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Improving Sesame Oil Quality: A Review of Metabolic Pathways, Genetic Regulation, and Breeding Strategies

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Citation: Abdulqader, A. A. Improving Sesame Oil Quality: A Review of Metabolic Pathways, Genetic Regulation, and Breeding Strategies. American Journal Of Biodiversity 2026, 3(2), 114-138.

Received: 05th Jan 2026

Revised: 20th Jan 2026

Accepted: 10th Feb 2026

Published: 28th Feb 2026



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Abstract: Seed oil percentage is not the only criterion to evaluate the improvement of sesame oil. The value of a breeding material is determined by the fatty-acid composition, the content of lignans, the content of tocopherols, the production of seeds, as well as their stability when grown under various conditions. These qualities are linked and an improvement in one does not necessarily lead to a similar improvement in the others. The review focuses on the use of genetically and molecular evidences reported in sesame for a more coherent approach to oil quality improvement. It explores how metabolism, variation (natural and induced), associations with the genome, and techniques for selection/modification of desired traits are related. This review focuses especially on evidence for individual targets. A gene identified by developmental expression or association analysis has a lesser level of support than a gene examined by biochemical characterisation, allelic analysis or experimental manipulation. The studies of fatty acid desaturation offer a practical link between sequence variation and oil composition while the studies of sesame lignans provide examples of well-defined enzymatic functions. New technologies such as mapping, transcriptomics, lipidomics and small-RNA studies have expanded the list of candidates to be explored. However, their value in breeding will rely on how those candidates are validated and put into appropriate genetic backgrounds. The evidence supports a coordinated approach integrating conventional breeding, mutagenesis, molecular selection and biotechnology, reflecting the guidance from biochemical phenotyping and evaluation across environments. The development of the materials should be assessed by what can be done with them, not by just the number of molecular discoveries.

Keywords: Sesamum Indicum, Oil Quality, Fatty-Acid Composition, Lignans, Genetic Variation, Molecular Breeding, Functional Validation, Environmental Stability

Introduction

Sesame, *Sesamum indicum* L., has significant importance in the oilseed crop due to the use of its seeds for their oil content and for a variety of other applications. Oleic and linoleic acids make a significant portion of the unsaturated fraction in sesame oil; in addition, other nutrients and functional compounds such as lignans, tocopherols and phytosterols are found in sesame oil. While there are a number of areas of improvement, there are also a number of challenges for the breeder. One genotype with a high seed oil percentage may not have the desired fatty-acid characteristics; and a plant line with very favourable fatty-acid characteristics may not be suitable because of seed output or adaptability.

The improvement objective should, therefore, specify the desired composition and the expected agricultural performance for the maintenance of this. [1]–[4].

There are multiple processes in the biological basis of this challenge. For oil to be stored in the seed, fatty acids need to be synthesized, modified and added to storage lipids. There are other pathways of production of specialized compounds, some more fully characterized than others. The genetic control of these processes is studied in various populations, tissues, and experimental systems, while the processes are coordinated during development. A candidate therefore cannot necessarily be assumed to have a definite metabolic function until the extent of its contribution to the composition of the product is well established. Pathway membership can be a useful piece of evidence for breeding, but is necessarily a more immediate question: what is the effect of a particular allele or intervention? [5]–[7]. With the resources provided by genomic research, we can now look at that question in more detail. The reference genome of sesame, the molecular-marker collections, the linkage maps, the association panels, and the expression datasets have enabled the linkage of variation in seed traits to specific genomic regions.

The biochemical studies have led to elucidation of some aspects of lignan metabolism, and transformation and targeted mutagenesis systems have provided opportunities for experimental testing of the function of genes. The range of questions that could be asked in sesame has been expanded by these developments. They have in addition compelled the necessary distinction between the identification of a possible target, its demonstration of biological effect, and its effective application in breeding programmes. [1], [4], [8], [9]. This review follows that line. It reflects the considerations on how the evidence of metabolic pathways and genetic variance can guide decisions that will enhance sesame oil quality without compromising on yield and adaptation. The topics discussed are related to the fatty acids, lignans and other components in the seeds, conventional selection, induced mutations, genomic discovery, and biotechnology. These areas can be grouped by a common breeding goal for the relationships to be easier to evaluate. It also gives the opportunity to assess the contribution of each method based on the problem it deals with and not on the technical complexity of the method.

Defining Oil Quality as a Breeding Objective

As the properties which make sesame oil better are not all interdependent, they must be determined individually before they can be used together. Seed oil content – the percentage of oil in the seed. Fatty-acid composition refers to the proportions of the different fatty acids contained in that oil. Seed yield refers to the production obtained from the plant, while nutritional composition refers to other compounds like lignans, tocopherols and phytosterols. These measurements don't necessarily have to be correlated in the same direction. A line can exhibit a positive alteration of a fatty-acid profile in the presence of a moderate oil content, or may yield a greater seed yield without a comparable improvement in the content of desired fatty-acids. [6], [10], [11].

These relationships have been well illustrated by conventional selection. Baydar identified some differences among selected types of sesame plants in yield, seed oil content, fatty-acid composition and total tocopherols. Oil content of the QTN type was 49.3% and that of high-yielding BMB type was 43.2%. For all types examined oleic acid ranged from 41.3% to 48.4% and linoleic acid from 36.6% to 43.1%. The results herein indicate that there is scope for agronomic selection to bring about changes in composition, but the direction of change needs to be measured. Different types of plants exhibited the best yields and the highest oil content, neither of which is necessarily the same. [10].

The same caution is advised in setting a fatty-acid goal. The oleic to linoleic acid ratio is the ratio that is informative because both are related by a desaturation reaction. Changes in selection that alters their balance can result in a different oil profile even if the amount of oil is comparable. Genetic studies of FAD2 variation and high oleate mutants demonstrate that this compositional target can be genetically reached. Their results should, however, be kept in relation to the measured phenotype. The higher the oleic acid content, the more the fatty-acid mix has changed; increased oil production claims must be supported by separate measurements of oil content and seed yield. [12], [13].

The quality objective is even more vague due to the presence of special constituents such as lignans. Among the characteristic constituents of sesame products are sesamin, sesamol and related compounds, and tocopherols and phytosterols for other desirable features. It is important to consider combinations not isolated concentrations when including them. There may be other compounds in the

same pathway that are affected by the intervention, and a change in abundance of one may result in a change in abundance of another. The breeder is thus required to be familiar with the profile that will result, how it will be expressed in combination with the major lipid fraction and the agricultural characteristics of the material. [8], [14]–[16].

Therefore, the expression of a practical definition of quality must be in terms of a set of measurements. The percentage of oil, fatty acids, lignans, tocopherols, phytosterols, yield, maturity and response to stress can be assessed in a single programme without losing the meaning of each term. This enables you to determine a helpful blend of characteristics and also to see if one improvement comes with a constraint in another. It additionally helps decide upon the best choice of selection method. If a particular composition and/or performance goal is associated with a well-supported allele, it can be targeted for selection, but if it's associated with a more general goal, it may need to be evaluated at multiple biochemical tests and multiple locations. [4], [17].

Metabolic Foundations of Sesame Oil Improvement

The synthesis of fatty acids takes place from the onset in developing seeds in plastids. In developing seeds, fatty-acid production starts in plastids. Acetyl-CoA carboxylase (ACC) is responsible for converting acetyl-CoA to malonyl-CoA which supplies the carbon source for subsequent chain-extension reactions. The fatty-acid synthase system is a repetitive series of condensation, reduction, dehydration and reduction. These steps are catalysed by four enzymes: ketoacyl-ACP synthases, ketoacyl-ACP reductase, hydroxyacyl-ACP dehydratase and enoyl-ACP reductase to produce predominantly 16- and 18-carbon acyl products. This portion of the pathway is important because it provides a source of precursor/building blocks for subsequent modifications and incorporation into storage lipids. [18].

It is important to note that an important upstream function is not equivalent to full control of the final phenotype of the oil. Once synthesized, fatty acids should be freed from the intermediate of the plastid, exported, activated and utilized in other lipid reactions. This means that they are not available for accumulation unless they are available on the market. Where the machinery at the downstream end can utilize the supply, an increase in that supply can help to lead to the formation of oil. Coordinated changes in genes involved in synthesis, transport, lipid assembly, and storage during seed filling of sesame are developmental evidence of this interpretation. [7], [18].

Those precursors undergo modification in their composition by desaturation. Stearoyl-acyl carrier protein desaturase converts stearoyl-ACP into oleoyl-ACP, and is linked to oleic-acid production. FAD2 is then involved in the conversion of oleic acid to linoleic acid in the endoplasmic-reticulum-associated glycerolipid system. Changes in the mix of fatty acids later to be incorporated into storage oil due to variation in these reactions. In the case of sesame, the reported linkage of FAD2 haplotypes to the oleic/linoleic balance provides a clear link between this metabolic step and a breeding phenotype. [13], [18].

Another aspect of the plant lipid network is provided by phosphatidylcholine. Bates and co. demonstrated that newly synthesized fatty acids could be used for acyl editing in cytosolic glycerolipids in pea leaves. They find that acyl groups can be transported in and out of phosphatidylcholine in the course of lipid metabolism. Here the context of the experiment is important. The study gives a mechanistic reference from pea leaves and the quantitative contribution of the same route to the sesame seed-oil formation requires investigation. The inclusion is useful for providing some possible metabolic linkage but not providing a quantifiable contribution for sesame. [17], [19].

The linkage of the fatty-acid pool and the main storage lipid of the seed is the triacylglycerol assembly. Triacylglycerol assembly is the linking of the fatty-acid pool and the main storage lipid of the seed. The first acylation in the Kennedy pathway is catalysed by glycerol-3-phosphate acyltransferase to produce lysophosphatidic acid. The next acylation takes place by lysophosphatidic acid acyltransferase to produce phosphatidic acid. Dephosphorylation results in the formation of diacylglycerol, which is further acylated to triacylglycerol by diacylglycerol acyltransferase. The sequence makes it easy to see why fat deposition requires more than just fatty-acid synthesis; the fatty acids synthesized must also be packaged into a storage form. [20].

Another pathway is through phospholipid acyltransferase. This enzyme removes an acyl group from a phospholipid and transfers it to diacylglycerol without the need for acyl-CoA for the transfer.

Biochemical work on developing sunflower and safflower seeds and evidence from *Arabidopsis* indicates that there are complementary enzymatic pathways for the synthesis of triacylglycerols in plants. These results provide information to guide investigation of sesame lipid assembly, but not the relative importance of sesame enzymes. Crop-specific evidence must be developed to identify the most beneficial reactions/alleles for improvement. [21]–[23].

Oil-body formation is essential for the storage of newly formed triacylglycerol (TAG). Seed oil bodies are surrounded by a phospholipid monolayer and proteins, and have a neutral-lipid core. Oleosins are related to the stability of these structures and the prevention of the merging of lipid droplets [24]. Oil-body organization and regulation have other additional functions of caleosins and steroleosins. It is therefore not surprising that these proteins are involved in the storage and maintenance of lipids in cells. Their involvement should not be confused with the direct production of fatty-acid precursors as these are separate points of control (POC) in the system. [25], [26].

Fatty-Acid Desaturation and the Breeding Relevance of FAD2

FAD2 is of special significance for an oil quality study of sesame that its biochemical function is related to a measurable compositional characteristic. One explanation for association of variation in their gene with variation in the conversion of oleic to linoleic acid is given directly. This provides a greater sense of a starting rationale for FAD2 than a candidate chosen just because of a difference in expression between samples. However, it is only the phenotype associated with the variant that determines its usefulness for any given individual, and the reliability of the association in the population from which the plants are drawn for breeding. [13].

Kim et al. investigated natural haplotype variation of 282 sesame accessions. They reported significant differences in fatty-acid composition associated with FAD2 haplotypes. The oleic/linoleic acid ratio was significantly higher for the materials with Hap1 than for the others (Hap2 or Hap3) and the difference in the oleic/linoleic acid ratio was correlated with the difference in the two fatty acid contents. This is valuable breeding evidence as it relates a natural genetic variation with a known oil phenotype. It provides a foundation to explore haplotypes in future parents and their manifestation in a breeding population. [13].

Wang et al., reported a more specific sequence–phenotype relationship. One accession (PI 263470) had a G425A substitution in FAD2 that results in an R142H change at amino-acid position 142. The content of oleic acid was around 54% for its origin while for the evaluated germplasm it was about 39.5%. The accession is thus a good example of natural variation linked to a significantly different fatty-acid profile. Although the suitability of the material for direct use or as a parent is also related to the remaining agricultural characteristics, its compositional value is evident from the reported evaluation. [12].

Wang et al. investigated induced variation using ethyl methanesulfonate (EMS) mutagenesis. Of their population 635 mutant plants were second generation mutants. Approximately 70% of some individuals were oleic acid and an improved 7th generation was greater than 75%. The source mentions M7-915-2 as an experimental material with a high oleate content. The results here demonstrate the ability to recover beyond the natural, high-oleate, example given in the same work a fatty-acid phenotype using mutagenesis and subsequent selection. The result reported is compositional change and the status of the material is left unchanged for experimental breeding. [12].

All high-oleate materials did not have the same genetic explanation. While the coding region of FAD2 was mutated in several induced lines, none contained further mutations. This finding is significant since it allows for the possibility of other genetic factors that all contribute to the phenotype. It does not identify them or their individual impacts, nor should it be used as evidence for a specific alternate mechanism. A high oleic-acid content is not necessarily correlated with another coding change in FAD2. An in-depth interpretation might necessitate a deeper look into that one sequence. [12]. Complementary are therefore the natural and induced findings. The application of variation existing in germplasm could be directed by haplotype diversity, and mutagenesis could provide supplementary materials of different composition. The latter might also prove to be useful in uncovering genetic elements not identified in the initial allele analysis. The relevant unit for the breeder is the measured oil profile, variation and plant performance. How useful an allele/mutant line is depending on the compositional effect of the line being preserved after inclusion of the line in an appropriate background.

The evidence reinforces the importance of FAD2 in the research of fatty acids in sesame and a need for precision in the description of what has been established. The pathway function, natural haplotype associations and reported high-oleate materials are related types of evidence. They are not necessarily interchangeable or every high-oleate line is agronomically better. The influence of the selected alleles must be assessed in conjunction with the total oil content, seed production and performance across the environments with the aim that the improvement in composition can be evaluated within the breeding objective [4], [12], [13].

Lignans, Tocopherols, and Phytosterols as Complementary Quality Targets

The fatty-acid fraction is a significant contributor to the oil quality phenotype, but other components also play an important role in the unique quality of sesame. Lignans are interesting for several reasons, as their biosynthesis has been studied using a number of complementary approaches. Selected genes have been associated with specific products through biochemical characterization, natural variation and targeted disruption. The body of evidence presented here provides a good example of how a nutritional target can be transformed from a description of a pathway to a supported pathway for experimental intervention. CYP81Q1 is thought to play a central role in the biosynthesis of sesamin [8], [9], [27]. It aids in the formation of methylenedioxy-bridge in the conversion of pinoresinol to sesamin. The catalytic role was confirmed by molecular and biochemical studies which directly showed the involvement of the enzyme in sesame lignan biosynthesis. It is easy to see why on target selection, CYP81Q1 is linked to an analysed biochemical reaction, not an expression pattern. This renders the anticipated result of researching the gene more specific. [27].

Follow-up studies on sesame sesamin synthase further validated the functional interpretation. Chandra and his team isolated the gene and expressed it in a heterologous system and showed its activity. The source also mentions increased activity when the sesame cytochrome P450 reductase CPR1 was co-expressed with CYP81Q1. This is a note of observation to the biochemical environment of a pathway enzyme. The effective activity of a catalytic target is still sensitive to associated molecular components, but can be well characterized. In order to improve, the question is then how does the reaction behave in the entire pathway and within the tissue(s) where the product of the reaction is deposited. Another well-defined point in lignan metabolism is the enzyme CYP92B14 [28] Murata and co. have shown that recombinant CYP92B14 can perform oxidative rearrangement of sesamin to sesamol and sesaminol. They also explained the synergic role played by the enzymes CYP81Q1 and CYP92B14 in the last step of sesame lignan formation. The results have led to links being established between specific enzyme activities and the location of the associated products. They can be of great value for a compositional breeding goal as they indicate that a change of the pathway can be a change in the balance of lignans and in their accumulation. [8]

Natural variation provided a genetic layer for evidence for CYP92B14. A variant of the gene was linked to the lack of sesamol, which is associated with a difference in sequence that resulted in a recognizable metabolite phenotype. A combination of catalytic characterization and genetic association gives a greater informative value for the target than either one of the two would yield. It also shows how to indicate which lignan there is a desired outcome. Changes to sesamol cannot be assumed to translate to changes in any other lignan or to the overall improvement in the nutritional profile. Downstream modification also affects the lignan composition [8] UGT71A9 & glycosyltransferases in the UGT94 family are discussed. The sequential, regio-selective glucosylation has been shown for the biosynthesis of sesaminol triglucoside by research of glycoside-specific glycosyltransferases. Such reactions make for a much more extended phenotype than would the quantity of the single unconjugated metabolite because the chemical forms in which compounds are found become relevant as well. The individual functions still have to be evaluated separately, however. A family designation is used to designate related genes and does not imply that all members are active or have the same breeding value [15].

Therefore, the practical implication is that a profile of pathway products should be used for evaluating lignan improvement. A change in one reaction could impact the availability of the other, or could change the ratio of related compounds. The combination that he or she creates must be measured before its value can be judged. The information provided in the evidence reviewed gives reasons to explore a few reactions and gene variants, but does not establish a clear preference for any particular

one of these for any breeding aim. There is still a need for a clear goal and an appropriate analytical evaluation in going from pathway manipulation to selection. Other constituents with genetic evidence for improvement are the tocopherols. [15], [17]. He and co-workers analyzed 96 accessions of sesame and found that a single locus accounted for 20.9% of the phenotypic variation in γ -tocopherol. This result indicates that the genomic association of the Vitamin E component variation could be studied. If it is to be reported numerically, the meaning of the percentage should be preserved, that is, it refers to explained variation in the study, not to a higher concentration of tocopherol that can be obtained by breeding. The results give an indication of a potential candidate that could go on to be evaluated for selection tool development [14]

The role of phytosterols is also subject of a big association panel. Wang and collaborators screened 402 sesame accessions for four important phytosterol traits in two environments and found 33 environmentally responsive single nucleotide polymorphism (SNP) locations. According to the source there are 18 environmentally stable sites and it suggests S1NPZ1100015 as a candidate gene. This gives both starting sites and evidence that some associations were maintained over the conditions examined. Their further use will depend on establishing the appropriate effects, differentiating the effects from those that are correlated, and evaluating the transferability of the relations to the desired breeding material. Not all these nutritional traits are equally evident with the same level of evidence. [16]. CYP81Q1 and CYP92B14 are directly biochemically supported and supported by additional experimental and/or genetic evidence. The studies of the tocopherols and phytosterols are mostly genomic associations with measured constituents. Both are involved in the breeding research but the next decision is different. A characterized enzyme can be investigated in a functional context or targeted manner, whereas an associated locus must be validated to be used with confidence as a selection target. Separating those contributions makes the research more actionable. A wider range of compounds should be used in a broader quality assessment. A desirable ratio of fatty acids does not show the composition of the same seed in terms of lignans, tocopherols or phytosterols. On the other hand, an appealing specialized-metabolite phenotype does not imply high oil concentration or seed production. By measuring the components together, combinations that are useful can be identified and what could be gained or lost made visible. This is the foundation of shifting from working on the improvement of an isolated constituent to working on the improvement of an appropriate breeding value, or seed-quality phenotype. [4], [14], [16].

Regulatory Genes and the Coordination of Lipid Accumulation

Enzymes involved in lipid formation are part of developmental programmes of a coordinated carbon metabolism, seed maturation and storage. Regulatory genes are crucial for the oil-biosynthetic process and are of interest for use in the breeding when several pathway steps are included in the breeding goal. Their role should, however, be taken with a pinch of salt as participation in a lipid program in a model organism does not necessarily predict their role in the control of the behaviour of sesame in response to expression changes or specific [5], [7]. One important example is WRINKLED1 (WRI1) whose involvement in transcriptional regulation of glycolysis and fatty-acid biosynthesis has been connected in Arabidopsis. These results provide a clue to how carbon metabolism is coordinated with storage lipid formation and provide the basis for testing other genes related to this process in sesame. The importance of the evidence from model systems is based on the mechanistic insights gained; the question for crops is what their targets are and what their role and effects are [5], [29].

Developmental analyses of sesame have highlighted WRI1 and its related genes as key candidates for lipid accumulation, alongside genes like ACCase and DGAT. While their expression aligns with seed development patterns, further evidence is required to confirm their role in altering oil phenotypes. In another study, Zhou and colleagues identified significant loci related to oil content in 400 sesame accessions, along with 515 differentially expressed genes across seed development stages, culminating in 20 candidate genes [7]. SiTPS1, which regulates fatty-acid and triacylglycerol metabolism, was recognized as a strong candidate due to the synthesis of population and developmental data, warranting further experimental investigation[30].

The study demonstrates that overexpression of SiTPS1 in Arabidopsis alters fatty-acid composition and boosts oil content, indicating a lipid-related response from the sesame gene manipulation. However, the implications of these findings are limited by species boundaries,

necessitating further examination of the allele and expression state in sesame for breeding applications. Additionally, an integrated analysis identified 220 differentially expressed microRNAs during sesame seed development, revealing regulatory relationships that extend beyond just transcription factors. This highlights the potential for exploring lipid development through these microRNA-target associations for future functional research [31].

Connections were found between genes related to unsaturated fatty-acid synthesis, notably FAD2, indicating a regulatory relationship pertinent to fatty-acid metabolism. While the study highlights specific microRNA–target pairs for further research, it cautions that not all inferred relationships are suitable for direct breeding applications [31]. Regulatory candidates should be evaluated based on evidence for each target and experimental context. Various methodologies, such as model-plant studies and crop-specific tests, must be utilized in conjunction to strengthen hypotheses while maintaining clear boundaries, avoiding overestimation of a regulator's impact on oil quality and yield.

Germplasm Diversity and Conventional Breeding

Useful genetic variation is essential for sesame improvement, with landraces and cultivars offering diverse agricultural and seed-composition traits. Some indigenous landraces from sub-Saharan Africa have valuable nutritional and sensory properties despite poor agronomic performance. Characterization of these materials is necessary. Geographic origin aids in describing collections, but specific traits must be measured [3], [17]. Marker studies have revealed molecular variation, such as inter-simple sequence repeat markers used to analyze Moroccan sesame populations, demonstrating polymorphism and differentiation. This supports germplasm characterization and helps in identifying optimal oil-quality variations through additional biochemical assessments [32].

Simple sequence repeats markers have been found to be useful for different applications in assessing molecular diversity. Asekova et al., 2018 [33], evaluated 129 accessions with polymorphic information content from 0.33 to 0.86 whereas Yue et al., 2012 [34], analyzed 545 accessions with Shannon information index of 0.4092 for three groups. In Ghana, Adu-Gyamfi et al. [35] evaluated polymorphic information content (PIC) values that ranged from 0.80 to 0.96 among 25 sesame landraces and found major and minor molecular groups. Also, a study used both the phenotypic traits and other markers to classify different landrace collections which shows the value of integrating molecular and phenotypic variation for optimal germplasm management. It should be noted that the results of different diversity measures are not comparable when comparing studies [36].

The breeder's decision needs to connect diversity with target traits, as marker systems can separate accessions with similar oil profiles. Molecular characterization should accompany direct trait measurements and the features of potential parents. Genome-wide marker resources enhance characterization but require a clear marker–trait relationship for effective quality trait selection [17], [37]. Conventional breeding methods like pure-line and pedigree approaches allow for the assessment of variation. Baydar's research on contrasting sesame genotypes demonstrated that agricultural and compositional traits can evolve together during selection, highlighting the importance of retaining each trait's contribution when evaluating resulting lines [10].

Hybridization merges complementary traits from selected parents, enhancing nutritional quality through an evaluation that includes yield performance and constituents such as oil concentration and fatty acids. Bhuyan and Sarma's study on 36 hybrid combinations of male-sterile lines and sesame cultivars illustrates that while hybrid systems may improve traits, thorough analysis is necessary to confirm nutritional benefits [38]. Additionally, the interplay between conventional and molecular breeding allows for effective variation tracking, with genomic information enhancing the reliability of selecting optimal plant combinations based on the resulting plants' maturity, architecture, production, adaptation, and composition.

Induced Mutagenesis as a Source of Quality and Agronomic Variation

Mutation breeding is an application of the use of physical or chemical mutagens to increase the variation of sesame in its characteristics, resulting in heritable variation which must be carefully selected for development. Generally, the numbers of individuals in the population and the efficiency of screening many mutations can be irrelevant to a breeding program. The goal is to develop characterized, stable materials, which would be used to impart desirable properties [17], [39], [40].

Historical examples illustrate a range of characteristics, including early maturity and yield, such as Babil and Rafiden, respectively, and recently a compact brace, the dt45 mutant. The examples demonstrate the wide range of agricultural advances that have been made using induced variation, and that such advances are not only desirable for their nutritional benefits [39], [40], [41].

The research by Wang et al. [12] establishes a link between oil composition and the genetic factors influencing fatty-acid profiles, achieved through chemical mutagenesis. This investigation emphasizes that while high oleic-acid content is valuable, it alone does not ensure agricultural performance necessary for cultivar release. Additionally, Gadri et al. [42] describe a mutation in *SiALS* that confers resistance to specific herbicides, demonstrating that targeted mutations can yield agriculturally advantageous traits, albeit not directly affecting oil profiles.

Stress-related materials enhance the understanding of breeding stability, with Moroccan mutant lines ML2-37 and ML2-72 evaluated for drought tolerance through physiological characteristics and stress indices under water deficit. Research also addresses germination, seedling vigor, and low-temperature tolerance, although broader claims of tolerance need further evaluation [43], [44]. Biochemical characterization studies have examined fatty-acid composition, bioactive compounds, antioxidant properties, and nutritional profiles under drought conditions, particularly for lines ML2-68, ML2-72, US2-6, and US2-7. These investigations link induced variation to direct seed composition and environmental response, providing a more specific value of mutants beyond mere appearance or singular traits [45], [46].

Recent studies highlight various mutant lines, such as Mut1 and Mut3, which demonstrate reduced phyllody incidence along with higher seed and oil yields. The officially registered mutant variety BINA til5 (SM-26) exhibits high yield and moderate waterlogging tolerance, while Binatil-3 is noted as a high-yielding released variety. These findings reflect different stages in the development process [47]–[49]. Dates require careful consideration, with 2013 marking the release of Binatil-3 and 2023 the registration of BINA til5, though related articles were published in 2024 and 2025. This distinction is crucial to avoid misinterpretation of the progress and categorization of mutant materials [17], [48], [49].

Yousri et al. [50] used gamma radiation and sodium azide mutagenesis to create experimental materials. They selected 3rd generation lines that showed changed fatty-acid profile, shorter stature and early maturity. VIG1 is associated with earliness, as is EW9, EW12, and EW3, and White-Seeds, EW11 and HNCW8 are associated with short stature. These materials will provide additional selection for the agricultural and compositional traits, and will be effective depending on the stability of the phenotype and the performance of the trait. The study highlights the need for molecular characterization and repeated selection for use in quality improvement programs; the need for accurate descriptions of genetic materials for use of research findings.

Genetic Architecture: Linkage Mapping and Genome-Wide Associations

Phenotypic variation in breeding has been identified through germplasm evaluation and genetic studies and this can be improved through understanding of genomic distribution. Linkage mapping and association studies can be used to define regions of the genome that are important for selection. The relationship of genomic information to measured traits is critical for quality enhancement of oils [4], [6], [11]. Of particular note, high-density mapping was conducted in sesame by Du et al. [51], who mapped 19 major-effect quantitative trait loci (QTLs) for seed traits that were valuable genomic resources for sesame. Furthermore, Wu et al. [52] used recombinant inbred lines for analysis of yield-related traits to show the importance of loci in an integrated breeding context, with the aim of optimizing compositional traits for production capabilities.

In an additional mapping effort, 430 recombinant inbred lines were used to identify 41 quantitative trait loci (QTLs) affecting plant height and 9 for seed-coat color. A separate study in 150 backcross individuals revealed the genes involved in basal branching and flowers/leaf axil, which underlines the importance of genetic investigation of the sesame architecture in breeding decisions. The results indicate that these traits are important for breeding for oil quality and that more than one of these architectural loci is required to have an effect [53], [54]. Determinate growth is associated with a phenotype-genome linkage and *QDt1* is located on linkage group 8 while *SiDt* is the determinacy gene,

which provides information for plant type selection for wider breeding purposes in agriculture, especially in reference to compositional traits [55].

Wei et al. [6] performed genome-wide association analysis using 705 accessions in four environments, and found 549 associated loci with 46 candidate genes associated with 56 agronomic traits. Of particular interest, 13 significant associations were reported, such as candidates that are associated to different phenotypes including *SiNST1* and *SiPPO*. The association patterns also indicate the complexity of these interactions between traits, and suggest that additional studies are needed to establish which genetic variants are responsible for the influence on several traits.

There are several candidate genes associated with fatty acid variation: *SiKASI*, *SiKASII*, *SiDGAT2*, *SiFATA*, *SiFATB* and *SiSAD*, of which *SiKASI* and *SiKASII* have been linked to the concentration of palmitic acid and palmitoleic acid respectively [6]. The biological relevance interpretation and future research on phenotype-associated variations based on these genomic results is important. In addition, Li et al. [11] studied 369 sesame accessions using 112 polymorphic markers, and found 19 oil-associated markers and 24 protein-associated markers, with individual oil-associated markers accounting for 4–29% of the phenotypic variation. This study makes associations between composition, marker variation and the neighbouring genes associated with lipids [11].

The explained-variation values should not be summed as independent contributions to the phenotype and do not guarantee the same effects in different breeding populations. Their role is to identify relationships for further evaluation. The design involving five environments and proximity of markers to lipid-related genes highlights the need for further investigation, while questions of transferability and causality remain. Interpretation varies based on population and environment, with association signals influenced by factors like population structure and growing conditions. Establishing a reliable selection target requires more than mere statistical significance; reproducible effects, allelic examination, and functional investigation are crucial for breeding reliability [4], [6], [11].

Transcriptomics and Lipidomics: Connecting Genetic Candidates with Seed Development

A genomic association is a region to explore but cannot provide insight into the development of the trait. The transcriptomic data shows gene expression, and the lipidomic data shows at the different species of lipids, and how their abundance was altered. A study of these in combination sheds light on the candidate functions related to periods of oil development, particularly those in seeds. It aims to provide a biological context of the candidate – and to do more than just annotate sequences. 481 lipid species were identified in a sesame study, and were found to accumulate between 21- and 33-days post-flowering, in association with genes associated with fatty-acid metabolism, triacylglycerol assembly, and lipid transport. For reference, the proposed candidates for the formation of oil (*ACCase*, *FAD2*, *DGAT*, and other *WRI1* related genes) are included in the table and are discussed below [7].

In addition to the measurements of mature seed, the developmental approach can offer a window into events that occur later in development, as the timing of lipid deposition is linked to expression changes, which can help with identification of candidate genes for lipid-deposition functions [7]. Observational relationships between genes, however, must be confirmed under experimental conditions. Wang et al. [56] highlighted the difference of lipid biosynthetic pathways of high and low oil sesame varieties/genotypes, highlighting certain pathways. However, differential expression does not definitely point to the fact that all the genes identified have a direct effect on the trait of interest (oil content in the case of the present invention), because some genes may correlate without having a direct effect.

Although there is some uncertainty about specific alleles and/or effect on oil concentration, *DGAT*'s contribution to the final acylation step suggests a high metabolic significance and this should be further investigated in sesame [7]. Similarly, the analysis of *ACCase* and *WRI1*-like candidates emphasizes the need to assess genetic variation in sesame. Developmental information combined with genomic associations can help narrow down candidate genes to those expressed at the time of lipid accumulation, associated with biochemical changes. Multi-omics analysis reveals the relationships between genetic variation, expression, lipid deposition and breeding phenotypes, and emphasizes the importance of testing candidates, and the informative power of both concordances and discordances between these layers [7], [30], [57].

Marker-Assisted Selection and Genomic Selection

Usefulness of a validated genetic finding is dependent on whether it can be used in a breeding judgment. Marker-Assisted Selection (MAS) is of special importance when a specific allele or major-effect region is known to have a stable association with a targeted phenotype. A suitable marker can be used to identify desirable plants prior to further testing with mature seeds. That benefit will be contingent upon the quality of the marker trait relationship. The marker should be for the relevant allele directly or be consistently associated with the allele, and the effect should be consistent in the genetic materials and environments in which selection will occur [4], [11].

Variation in the *FAD2* sequence provides a breeding opportunity to correlate sequence variation with oleic/linoleic ratio. A special high-oleate variant facilitates the identification of alleles and targeted investigations, but needs to be evaluated in its background, because not all allelic markers of *FAD2* are necessarily associated with high-oleate phenotypes. More than one genetic region and environmental effects contribute to total oil content [12], [13]. The complexity of marker assisted selection must be taken into account when expected outcomes are considered, as they may pinpoint validated loci. Selection may have to be done in conjunction with desirable regions and direct phenotyping to establish the desired oil content and composition. The molecular insights contribute to the improvement of selection only if related to the targeted phenotype [6], [11].

Genomic selection is a paradigm for the use of contributions of multiple loci in the genome, which has been found suitable for complex traits with large training populations that have accurate phenotypes and whole genome wide marker data. It has potential advantages by utilizing the distributed genetic information, including the information of small effect. The review mentions, however, that universal prediction accuracy or universal improvement in the quality of sesame oil is not guaranteed. It points out the need for data needs and validation prior to the use of a reliable prediction strategy [4], [17]. The selection method should be matched to the phenotype and its genetic basis; selection using marker systems is appropriate for those traits that are strongly influenced by few major-effect genes, while more extensive genomic prediction is required for those traits with many genes and, in particular, yield and environmental responses. Biochemical assessment is essential for accuracy or if it is not done, genetic tracking can continue with a lack of clarity regarding the performance and composition of the resulting traits.

Multiple-trait selection requires some consideration: high oil concentration may not be desirable for fatty-acid and/or lignan content. This framework should include major effect alleles, as well as the effects of the broader genome, and should include information on oil percentage, composition, lignans, anti-oxidant constituents, yield, maturity, and stress tolerance [4], [17]. While molecular selection can aid breeding decisions identifying the promising materials and monitoring favorable genetic variation, biochemical validation and field tests should be included to guarantee expression of expected traits. The ultimate goal of this process is to generate a line which will have a quality advantage in appropriate agricultural environments, based on molecular insights to ensure a reliable selection.

Transformation, Genome Editing, and Metabolic Engineering

Experimental manipulation facilitates hypothesis testing in genetics, especially with the progress in sesame through genetic transformation. Yadav et al. [58] demonstrated *Agrobacterium*-mediated transformation, allowing for gene function analysis directly in sesame, thus extending knowledge beyond heterologous systems. Chowdhury et al. [59] established a high-frequency transformation method using de-embryonated cotyledons, emphasizing that factors such as explant type, genotype, and culture conditions influence transformation outcomes. This variability necessitates adjustments in protocols for different genetic materials, underscoring the importance of reproducibility for effective breeding research.

Transformation relates proposed candidates to tested responses, and looks at the contribution of the gene to the biochemical characters and alignments of the phenotype. Very important are different experiments for validation and cultivar development stages. If the manipulation is successful, it will show gene function; for the use in agriculture, additional research is required with the manipulated material. Targeted mutagenesis by CRISPR/Cas9 in *Agrobacterium rhizogenes*-mediated sesame hairy-root system exhibited mutation frequencies of 90.63% and 93.33% for the *CYP81Q1* and *CYP92B14* genes, respectively, as demonstrated by research led by You and colleagues [9]. This work helps to

establish importance of genes with biochemical significance in targeted testing of genes for lignans metabolism [9], [58]–[60].

The mutation frequencies reported in the hairy-root system should not be extrapolated to whole-plant regeneration or cultivar development, which have to be validated individually. The study emphasizes that efficient targeted investigation is the key, and regeneration and genetic stability are essential for success in agriculture. Also, selection of targets for oil quality improvement is important and requires good biochemical relationships for effective interventions. The lignan-pathway research is a prime example, calling for further research to link the genetic edits to the predicted biochemical changes and their phenotypic effects and to not presume an outcome based on the level of molecular precision [4], [9]. Metabolic engineering is introduced in the context of tissue and pathway interactions, including the expression tools used in seeds such as the 2S albumin of sesame, and studies on fatty-acid metabolic engineering. Such studies are essential for effective targeting of seed oil manipulation interventions during development in the process of oil accumulation. The fact that these resources are available does not mean that all proposed methods have resulted in sesame cultivars with proven field performance and better composition. Biotechnology and breeding thus complement each other: transformation/edits evaluate and generate specific changes, crossing and selection combine these changes with other traits and environmental evaluation is necessary to assess performance. Efficient interventions require a match between molecular specificity and breeding success in terms of plant and seed composition under relevant conditions [61], [62].

Environmental Stability and the Interpretation of Oil-Quality Traits

The characteristics and genotype expression of sesame is greatly influenced by growing conditions. The availability of water affects seed production, oil accumulation and fatty acid composition; these differ depending on material. Kadkhodaie et al. [63] showed that there was a difference in oil content and composition as a result of different irrigation regimes, which showed the relationship between environmental assessment and quality. These variations have been further investigated in recent studies, such as those of Elsafy et al. [64], [65], which highlighted genotype-by-environment interactions and the implications for breeding objectives, highlighting the importance of understanding genetic relationships under relevant conditions.

An attractive composition can indicate various possibilities influenced by genetic effects, environmental responses, or their interaction. Repeated assessment helps relate biochemical phenotypes to agricultural performance and determines material suitability for diverse conditions [17], [63]. For instance, a phytosterol association study showed that 18 out of 33 associated sites were stable across two evaluated environments, suggesting their prioritization for breeding. However, this stability does not guarantee consistency across all climates, thus emphasizing the need for validation tailored to specific applications [16].

The analysis of stress response mutants gives clues on the evaluation of drought-tolerant material and lines for low-temperature germination. These adaptations signify the importance of choosing traits that are important for oil quality as well as tolerance phenotypes and seed composition [43], [44], [46]. Breeding aims are based on the integration of these characteristics at critical developmental times and under certain conditions; environmental assessments are used to guide the selection of materials. This method can help define reliable alleles and phenotypes, and improve quality improvement statements in the agricultural context.

Assessing the Strength of Evidence

An effective review will help to distinguish evidence for each of the targets. Biochemical characterisation, allelic analysis, association mapping and developmental expression are all methods that have the potential to provide unique insights and can be used together to draw broad conclusions. Multiple investigative approaches are exemplified for the gene functions involved in the metabolism of lignans, such as *CYP81Q1* and *CYP92B14* [4], [17], [57]. Moreover, the continuous breeding programme aims to improve metabolite profiles and to consider the response of plants, but the use of the plants in agriculture is another point that needs to be evaluated [8], [9], [27].

The pathway function of *FAD2* explains biochemical differences, with a correlation between the sesame haplotypes and fatty-acid balance, and a natural sequence variant and accession with high oleate content. This indicates that not all *FAD2* coding mutations are essential and further genetic study

of some of the mutant phenotypes is warranted due to the presence of high-oleate lines. Because of its functional testing and population and transcriptomic data, it is a strong candidate, but needs to be tested directly on the sesame allele to confirm *SiTPS1* [12], [13]. Pathway and developmental information is provided by the genes of ACCase, DGAT, and WRI1-like; additional functional studies are needed to confirm their involvement. Functional testing, allelic validation and perhaps testing of some candidates as selection tools in specific populations are next steps [7], [30].

Stable and transferable oil content, tocopherol and phytosterol marker development has been emphasized through research. Cultivar release is a sign of progress in the development of promising experimental material. Knowing the process of building evidence helps you identify significant pieces of evidence from common applications of the breeding process. A larger candidate set helps to get research started but not necessarily helps the number of confirmed selection targets [11], [14], [16], [17]. An efficient editing system benefits functional investigation but may not necessarily reflect in the field. Even though there are some unexplained mechanisms, a stable association can help in the selection of the achievement, as these aspects should be considered in the context of every crop improvement achievement.

Table 1. Biochemical and genetic evidence relevant to improving sesame oil composition and seed nutritional quality

Target or evidence set	Trait or metabolic role	Main findings and experimental context	Interpretation for sesame breeding	References
Acetyl-CoA carboxylase (ACCase)	Formation of malonyl-CoA for fatty acid biosynthesis.	The supplied review describes its established biochemical role. Integrated transcriptomic and lipidomic analysis identified ACCase among candidates associated with lipid accumulation during sesame seed development.	A candidate for functional investigation of fatty acid synthesis. Developmental expression does not establish that increasing its activity will improve seed oil content. Relevant to fatty acid	Biochemical background: (Ohlrogge & Browse, 1995, as cited in Mushtaq et al., 2026). Sesame developmental evidence: (Y. Zhang et al., 2023).
Stearoyl-ACP desaturase (SAD/SiSAD)	Conversion of stearoyl-ACP to oleoyl-ACP.	Its biochemical role provides the basis for examining oleic acid formation. SiSAD was identified as a candidate associated with fatty acid variation in a panel of 705 sesame accessions .	composition, although the sesame association requires functional confirmation before a particular allele can be treated as a validated breeding target.	Biochemical background: (Ohlrogge & Browse, 1995, as cited in Mushtaq et al., 2026). Sesame association: (Wei et al., 2015).
FAD2 haplotypes	Oleic acid desaturation and the oleic-to-linoleic acid ratio.	Agronomic traits and fatty acid composition were evaluated in 282 accessions . FAD2 haplotypes were examined in 23 selected	Supports further evaluation of FAD2 variation. The selected subset limits extrapolation of	(Kim et al., 2024).

		accessions; Hap1 had a higher oleic-to-linoleic acid ratio than Hap2 and Hap3.	the haplotype results to the entire collection or wider sesame germplasm.	
Natural FAD2 variation in PI 263470	Elevated oleic acid proportion.	PI 263470 carried a G425A substitution corresponding to R142H in FAD2. Its oleic acid proportion was approximately 54% , compared with approximately 39.5% for the germplasm average discussed in the study.	Identifies a natural genetic resource for investigating elevated oleic acid content. The accession's broader agronomic value requires separate assessment.	(M. L. Wang et al., 2023).
High-oleate mutants induced by ethyl methanesulfonate	Modification of seed fatty acid composition.	A population of 635 M₂ plants was generated, followed by seed fatty acid analysis and advancement of selected lines. Several lines approached 70% oleic acid , and M7-915-2 exceeded 75% . No additional FAD2 coding-region mutation was identified in the examined induced lines.	Demonstrates recoverable variation beyond the starting accession. The absence of an additional detected FAD2 coding mutation leaves the genetic explanation for the further increase unresolved. Candidates for examining saturated and monounsaturated fatty acid variation; association alone does not establish causal alleles.	(M. L. Wang et al., 2023).
SiKASI and SiKASII	Candidate genes related to fatty acid composition.	Genome-wide association analysis of 705 accessions implicated these genes in variation in palmitic and palmitoleic acid concentrations.	Provide hypotheses for functional analysis rather than demonstrated outcomes from modifying these genes in sesame.	(Wei et al., 2015).
SiACNA, SiFATA and SiFATB	Candidate components associated with fatty acid variation.	These genes were identified among candidates underlying fatty acid composition in the sesame association panel.		(Wei et al., 2015).
Glycerol-3-phosphate	Initial acylation step in glycerolipid synthesis.	The Kennedy pathway provides the biochemical	Links pathway knowledge with sesame	Pathway background: (Kennedy,

acyltransferase (GPAT)		framework. Sesame developmental analysis detected higher transcript levels of GPAT members at 33 days after flowering , alongside changes in diacylglycerol and triacylglycerol species.	expression evidence. Experimental manipulation is needed to determine whether individual GPAT members influence seed oil accumulation. Supports investigation of specific members involved in triacylglycerol precursor formation; the expression result does not validate the whole gene family as a breeding target. Combines sesame association and expression evidence with functional support from another species. Individual sesame DGAT genes still require direct evaluation.	1961, as cited in Mushtaq et al., 2026). Sesame expression: (Y. Zhang et al., 2023).
Lysophosphatidic acid acyltransferase (LPAAT/LPAT)	Acylation of lysophosphatidic acid to form phosphatidic acid.	The sesame developmental study, which used the abbreviation LPAT, detected higher transcript levels of two LPAT members at 33 days after flowering .		Pathway background: (Kennedy, 1961, as cited in Mushtaq et al., 2026). Sesame expression: (Y. Zhang et al., 2023).
DGAT family, including SiDGAT2	Final acylation step in triacylglycerol synthesis.	SiDGAT2 was a sesame association candidate, and developmental analysis detected higher DGAT transcript levels at 33 days after flowering . Functional evidence for DGAT1 and its overlapping role with PDAT1 was obtained in Arabidopsis .		Sesame association: (Wei et al., 2015). Sesame expression: (Y. Zhang et al., 2023). Arabidopsis function: (M. Zhang et al., 2009).
Phospholipid acyltransferase (PDAT)	Acyl-CoA-independent triacylglycerol formation.	PDAT-mediated transfer of acyl groups from phospholipids to diacylglycerol was characterized in yeast and plants. Additional evidence concerns Arabidopsis and microsomal preparations from developing sunflower and safflower seeds .	Establishes an alternative route for triacylglycerol synthesis. These sources do not demonstrate an oil-quality improvement produced by manipulating PDAT in sesame.	Enzymatic route: (Dahlqvist et al., 2000). Arabidopsis function: (M. Zhang et al., 2009). Sunflower and safflower activities: (Banaś et al., 2013).
Oleosins	Oil-body organization and	Structural work describes seed oil-body	Relevant to storage-lipid	Structural background:

	storage-lipid compartmentalization.	organization. Evidence discussed for oleosin-deficient Arabidopsis mutants supports a role in preventing abnormal oil-body fusion and maintaining seed germination.	organization, but these findings do not establish that modifying sesame oleosin abundance increases oil content or nutritional quality. Provides	(Tzen & Huang, 1992, as cited in Mushtaq et al., 2026). Physiological evidence: (Shimada & Hara-Nishimura, 2010).
Caleosins	Oil-body-associated protein family.	Caleosins are identified as one of the principal protein families associated with plant seed oil bodies. The cited source does not establish a sesame breeding outcome from their manipulation.	background on oil-body composition. A specific oil-improvement claim would require additional gene-specific evidence.	(Shimada & Hara-Nishimura, 2010).
Steroleosins	Oil-body-associated protein family.	Steroleosins are classified among plant oil-body membrane proteins. This classification does not demonstrate that manipulating them improves sesame oil storage or nutritional composition.	Their inclusion identifies a component of oil-body biology, rather than a validated sesame improvement strategy.	(Shimada & Hara-Nishimura, 2010).
WRINKLED1 and WRI1-like genes	Transcriptional regulation associated with carbon metabolism and fatty acid synthesis.	Functional studies established WRI1 involvement in regulating glycolytic and fatty acid biosynthetic genes in Arabidopsis . Sesame developmental analysis identified expression patterns consistent with a possible regulatory role.	Provides a rationale for testing sesame WRI1-related genes. The strength of Arabidopsis evidence should be distinguished from sesame expression-based inference.	Arabidopsis regulation: (Baud & Lepiniec, 2009; Baud et al., 2009). Sesame expression: (Y. Zhang et al., 2023).
Glycerol-3-phosphate dehydrogenase and phosphoenolpyruvate carboxylase	Carbon metabolism and precursor supply associated with lipid accumulation.	Integrated sesame transcriptomic and lipidomic analysis identified these enzymes among candidates associated with developmental changes in lipid	Suggests that precursor supply deserves attention alongside lipid-pathway enzymes. Their contribution requires testing	(Y. Zhang et al., 2023).

		biosynthesis and accumulation.	beyond expression and metabolite correlations.	
SiTPS1	Candidate regulator associated with oil content and fatty acid composition.	Analysis of 400 sesame accessions identified 43 loci . Transcriptomic comparison identified 515 differentially expressed genes , and integration of the datasets prioritized 20 candidates . SiTPS1 overexpression altered oil content and fatty acid composition in Arabidopsis . The study reported 220 differentially expressed microRNAs and identified 65 novel microRNAs in its degradome analysis . It reported 32 negatively correlated microRNA-target relationships , with 12 pairs examined by reverse-transcription quantitative polymerase chain reaction .	Offers stronger support than association alone, while leaving its effects in sesame plants and breeding populations to be established.	(Zhou et al., 2022).
MicroRNA-target networks	Post-transcriptional regulation associated with seed lipid metabolism.		Provides regulatory candidates. Expression verification supports the observed patterns but does not demonstrate that manipulating each pair changes sesame oil composition.	(Y.-P. Zhang et al., 2021).
SiNST1	Association with oil, lignan and protein content.	In the sesame association panel, SiNST1 was implicated in variation in oil content, sesamin, sesamolin and protein content.	Relevant to evaluating several seed-quality traits together. Functional confirmation is needed to resolve the causal contribution and consequences of particular alleles.	(Wei et al., 2015).
SiPPO	Association linking seed-coat colour with seed composition.	Association, sequence and expression analyses implicated SiPPO in seed-coat colour and oil-related variation.	Suggests a connection worth investigating between pigmentation and seed	(Wei et al., 2015).

Additional oil-content candidates: CXE17, GDSL-like lipase and lipid-transfer proteins	Candidate processes associated with lipid turnover and transport.	The study detected 13 significant oil-content associations and identified candidates including two lipases and two lipid-transfer proteins .	composition. The association does not establish that coat colour directly determines oil content. Extends candidate selection beyond biosynthetic enzymes; functional testing remains necessary to establish their effects.	(Wei et al., 2015).	
	CYP81Q1	Conversion of pinoresinol through piperitol to sesamin.	Biochemical and heterologous-expression studies characterized sesamin synthase. In a separate sesame editing study, targeted mutations were detected in 90.63% of the examined transgenic hairy-root lines .	A biochemically characterized lignan-pathway target. Hairy-root editing provides a functional research tool, but does not establish a field-tested edited sesame cultivar.	Enzyme characterization: (Chandra et al., 2019; Ono et al., 2006). Hairy-root editing: (You et al., 2022).
	CYP92B14	Formation of sesamolin and sesaminol from sesamin.	Recombinant-enzyme experiments characterized the relevant conversions, and natural variation was associated with sesamolin deficiency. A separate editing study detected targeted mutations in 93.33% of the examined transgenic hairy-root lines .	Supports investigation of lignan-profile modification. The reported mutation frequency measures editing in hairy-root lines, not improvement of seed lignan content.	Enzyme function and natural variation: (Murata et al., 2017). Hairy-root editing: (You et al., 2022).
UGT71A9 and selected UGT94 members	Sequential glucosylation in sesaminol triglucoside biosynthesis.	Gene-specific biochemical and genetic evidence characterized regioselective glucosylation steps involving UGT71A9 and selected UGT94 enzymes.	Supports investigation of lignan glycosylation. Evidence for particular enzymes should not be generalized to every member of	(Ono et al., 2020).	

γ-Tocopherol-associated locus	Variation in vitamin E composition.	Genome-wide association analysis of 96 sesame accessions identified a significant γ -tocopherol-associated locus accounting for 20.9% of phenotypic variation .	the UGT94 family. Provides a candidate locus for validation. The percentage represents variation explained in the study, rather than a demonstrated increase in tocopherol content. (He et al., 2019).
Phytosterol-associated loci and SINPZ1100015	Variation in campesterol, stigmasterol, β -sitosterol and $\Delta 5$ -avenasterol.	Analysis of 402 accessions in two environments reported 33 significant single-nucleotide polymorphism loci . The authors highlighted Ch6-39270 and Ch11-142842 for campesterol/stigmasterol associations across the environments and proposed SINPZ1100015 as a candidate gene.	Supports further validation of phytosterol-associated variation. The candidate gene and highlighted loci should not be presented as established breeding products. (Z. Wang et al., 2022).
Simple sequence repeat markers associated with oil and protein content	Marker associations for seed oil and protein traits.	Analysis of 369 accessions across five environments , using 112 markers , identified 19 oil-associated and 24 protein-associated markers . Individual oil-associated markers explained approximately 4–29% of variation. Nineteen markers were associated with both traits , and 17 oil-associated markers were near lipid-pathway genes.	Provides markers for further evaluation in breeding populations. Individual percentages should not be summed, and proximity to a pathway gene does not establish causality. (C. Li et al., 2014).

An Integrated Breeding Framework for Oil-Quality Improvement

The evidence provides a pathway linking germplasm evaluation to improved germplasm, consisting of characterization, biological validation, deployment in the breeding process, and pre-release evaluation. This framework identifies the activities for each method and shows how results from one phase inform the activities in the next (which are not always complete for each trait/target). It

highlights the deliberate links that are created. The first step in the process involves the definition of phenotypes and the measurement of the variation of oil contents, fatty acid composition, lignan and tocopherol contents, and phytosterols, which are important to identify materials that have complementary properties and to evaluate prospective parents. Biochemical characterization by direct assays is important since visual performance and molecular diversity measures are not sufficient to assess seed quality. Objectives need to be aligned with subsequent assessment for improvements [10], [11], [17].

Genetic characterization links phenotypic variation to genomic regions through methods like linkage mapping and association studies. The effectiveness of candidates is prioritized based on their relationship consistency, effects, and biological relevance, leading to hypotheses for selection. Distinction between trait-associated regions and the specific variants is crucial [4], [6], [51]. Biological validation tests the proposed relationships through context-driven data and various methods such as allelic investigation and biochemical characterization. Integrated studies in lignans and lipid expression highlight the importance of evidence convergence, as seen in *SiTPS1* and developmental lipid studies in sesame, emphasizing the need for tailored validation methods depending on the uncertainty of the target [8], [9], [30], [57].

The deployment in the breeding needs to be coordinated with the defined trait architecture. For major effect alleles, diagnostic markers are used to monitor them and for phenotypes affected by many loci, extensive genomic and phenotypic information is needed. Mutagenesis/editing can be used to induce variation depending on evidence and goals [4], [12], [13]. The chosen variety should be appropriate to an agricultural production environment, with regard to the production objectives regarding fatty acids, oil concentration, yield, maturity and adaptation. Also, the assessment of the lignan target and antioxidant targets should be done together with other parts of the seed. This stage emphasizes trade-offs and combinations for progress, and provides the point of molecular selection in concert with traditional breeding to ensure the marker or edited allele is a meaningful progress in plant phenotype [6], [10], [17].

Evaluation in different environments is essential to ensure that lines selected for production retain biochemical characteristics and good production under relevant environments. In transformed materials, plant regeneration and subsequent assessment of changes is included. Evidence should be provided to describe the status of the material – experimental or developed as a cultivar [9], [60], [64]. The series of decisions includes related work with germplasm, genomic analysis for relationships, functional research to test, selection of useful traits, and environmental assessment for performance. Program strength is determined by the quality of links, with more candidates not filling the gap for unresolved phenotypes and an evaluation of the plants not filling the gap for interventions.

Results and Discussion

Comparative Analysis of Quality Targets and Genetic Mechanisms

The synthesized evidence reveals that sesame oil quality cannot be attributed to a single genetic locus or pathway. Instead, it relies on a multi-tiered regulatory system comprising structural enzymes (e.g., *FAD2*, *SAD*, *ACCase*), specialized secondary metabolic routes (e.g., *CYP81Q1*, *CYP92B14* for lignans), and complex transcriptional networks (e.g., *WR11*, *SiTPS1*, microRNAs) [5]–[9], [13].

A critical finding from comparative evaluation is the hierarchy of evidence supporting different targets:

1. **High-Confidence Targets (Biochemically and Allelically Validated):** *FAD2* stands out as the most actionable target for modifying the oleic/linoleic acid ratio [12], [13]. Specific point mutations (such as G425A / R142H) and induced alleles consistently demonstrate large-effect phenotypic changes, achieving oleic acid concentrations exceeding 75% [12]. Similarly, *CYP81Q1* and *CYP92B14* offer concrete enzymatic control points for sesamin and sesamolin accumulation [8], [9], [27].
2. **Medium-Confidence Candidates (QTL and GWAS Loci):** Markers identified for oil content, protein content, tocopherols, and phytosterols (e.g., *SiNST1*, *SiPPO*, *SINPZ1100015*) account for significant phenotypic variance (4–29%) [6], [11], [14], [16]. However, their application in marker-assisted selection (MAS) remains restricted by context dependency and unresolved causal variants.

3. **Exploratory Candidates (Developmental Omics & Model-Plant Homologs):** Genes identified via transcriptomics or lipidomics during seed filling (e.g., *GPAT*, *LPAT*, *DGAT2*) provide insights into temporal lipid assembly but lack crop-specific functional validation in field environments [7], [30].

Trade-offs Between Quality Traits and Agronomic Performance

A central challenge highlighted across studies is the trade-off between improving specific oil quality parameters and maintaining agronomic traits such as seed yield, stress tolerance, and environmental adaptability [10], [63], [64]. For instance, selection for maximum oil percentage often yields lines with reduced overall seed production, while high-oleate mutants may exhibit penalties in seedling vigor or field establishment if not properly backcrossed into elite backgrounds [10], [12].

Furthermore, specialized metabolites like sesamin and sesamolin contribute to the exceptional oxidative stability of sesame oil [8]. However, altering upstream fatty acid fluxes can indirectly shift lignan profiles, reinforcing the need for multi-trait evaluation during selection cycles [15], [17].

Strategic Roadmap for Molecular Breeding

To bridge the gap between genomic discovery and cultivar release, breeding programs must transition from single-gene focus to an integrated selection framework:

- **Marker-Assisted Introgression:** Validated functional markers (e.g., *FAD2* Hap1 and EMS-induced high-oleate alleles) should be deployed immediately for backcross breeding [12], [13].
- **Genomic Selection (GS):** Polygenic traits like total seed oil percentage and seed yield under drought/waterlogging conditions should be targeted using GS models built upon multi-environment phenotypic data [17], [64], [65].
- **CRISPR/Cas9 and Functional Genomics:** High-efficiency editing systems validated in hairy roots must be extended to whole-plant regeneration systems to validate candidate transcription factors (*SiTPS1*) and fine-tune lignan pathways [9], [30].

Research Gaps and Priorities

The most significant missing link is moving from identification to contribution in sesame. Many regions or genes have been mapped and studied using the omics approach that are linked with oil accumulation and/or composition; however, the evidence supporting this is not uniform. Many targets require direct investigation of the crop, whereas expression and association are useful for prioritization. A fruitful research direction would thus be to identify some of the candidates with converging evidence and relate their impact to the breeding phenotype. This provides the information with a more useful form than a representation of adding to a list of candidates as a parallel growth of targets [7], [17], [57].

Marker relationships can transfer differently across populations and environments and need to be explored in pertinent environments when developing markers for trait selection. Good phenotyping and independent validation is essential for successful genome-wide predictions [6], [11], [64]. Furthermore, transformation and regeneration processes in molecular interventions hinder cultivar improvement: factors like genotype and culture conditions affect results. Hairy-root system and whole-plant use offer some special advantages for the study of lignan genes, and would need increased regeneration and inheritance studies [9], [58]–[60]. Improved genomic prediction and candidate validation by linking extensive molecular data to actual measurement of seed phenotype is crucial, and requires standardized biochemical assessment while not being an alternative to direct assessment of the traits [17], [57].

Quality and environmental factors should be examined in conjunction with each other because irrigation variations, drought and other factors may affect oil traits. The data obtained from studies measuring composition as well as field performance can be used to give insights that correlate with breeding objectives. It is critical to maintain a balance in selected materials for intended agricultural conditions [46], [63], [66]. Furthermore, a transition from focusing on individual nutrient targets to comprehensive analyses of fatty acids, lignans, tocopherols and phytosterols should be achieved, representing different opportunities. Emphasis is placed on finding reliable combinations which can be reproduced consistently; existing genetic and functional evidence is assessed at the seed and plant level [14], [16], [17].

Conclusion

There is a solid base of metabolic, genetic and breeding research for the improvement in oil quality of sesame. Natural *FAD2* variation and induced high-oleate lines allow the connection between genetic variation and a specific fatty-acid phenotype. Two studies have been performed to associate the functions of characterized enzymes to the composition of the lignans, both of which were performed on CYP81Q1 and CYP92B14. Mapping and integrated omics have broadened the spectrum of candidates for oil storage as well as for other nutrients and have shown how variable the evidence is among targets.

Results indicate a preferred organization around the desired phenotype. The test should measure directly the composition, candidates should be arranged according to their support and the selection should take into consideration the genetic basis of the trait. Conventional breeding and mutagenesis provide and combine variation. It can be identified and followed with the genomic information and can be tested or edited by means of transformation and editing of selected targets. They have been proven to be useful to agriculture by the retention of the desired composition as well as acceptable performance characteristics in the materials created.

Then is the central question whether a molecular finding is the basis of a reliable breeding decision. The usefulness of a characterized enzyme, a reproducible allele–trait relationship, and a transferable marker are all different. The inclusion of them in the same programme and the subsequent evaluation by different environments provides a more defined path to improvement than does the promotion of materials based on a single favourable biochemical measurement or a single molecular result. The goal is to create a well-balanced mix of quality and agricultural value with evidence relevant to each developmental phase.

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