sorghum bicolor* L. TF, *SbAP37 (SbAPETALA37)*, in sesame and observed improved tolerance against experimental salinity stress.

Sesame is the largest reservoir of lignans among crops. Sesame-specific sesamin and sesamolin are major lignans of it. Lignans primarily act as antioxidants and exert numerous health benefits such as anti-ageing, anti-cancer, anti-diabetic, anti-inflammatory, analgesic, cardioprotective,

Table 10 Reports of functional gene delivery using transformation in sesame

Explant	Transformation method	Transformation frequency	Transformed gene	Gene function	References
Seedling shoot	Conventional <i>Agrobacterium</i> -mediated transformation	–	<i>CAM-4</i> (Calmodulin)	Secondary metabolite biosynthesis-mediated defence	Mitsuma et al. 2004
Hairy roots	<i>Agrobacterium rhizogenes</i> -mediated transformation	50–60%	<i>PHYTASE</i>	Feed supplement	Jin et al. 2005
Apical shoot tip	Conventional <i>Agrobacterium</i> -mediated transformation	1.12%	<i>Chi I</i> (Chitinase)	Protection against phytopathogenic fungus	Raja 2012
Cotyledon (de-embryonated)	Conventional <i>Agrobacterium</i> -mediated transformation	–	<i>OLP</i> (Osmotin-like proteins)	Drought, salinity, and root rot tolerance	Chowdhury et al. 2017
Cotyledon (de-embryonated)	Conventional <i>Agrobacterium</i> -mediated transformation	23.1%	<i>DGAT1</i> , <i>PDAT1</i> , <i>FAD3</i> , and <i>Cyt b5</i>	Oil content increase	Muthulakshmi et al. 2021
Hairy root	Conventional <i>Agrobacterium</i> -mediated transformation	–	CRISPR-Cas9-edited <i>CYP81Q1</i> and <i>CYP92B14</i>	Sesamin and sesamol biosynthesis	You et al. 2022
Cotyledon (de-embryonated)	Conventional <i>Agrobacterium</i> -mediated transformation	–	<i>SbAPETALA37</i>	Salt stress tolerance	Shetty et al. 2023
Cotyledon (de-embryonated)	Conventional <i>Agrobacterium</i> -mediated transformation	1.71%	<i>GN13</i>	β -1,3 Glucanase gene promoter	Debnath et al. 2025

“–” indicates that no information is available

hepatoprotective, neuroprotective, and wound healing properties towards humans and other animals. Lignans are an important antioxidant system component that protects plants from various (a)biotic stresses. Therefore, modulation of lignan biosynthesising genes can improve the stress tolerance of sesame (Andargie et al. 2021; Ražná et al. 2021). The cytochrome P450 (CYP450) and dirigent (DIR) proteins are key enzymes for biosynthesising several sesame lignans such as sesamin and sesamol. The *CYP450* and one of its family members, *SiCYP76C7*, have been identified in sesame that are associated with drought and salt tolerances in sesame (Li et al. 2018; Dossa et al. 2017b, 2019a). The *SiDIR* has been found to control Fusarium wilt tolerance in sesame (Miao et al. 2024). Research regarding genome editing of sesame is in its infancy. In a recent report, You et al. (2022) introduced CRISPR-Cas9 system-mediated targeted insertion–deletion (InDel) mutagenesis to generate two CYP450 knockdown lines, *CYP81Q1* and *CYP92B14*, with 90.64% and 93.33% mutation frequencies, respectively. Among the mutant lines, sesamin biosynthesis was improved in *CYP92B14*-knockout lines. Such high sesamin-containing mutants could be useful for stress adaptation studies in sesame.

The potential of genome editing for crop improvement has been proven in many studies. CRISPR-edited mutated lines for *INDEHISCENT*, *ALCATRAZ*, and

SHATTERPROOF genes in *Brassica napus* (Zhai et al. 2019; Zaman et al. 2021) and *Capsella rubella* (Dong et al. 2019) were less prone to the early capsule-shattering problem. Genome editing of *OsDEP1* and *OsROC5* enhanced heat resistance in rice (Malzahn et al. 2019), *ZmG6PDH1* improved cold resistance in maize (Li et al. 2023), *HvGSK1.1* enhanced salinity tolerance in barley (Kloc et al. 2024), *TaARR12* improved drought resistance in wheat (Li et al. 2024), and *OsNIP3* reduced arsenic accumulation in rice (Xu et al. 2024). Moreover, CRISPR-edited *Solyc08g075770* enhanced Fusarium wilt susceptibility in tomato (Prihatna et al. 2018), *OsSWEET11*, *OsSWEET13* and *OsSWEET14* promoters enhanced broad-spectrum bacterial blight resistance in rice (Oliva et al. 2019; Xu et al. 2019), *VvMOL3* enhanced powdery mildew resistance in grapevine (Wan et al. 2020), and *SIDMR6-1* improved bacterial speck, Phytophthora blight and bacterial spot resistance in tomato (Thomazella et al. 2021). Furthermore, *OsGS2/GRF4*, *TaRPK-1*, and *GW2.1* gene editing improved rice (Wang et al. 2022), wheat (Abdul Rahim et al. 2024), and barley (Kis et al. 2024) yield, respectively. Several contemporary review articles summarised the recent advances in crop improvement using genome editing (Li et al. 2022; Rahman et al. 2022; Erdoğan et al. 2023; Kumar et al. 2023; Chen et al. 2024).

However, such genome editing works are completely absent in sesame and are highly needed to improve this crop.

Researchers have put their best effort into sesame gene Manipulation studies in the past 2 decades. However, the outcome is minuscule. Current and future sesame improvement programmes should focus on yield enhancement that could include adaptability to stress factors, the introduction of capsule non-dehiscent trait, amenability to machine harvesting, seed and capsule number increase, and oil content increase by biosynthesis gene manipulation. Such approaches could make the crop industrial application-friendly and satisfy the UN's goal.

Conclusions and future perspectives

Sesame is one of the oldest oilseed crops in the world. Despite its wide cultivation area in tropical and subtropical regions, its yield remained lower than that of other oilseed crops. The low yield of sesame is the primary reason hindering its successful commercialisation. Besides low oil yield, the major problems associated with this crop are early pod shattering and susceptibility to various abiotic and biotic stress factors. Modern biotechnological tools could plausibly improve this crop. Targeted trait improvement using the molecular-genetic approaches of gene manipulation could be a potential way to solve these problems. Many researchers are identifying key genes and QTLs for various pathways to improve this crop. However, a few knowledge caveats, such as discovering a proper genetic basis for important phenotypic traits like capsule shattering, remain. Moreover, detailed studies on host–pathogen interactions of sesame could reveal more genetic backgrounds of its biotic stress susceptibility. The wide availability of marker profiles facilitates the MAB programmes of sesame yield improvement. However, much more effort is needed to exploit molecular heterosis in sesame. The unavailability of a universally working, suitable regeneration and transformation system, a prerequisite for gene manipulation studies, is a major bottleneck for applying biotechnological trait improvement studies. Besides conventional *Agrobacterium*-mediated transformation techniques, more research on alternative transformation methods such as SAAT, biolistic, and in-planta transformation can potentially improve transformation strategies in this crop. Cumulatively, all these efforts could pave the way for improving the yield of this important oilseed crop.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11816-025-01014-7>.

Author contributions AJD: conceptualisation; AJD, DE, LH, and MK: writing—original draft preparation; AJD: data curation and formal

analysis; DB and SRS: resources, supervision, and validation; AJD, DE, LH, MK, DB, and SRS: writing—review and editing.

Funding Open access funding provided by The Ministry of Education, Science, Research and Sport of the Slovak Republic in cooperation with Centre for Scientific and Technical Information of the Slovak Republic. Not applicable.

Availability of data and materials The data sets of the current article are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors have declared that no competing interests exist.

Ethical approval and consent to participate Not applicable.

Consent for publication Not applicable.

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