

REVIEW

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Importance of cottonseed oil and improvement of its quality and quantity through different breeding strategies

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Abstract

Upland cotton (*Gossypium hirsutum*) is the most important fiber and oilseed crop globally. Cottonseed produces approximately 15% of the farm-gate value in cotton production. Cottonseed oil is one of the major sources of vegetable oil which has higher value than any other by-products of cotton. Thus, increasing the quantity and quality of cottonseed oil can significantly increase the economic return of cotton production for producers without the need for additional land use and investment. This review aims to understand the importance of cottonseed oil and consumer's acceptance, biosynthetic pathways and associated genes, genetic variation in oil content, as well as conventional breeding and modern genomic approaches to improve cottonseed oil content and quality.

Keywords Cottonseed oil, Applications, TAG biosynthesis pathway, Genes, Breeding techniques

Introduction

Cotton belongs to the *Gossypium* genus in the Malvaceae family, which comprises approximately 54 species, including 47 diploids ($2n=2x=26$) and seven allotetraploids ($2n=4x=52$) (Gallagher et al. 2017). The tetraploid species originated from the interspecific hybridization of two extant diploid species, similar to *G. arboreum* (AA) and *G. raimondii* (DD), approximately 1–2 million years ago (Cronn et al. 2002; Adams et al. 2005; Li et al. 2014b). Although tracing the original habitat of cotton cultivation is difficult, scientists found cotton boll fragments and fibers in Mexico approximately 7 000 years ago. *G. hirsutum*, also known as upland cotton, was the first cultivated cotton produced by the Mayan civilization in Mexico (The Australian Government Office of the Gene Technology Regulator

2008; Negm 2020). It is grown in tropical and subtropical regions such as America, Africa, Australia, and Asia. It is planted in more than 97% of cotton-cultivated areas in the US because of its wide adaptability and high yield. However, *G. barbadense*, also known as American Pima or extralong staple (ELS) cotton, produces strong, fine, and extralong fibers. It accounts for approximately 3% of cotton production because of its low yield and narrow adaptability.

Normally, a cotton plant produces approximately 1.6 kg of seed for every kilogram of lint (O'Brien et al. 2005). The typical composition of cottonseed is 5%–12.8% moisture, 15.2%–22.7% oil, and 17.1%–27.6% protein (Cherry et al. 1981). Cotton, a lucrative commercial crop, produces food, feed, and fiber. It is primarily grown for fibers to produce textiles and clothing. In addition, it is one of the major sources of vegetable oil, which has a higher value than any other by-products of cotton. Cottonseed meal, the remaining by-product after oil extraction, is an important source of plant protein after soybeans. Cottonseed meal or whole cottonseed can be used as animal feed and organic fertilizer. Cottonseed by-products support the integrated farming systems. Utilizing cottonseed

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increases farmers' income in addition to fiber production from the same land area and investment.

In approximately 1820, cottonseed oil utilization started commercially along with cotton plantations in the New World. Primarily, it was used in lamps, lubricants, and soaps. It dominated the vegetable oil market until soybean and canola oil rose in the 1950s (Wu et al. 2022). After that period, it remained important in some sectors, such as snack food processing and frying oil. Until the 1940s, it was the major vegetable oil produced in the US, and it became a part of the diet in the US for more than a century (Sekhar et al. 2011). As upland cotton cultivation has expanded from the US to other countries, the use of cottonseed oil as a food has globally become common in all cotton-growing areas. Cotton is now considered the fifth most common oil-producing crop, following soybean, canola, sunflower, and palm, and it is the second major source of plant protein after soybean (Wang et al. 2019; Sharif et al. 2019).

Because of the worldwide increasing demand for vegetable oil, cottonseed oil's nutritional components and quality have attracted much attention. The global cottonseed oil market size was valued at approximately USD 5.12 billion in 2022 and is projected to reach USD 6.87 billion by 2030 at a 3.75% compound annual growth rate (Zion Market Research 2023). There is a significant rise in the market for cottonseed oil because of the growing awareness of the health benefits of cottonseed oil and the rising standard of living. The importance of cottonseed oil as food, feed, and fuel, as well as its sustainable production without the need for additional land use, encouraged researchers to develop ways to genetically enhance cottonseed products (Alford et al. 1996). Although cotton has a complex genetic basis, considerable progress has been made in the understanding of the molecular and biochemical mechanisms involved in the biosynthesis of cottonseed oil and the genetic improvement of its oil and fatty acid contents (Wu et al. 2022).

Sharif et al. (2019) reviewed biosynthetic pathways and different breeding and genetic engineering techniques to increase cottonseed oil content and quality by modifying fatty acid composition. In addition, Wu et al. (2022) reviewed biosynthetic pathways, the genetic basis of cottonseed oil and fatty acids, and advancements in genetic engineering, including genome editing, to improve the production of cottonseed oil and fatty acids. However, this review paper discusses the multifaceted importance of cottonseed oil, including its nutritional and economic significance, association of cottonseed oil with other parameters, as well as the cottonseed oil market and consumer acceptance. In addition, this review highlights fatty acid profiles in cottonseed oil, successful cases and potential challenges of conventional,

molecular and biotechnological techniques besides the inclusion of fatty acid biosynthetic pathway, exploration of genetic variation in oil content, as well as conventional breeding and modern genomic approaches.

Uses of cottonseed oil

Cottonseed oil is naturally hydrogenated because of the balanced amount of stearic, palmitic, and oleic acid, which ensures stable frying without additional processing or the formation of trans fatty acids (Malik et al. 2016). It has a light, non-oily consistency and high smoke point, making it the most desirable for frying in cooking, as it also imparts a toasted aroma to fried products. It can be applied in a wide range of food processing, as it maintains the flavor of the items to be cooked because of its bland or neutral flavor (Zhang et al. 2022a, b; Wu et al. 2022). Approximately 56% is consumed as salad or cooking oil, whereas approximately 36% as baking and frying fats, and a small amount is consumed in margarine and other uses (Sekhar et al. 2011).

Besides the food sector, cottonseed oil is used in the preparation of industrial bioproducts, including alkyl resins for interior paints, cosmetic products, specialty soaps, and detergents (Saxena et al. 2011). Additionally, it is used in the pharmaceutical industry for protective coatings, fabric dispersants, rubber manufacturing, inks, and plastics (Wakelyn et al. 2010). As the production and sourcing of diesel from fossil fuels have adverse environmental and health effects, there is a high demand for the substitution of petrodiesel (Unosson et al. 2021). Biodiesel can be a potential substitute for petrodiesel because it is eco-friendly, biodegradable, renewable, and nontoxic. Biodiesel consists of fatty acid alkyl esters, which are produced by chemically converting triglycerides from raw materials into usable fuel through processes such as transesterification. Compared with mineral diesel, biodiesel from cotton has high quality, high density ($0.875 \text{ g}\cdot\text{cm}^{-3}$), low viscosity (6.00 cSt at 37.8°C), low oxygen content ($\sim 11\%$), fewer CO_2 emissions, no corrosion, no sulfur, and greater flammability (Freire et al. 2009). Therefore, fuel properties and a suitable carbon chain length in cottonseed oil have attracted considerable attention as sources of biodiesel (Yesilyurt et al. 2020; Zhu et al. 2021; Yesilyurt et al. 2020).

However, cottonseed oil must be chemically refined to remove gossypol, a naturally occurring toxin that protects cotton plants from damage caused by insects (Kanoi 2005). Therefore, unrefined cottonseed oil is sometimes used as a pesticide. Gossypol, a polyphenolic antinutritive compound, is produced in the pigment glands of cotton stems, leaves, seeds, and flower buds (Gadelha et al. 2014). Plant breeders have developed glandless cotton varieties with ultralow gossypol contents that are safe for use as food or feed (Zhang et al. 2014a,

b). These breeding efforts involved cross-breeding in introducing glandless genes, or silencing the σ -cadinene synthase gene, which minimizes the gossypol level in seeds by 97% without affecting terpenoids, which are involved in defense against insects and diseases (Rathore et al. 2020). The oil with practically no gossypol is pale yellow in color, soft in flavor, and rich in vitamin E.

Nutritional importance of cottonseed oil

Cottonseed oil is considered one of the healthiest vegetable oils because it contains various fatty acids, such as palmitic, stearic, oleic, and linoleic acids, in adequate amounts. One tablespoon of cottonseed oil provides 120 cal and 3.5 g of saturated fatty acids (SFAs), along with vitamins A and K, antioxidants, and amino acids (Malik et al. 2016). In addition, it provides essential amino acids from lipases, phytases, and lecithin. Tocopherols inhibit the development of rancidity in cottonseed oil, increasing its stability and enabling a long shelf life. High amounts of natural antioxidants and alpha-tocopherols (35 mg per 100 g) with varying degrees of vitamin E activity prolong the shelf-life of cottonseed oil (Agarwal et al. 2003). In addition, high levels of oleic acid and tocopherol enhance cottonseed oil's thermal and oxidative stability (Brien et al. 2000; Sekhar et al. 2011). It has no trans fatty acids; however, it contains more than 50% omega-6 fatty acids and only a small amount of omega-3 fatty acids (Sekhar et al. 2011). Therefore, cottonseed oil with a high proportion of polyunsaturated fatty acids with a balanced amount of omega-3 and omega-6 fatty acids, as well as vitamins A and E, is beneficial to human health (Ashokkumar et al. 2011). Thus, a slight improvement in the composition of cottonseed oil can significantly expand its market value.

Fatty acid profile of cottonseed oil

A person's risk of heart disease can be determined by the type of oil consumed. Chemically, all fats and oils are esters of glycerol and fatty acids. Fatty acids are essential to produce multiple hormones that enable the internal vital organs of the human body to function properly. All cooking oils are classified as saturated, monounsaturated, or polyunsaturated based on the relative proportions of fatty acids in the oil (Dohlman et al. 2003). Saturated fat, which is solid at room temperature, is found in animal fat, such as butter, ghee, and lard. These fats are good for infants and young children but not for heart health, as they increase low-density lipoprotein (LDL, bad) cholesterol while reducing high-density lipoprotein (HDL, good) cholesterol in the blood (Tomek et al. 2001). Palm oil (palmolein) and coconut oil are examples of high saturated fat content (Cheng Hai 2002). However, monounsaturated fatty acids (MUFAs) and polyunsaturated fatty acids (PUFAs) lower

LDL cholesterol and are considered good fats. The ideal cooking oil has a balanced level of MUFAs and PUFAs as well as higher omega-3 fatty acids, which benefit the heart. Therefore, mustard, rapeseed (canola), olive, groundnut, and sesame (gingelly) oils are good vegetable oils because of the balanced combination of good and bad fatty acids. However, soybean, corn, sunflower, and safflower oils have lower saturated fatty acid contents, and their PUFA contents are higher than their MUFA contents, which is undesirable.

Actually, fatty acids are vital raw materials for the formation of plant oils and crucial precursors of biological membranes (Cui et al. 2017; Wang et al. 2017a, b). Fatty acid composition is a major determinant of plant oils' quality and nutritional value. Cottonseed oil contains approximately 65%–70% unsaturated fatty acids and 26%–35% saturated fatty acids, with linoleic acid (55%) being the most prominent, followed by palmitic acid (26%), oleic acid (15%), and finally stearic acid (2%) (Hui 1996). A greater percentage of saturated fatty acids is responsible for the oxidative stability of cottonseed oil during frying, which compensates for the instability of unsaturated fatty acids (Lindsey et al. 1990). However, saturated fatty acids produce trans fatty acids as a by-product during vegetable oil hydrogenation (Mozaffarian et al. 2007). Trans fats cause diabetes and heart disease by excessively increasing weight and abdominal fat.

On the other hand, PUFAs are easily oxidized and become rancid upon exposure to oxygen when stored under general conditions (Carvalho et al. 2019). Because of their oxidative instability, unsaturated fatty acids are converted into short-chain hydroperoxides, aldehydes, and keto derivatives upon long deep-frying. Those short-chain products are responsible for the off-type flavor and shorter shelf life (Liu et al. 2002). Partial hydrogenation can be used to increase oil stability by converting polyunsaturated fatty acids into monounsaturated and saturated fats by keeping the oil in a liquid state (Liu et al. 2002). However, it has side effects, particularly the production of trans fatty acids, which increase the level of LDL cholesterol and reduce HDL cholesterol in blood serum (Mozaffarian et al. 2006; Horn et al. 2014). Therefore, cottonseed oil rich in palmitic, oleic, and stearic acids could eliminate the need for partial hydrogenation of vegetable oils. Nevertheless, oil with high levels of palmitic acid is undesirable because of its associated health risks of cardiovascular diseases (Liu et al. 2017; Qian et al. 2016; Zong et al. 2016). However, an increase in palmitic acid content is necessary for the oxidative stability of oil to make margarine, shortening, and confectionery products (Liu et al. 2017). Among saturated fatty acids, stearic acid is classified as a desired dietary component compared to palmitic and myristic

acids, as it may lower LDL cholesterol (Dougherty et al. 1995). It enhances the solidity and plasticity required for margarine and shortening (Tarrago-Trani et al. 2006). Additionally, it increases the melting point and may provide a substitute for the extensive usage of hydrogenated oils (Liu et al. 2002). Monounsaturated fatty acid (oleic acid) is relatively stable toward oxidative decomposition at high temperatures, even though oleic acid has a LDL-lowering effect similar to that of linoleic acid. Oils with high oleic acid contents improve cooking stability for deep frying and benefit human health (Liu et al. 2002, 2017, 2009). The healthy oils with high oleic acid contents, such as olive oil, have low levels of SFAs and no need for chemical hydrogenation (Schwingshackl et al. 2014). Therefore, oils with high oleic acid and low linoleic acid contents have nutritive benefits and better oxidative stability at frying temperatures, which is more appealing to health-conscious consumers (Hernandez et al. 2012). Thus, increasing the level of oleic acid above its typical range of 15%–19% is the primary target for the genetic improvement of cottonseed oil. Furthermore, increasing saturated fatty acids such as stearic acid can improve the functionality and plasticity of cottonseed

oil without the need for partial hydrogenation, a nutritionally undesirable quality. Understanding the genetic mechanisms underlying cottonseed oil biosynthesis can contribute to the development of improved cotton varieties.

Cottonseed oil biosynthesis

Oil accumulates in cottonseed during the maturity stage of the embryo. The cottonseed oil is stored in the form of triacylglycerols (TAGs) comprising three fatty acids esterified on a glycerol backbone (Troncosoponce et al. 2011). Oil synthesis and accumulation occur in four main stages (Fig. 1): the conversion of sucrose into pyruvate, de novo biosynthesis of fatty acids, TAG synthesis, and oil-body assembly (Zhang et al. 2022a, b). Sucrose is the primary source of oil stored in seeds. In higher plants, the de novo fatty acid biosynthesis pathway produces fatty acyl precursors for fatty acids of different chain lengths and saturation levels in plastids. In addition, this pathway produces glycerol 3-phosphate (G-3-P) in the cytoplasm, as well as TAG assembly via dehydration condensation of acyl-CoA and G-3-P in the endoplasmic reticulum (ER) (Song et al. 2022).

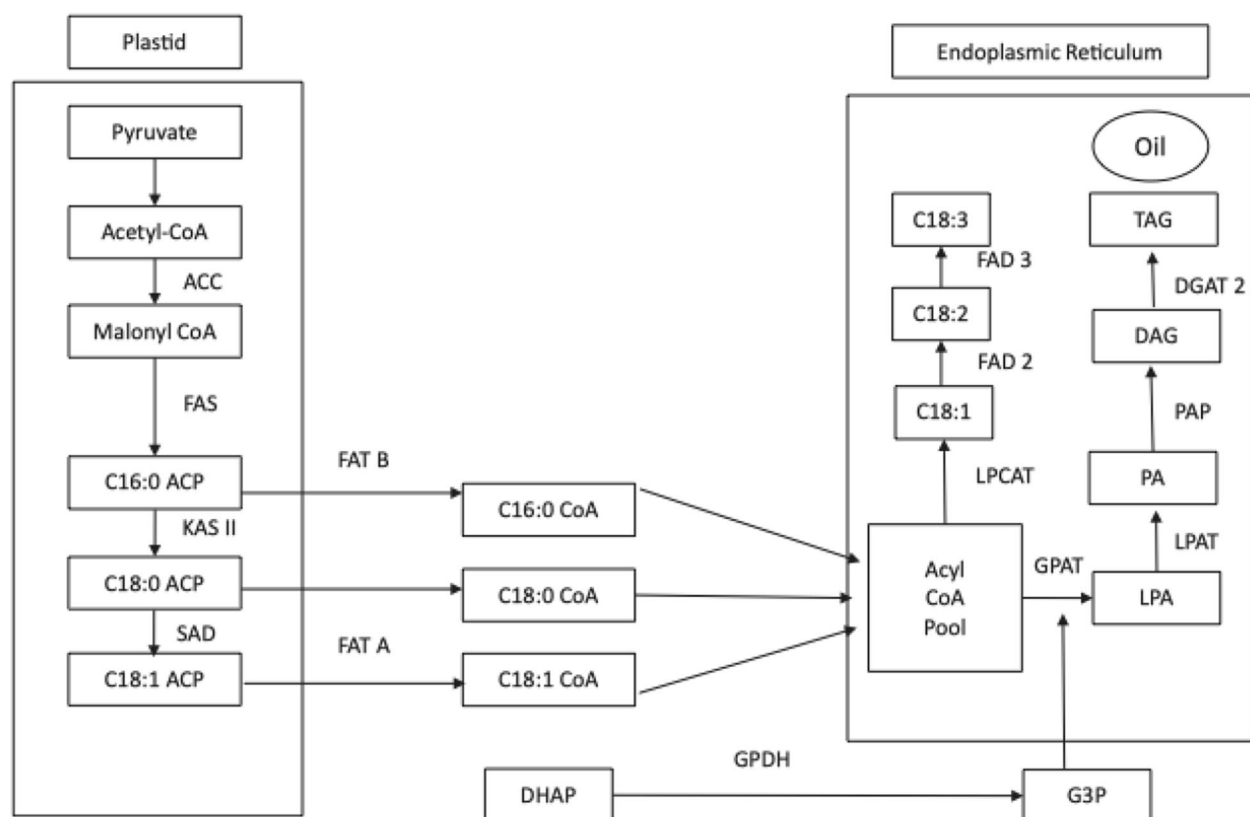


Fig. 1 Triacylglycerol (TAG) biosynthesis pathway in cottonseed (ACC: acetyl-CoA carboxylase; FAS: fatty acyl synthase; KAS II: beta-ketoacyl-ACP synthase II; SAD: stearyl ACP desaturase; FAT B: fatty acyl ACP thioesterase B; GPAT: glycerol-3-phosphate acyltransferase; LPAT: lysophosphatidyl acyltransferase; PAP: phosphatidic acid phosphatase)

De novo fatty acid biosynthesis is catalyzed by a complex of proteins known as fatty acid synthases (FASs). A palmitoyl-acyl carrier protein (C16:0-ACP) is synthesized by the addition of two carbons during each cycle of 'condensation reduction-dehydration-reduction' to generate the acyl carbon chain of fatty acids. The β -ketoacyl ACP synthetase II (KASII) extends C16:0-ACP (acyl carrier protein) to stearyl-ACP (C18:0-ACP) with the addition of two carbon atoms. Most C18:0-ACP is desaturated by stearyl-ACP desaturase (SAD) to produce oleoyl-ACP (C18:1-ACP). Free fatty acyl thioesterase (FAT) releases the free fatty acid (FA) chains C16:0, C18:0, and C18:1 from C16:0-ACP, C18:0-ACP, and C18:1-ACP, respectively (Fig. 1). For example, the palmitoyl-ACP thioesterase (FatB) can cleave palmitic acid from palmitoyl-ACP. These free fatty acids are transported into the cytoplasm, where they are activated by acyl synthase to form fatty acyl-CoA. These fatty acyl-CoAs are carried into the endoplasmic reticulum for further re-extension, desaturation, modification, TAG assembly, and synthesis of possible fatty acids (Salas et al. 2014; Aznar-Moreno et al. 2014). The modified fatty acid chain is further processed into triacylglycerol via the Kennedy pathway (Gnan et al. 2014; Mao et al. 2020). The Kennedy pathway [diacylglycerol (DAG) acyltransferase-catalyzed DAG to TAG] is the major pathway of TAG synthesis for oil production. The final step of TAG assembly in the Kennedy pathway is the acylation of the sn-3 position of 1,2-diacylglycerols into TAG by the catalyzation of diacylglycerol acyltransferase (DGAT) (Guo et al. 2017). The Kennedy pathway plays an important role in determining the oil content in cotton seeds and is also considered a rate-limiting step. The resulting TAG molecules accumulate into a spherical structure known as lipid droplets or oil bodies covered by a monolayer of phospholipid membranes. These decorated lipid droplets are associated with proteins such as oleosin, caleosin, and stereoleosin (Wu et al. 2022). These lipid droplets are released into the cytoplasm after reaching a specific size.

Gene expression during oil accumulation

Fatty acids are stored in the form of triacylglycerol in seeds. The TAG biosynthesis pathway is governed by the interactions of several genes forming a complex network, which differs among species, leading to variations in the content and composition of oil in different species (Zhu et al. 2021). As fatty acyl-ACP thioesterase (FAT) determines the carbon chain length and fatty acid types in plants, understanding the characteristics of GhFAT expression could guide genetic improvement of the quality of cottonseed oils (Qu et al. 2012; Cao et al. 2013). FATS are categorized into two subfamilies, FATA and FATB, based on their amino acid

sequence and substrate preference (Ghosh et al. 2007; Aznar-Moreno et al. 2014). In general, FATA is a class of 18:1-ACP thioesterases whose level is 18:1 in most plants (Beisson et al. 2003; Moreno-Pérez et al. 2011). FATB is also involved in the biosynthesis of unsaturated acyl-ACP fatty acids, but the gene encodes 16:0 ACP thioesterases that catalyze the formation of C16:0 in most plants (Moreno-Pérez et al. 2011; Zhou et al. 2007). Major genes, such as *FATA* and *SAD6* (Table 1), are involved in de novo fatty acid biosynthesis and oil accumulation. Generally, DGAT1 plays an important role in TAG production, as it catalyzes the rate-limiting step to convert DAG into TAG (Wu et al. 2022). The overexpression of the *GhDGAT1* gene via a seed-specific promoter in cottonseed increased the total oil content from 4.7% to 13.9% in a transgenic population, and the oil composition changed from mainly linoleic acid to oleic acid (Wu et al. 2021). In addition, transcription factors (TFs) play important roles in regulating gene expression and are essential for plant growth and development. WRI1 is vital in regulating many enzymes to facilitate carbon reallocation toward de novo fatty acid biosynthesis in plastids (Kong et al. 2019). WRI1 and NF-YB6 are highly expressed and contribute to oil accumulation in cottonseeds (Zhao et al. 2018b). Some key genes, such as TFs (*TTG1*, *TT8*, *WRI1*, and *NF-YB6*), FA synthesis genes (*FAD2* and *FAD3*), oil body proteins (*OLE1*, *OLE2*, and *OLE4*), and TAG assembly genes (*GPAT*, *LPAAT*, *LPCAT*, and *PDAT*), are required for the high oil content of *G. hirsutum* (Gao et al. 2023). These genes and enzymes are more highly expressed in *G. barbadense* than in *G. hirsutum*, implying divergence between the two closely related allotetraploid species (Zhu et al. 2021).

Table 1 Key cottonseed oil synthesis regulatory genes

Pathway	Gene	Gene annotation
Fatty acid synthesis	<i>ACCase</i>	Acetyl-CoA carboxylase
	<i>FASs</i>	Fatty acyl synthases
	<i>KAS</i>	β -ketoacyl-ACP synthase
	<i>SAD</i>	Stearyl-acyl carrier protein desaturase
	<i>FATA & FATB</i>	Fatty acid thioesterase
	<i>LPCAT</i>	Lysophosphatidyl choline acyltransferase
	<i>FAD</i>	Fatty acid desaturase
TAG synthesis	<i>GPAT</i>	Glycerol-3-phosphate acyltransferase
	<i>LPAAT</i>	Lysophosphatidic acid acyltransferase
	<i>PAP</i>	Phosphatidic acid phosphatase
	<i>DGAT</i>	Diacylglycerol acyltransferase

Association of the cottonseed oil content with other parameters

The relationships among traits are important in cotton breeding programs, which combine favorable traits into a single line to meet the needs of cotton growers and the industry. Breeders should know the direction and magnitude of genetic correlation between economically important traits to aid in the selection of breeding strategies. The seed oil content is positively correlated with seed index (Taneja et al. 1993), boll weight (Azhar et al. 2000), okra-type leaf, long fruiting branches (Liu et al. 1994), seed vigor (Snider et al. 2014), fuzzless seeds (Bellaloui et al. 2015), and seed size (Pahlavani et al. 2009). A strong linear relationship occurred between seed weight and oil content in an experiment conducted at Gorgan University of Agricultural Sciences (Pahlavani et al. 2009). Feng et al. (2023) reported that the oil content was positively correlated with seed vigor, palmitic acid, and linolenic acid. Selecting high oil-containing lines will help determine genotypes with economically important morphological traits. Lipids and proteins, which constitute cottonseed chemical reserves, are the major nutrients for energy during post-germinative growth in cotton, leading to improved seed vigor. Consequently, larger seeds indicate a greater chance of emergence and reserves for oil and protein. Therefore, selection based on seed yield, bolls per plant, and boll weight could assist breeders in developing genotypes with high oil content (Qayyum et al. 2010).

Factors affecting cottonseed oil content

Cottonseed oil content is affected by the genotype, environment, and their interactions. It varies among growing seasons, locations, and years (Ye et al. 2003). The interactive effect of genotype and environment depends on environmental factors (water, soil, temperature, and light) and the relative contribution of parent genotypes to the trait (Hom et al. 2015). However, fatty acid composition is mainly determined by the genotype of the developing cottonseed embryo (Velasco et al. 2004). Generally, the quality of oil and fatty acids depends on the quality of seeds and plant species or varieties. A high-quality oil is obtained from the seeds growing in the dry season, but it is lower in wet weather in the field or when stored with high moisture. The above is an example of the environmental effect on cottonseed oil, whereas the lower one is the effect of genetics. The diploid, *G. arboreum* and *G. herbaceum* have lower percentages of oil than New World cotton, *G. hirsutum* and *G. barbadense*, because the diploid cotton produces smaller seeds (Gopalakrishnan 2007; Pahlavani et al. 2009).

Genetic variability in cottonseed oil content

G. lobatum (24.82%) and *G. harknessii* (24.22%) have the highest, while Old World wild species such as *G. stocksii* and *G. somalense* possess the lowest oil content (11.22%) (Sharif et al. 2019). Likewise, diploid species, except for the A- and K-genome species, possessed the lowest, whereas tetraploids (21.7%) and D-genome species had the highest oil content among 33 *Gossypium* species analyzed (Hinze et al. 2015). In addition, cultivated tetraploids possessed higher oil content (22.7%) compared to wild tetraploid accessions (20.9%) (Hinze et al. 2015). Therefore, the genetic variability present in cottonseed oil within the *Gossypium* genus could be used to make genetic gains (Horn et al. 2011). However, low genetic diversity among elite upland cotton (*G. hirsutum*), because of extensive selection within the species toward improving lint yield and quality, limits the chance for genetic breeding within the species to improve seed oil content (SOC) (Kaur et al. 2017). Therefore, *G. hirsutum* can be crossed with *G. barbadense* followed by selection to improve oil accumulation by overcoming the bottleneck of low genetic variation within existing upland cotton. *G. barbadense* is often used as an important germplasm donor to improve yield (Li et al. 2016), fiber quality (Jenkins et al. 2018), disease resistance, and oil content in *G. hirsutum* (Zhao et al. 2018a). Many QTL alleles from *G. barbadense* were shown to be very favorable for improving the seed oil content of introgressed *G. hirsutum* lines (Zhu et al. 2020). Therefore, introgression breeding between *G. hirsutum* and *G. barbadense* may greatly increase the quantity and quality of cottonseed oil. The interspecific introgression line populations of *G. hirsutum* and *G. barbadense* have been frequently used to determine the genomic regions associated with interesting quantitative traits in cotton (Zhang et al. 2014a, b). Some studies have used *G. barbadense* in the background of *G. hirsutum* to improve SOC. Wu et al. (2009) and Yu et al. (2012) verified the importance of *G. barbadense* in improving SOC in the background of *G. hirsutum* while studying the correlations between cottonseed traits. Additionally, Hinze et al. (2015) and Shockey et al. (2016) confirmed that *G. barbadense* accessions have high SOC characteristics among cotton germplasm resources. Thus, the genetic variation in cottonseed oil in the *Gossypium* genus can be used to improve the cottonseed oil content and quality while maintaining the desired yield and fiber quality at acceptable levels (Sharafi et al. 2015; Azhar et al. 2008).

Breeding to increase cottonseed oil and fatty acid contents

Conventional breeding

Different breeding approaches have been used to improve oil content and quality. Researchers have

used various strategies, such as pedigree selection, mass selection, backcrossing, and mutation breeding, to improve the oil content of cotton. However, pedigree breeding was found to be effective, with a 2%–3% increase in oil percentage (Singh et al. 1991). Maternal effects play a crucial role in cottonseed oil determination (Dani et al. 1989), as seed and embryo size, which depend on the maternal parent, are positively related to oilseed content.

Natural variation or induced mutations in selective breeding programs can be used to develop crop varieties with increased oil content (Ashokkumar et al. 2011). Chemical mutagenesis has been used to reduce fuzzy lint on the seed surface, which increases oil extraction efficiency along with an increase in the percentage of seed oil (Lowery et al. 2007). A naturally occurring mutant of the *fatty acid desaturase-2* (*FAD2-ID*) gene has been identified in accession GB-713 of the *G. barbadense* mutant (FAD2), a potential candidate line for the high-oleate trait with less linoleic acid in *G. hirsutum* (Shockey et al. 2017). However, traditional breeding approaches, along with induced mutagenesis, are not enough for significant improvement of cottonseed oil quality owing to the narrow genetic basis for fatty acid composition and the polyploidy nature of the cotton genome.

Molecular breeding

As many enzymatic reactions are responsible for oil synthesis, conventional and molecular breeding approaches are necessary to improve the cottonseed oil content and modify the fatty acid composition.

Cottonseed oil, a polygenic trait, is significantly affected by environmental factors. Along with conventional breeding approaches, molecular techniques facilitate mapping genes/quantitative trait loci (QTLs) involved in oil biosynthesis. Various molecular markers associated with QTLs could be used for direct selection, which improves selection efficiency by avoiding tedious phenotypic selection (Gopalakrishnan 2007) and increasing breeding efficiency by reducing backcross generations (Qayyum et al. 2009).

Linkage mapping and association mapping

As many genes control oil biosynthesis, knowledge of QTLs associated with cottonseed oil content and quality would be helpful for their improvement (Table 2). Linkage mapping is often used to detect QTLs associated with cottonseed oil content by using different genetic materials (Wang et al. 2015). Liu et al. (2015a) reported 64 QTLs for six seed nutrient traits (crude oil, crude protein, linolenic acid, stearic acid, oleic acid, and palmitic acid contents) in a *G. hirsutum* intraspecific recombinant inbred line (RIL) population via a high-density upland cotton genetic map (Yuan et al. 2018). Yu et al. (2012) identified 17 QTLs governing oil content (OC) on twelve chromosomes via a backcross inbred line (BIL) population of 146 lines. Furthermore, Shang et al. (2016) identified 40 QTLs for OC via two RIL and two BIL populations (Table 2). Four QTLs controlling OC were found in an immortalized F_2 population (IF_2) by Alfred et al. (2012), whereas 15 QTLs for OC were reported in an $F_{2:7}$ population by Liu et al. (2015a). Three major QTLs associated with kernel percentage, kernel oil percentage, and kernel protein percentage were reported in a *G.*

Table 2 Quantitative trait loci (QTLs) mapped for cottonseed oil content and fatty acids

Mapping population	Marker numbers	Traits	No. of QTL	QTL details	References
2 RIL pop and 2 BC pop, <i>G. hirsutum</i> (Gh)	1 053 SSRs	Fatty acids	24	On 13 chromosomes	Shang et al. (2016)
503 accessions, Gh	179 SSRs/11 975 SNPs	Oil	8	On chr 1, chr 10, chr 12, chr 13, chr 15, chr 17, chr 24	Zhao et al. (2019)
90 + accessions, Gh	15 369 SNPs	Oil	13	On 13 chromosomes, including one on D05 with a candidate gene	Ma et al. (2019)
376 IF_2 from 188 RILs, Gh	388 SSRs	Oil	8	Including a QTL on A02 with two candidate genes	Liu et al. (2020)
325 chromosome segments substitution lines (CSSLs), Gh × <i>G. barbadense</i> (Gb)	11 653 661 SNPs	Oil	15	On chromosomes A01 (4), A03, A05, A07, A11, A12 (2), A01 (2), A03 (2), and A10	Zhu et al. (2020)
196 Gh × Gh RILs	8 295 (458 SSRs, 5 521 SLAF-SNPs and 2 316 chip-SNPs)	Oil	39	chr 1(1), chr 3(1), chr 4(5), chr 5(2), chr 6(1), chr 7(2), chr 9(1), chr 10(3), chr 11(1), chr 12(2), chr 13(3), chr 14(4), chr 15(3), chr 17(1), chr 19(1), chr 20(1), chr 22(1), chr 24(8)	Zhang et al. (2022b)
188 Gh × Gh RILs	388 SSRs	Oil, fatty acids	15	On chr3(1), chr18(4), LG 3(2), LG 7, LG 8, chr 15(1), LG 6(3), chr 16(1), chr 15(1)	Zhang et al. (2022a)

hirsutum × *G. barbadense* BC₁S₁ population (Song et al. 2007). The sufficient availability of molecular markers in the past two decades has made linkage mapping a routine process to tag QTLs harboring functional genes. Therefore, many QTLs have been identified for agronomically important traits in cotton (Said et al. 2013), including QTLs for cottonseed oil (Song et al. 2007; An et al. 2010; Liu et al. 2012; Alfred et al. 2012; Yu et al. 2012; Liu et al. 2013). However, approximately 80% of the QTLs identified through linkage mapping could not be confirmed in subsequent studies (Lacape et al. 2010; Said et al. 2013). According to the reported results, most of the QTLs governing cottonseed oil were identified in a single environment or single population. Very few were found in multiple environments or multiple genetic backgrounds and rarely used in marker-assisted selection (MAS) of cotton breeding programs for high oil content. This might be due to QTL population specificity, large QTL confidence intervals, QTL × genetic background, and QTL × environment interactions. This makes it difficult to tag QTLs at high resolution, thereby obstructing their application in practical breeding (Mackay et al. 2007; Cavanagh et al. 2008; Qi et al. 2011). In addition, the limited recombination events and low genotype variation in the designed populations are major bottlenecks in determining more QTLs at an acceptable level via conventional linkage mapping (Huang et al. 2014). Therefore, more loci for cottonseed nutrient traits need to be explored in diverse genetic backgrounds through different techniques.

Association mapping is a complementary approach to understanding the genetic basis of quantitative traits. It involves identifying QTLs based on the recombination events that occurred during the evolution of a panel of diverse germplasms and simultaneously evaluating the effects of many alleles of target loci. Therefore, it provides the advantage of dissecting larger numbers of alleles (Yu et al. 2006; Rafalski 2010; Tian et al. 2011; Saïdou et al. 2014). It has been widely used to study the genetic variants underlying traits such as seed protein, oil, and fatty acid composition in oil crops such as soybean (Cao et al. 2017), rapeseed (Gacek et al. 2017), and sesame (Li et al. 2014a). A whole-genome association study (GWAS) investigates genome-wide genetic variants in different individuals to determine the associations of any genetic variant with a trait. Du et al. (2018a, b) reported 16 significant SNPs associated with OC through GWAS by using 316 upland cotton accessions. Furthermore, Badigannavar et al. (2015) detected six QTLs related to OC in 75 upland cotton germplasm lines with 234 polymorphic amplified fragment length polymorphisms (AFLPs). An association analysis using 228 simple sequence repeat (SSR) markers in a panel of 180 elite upland cotton cultivars and breeding

lines detected 86 marker–trait (seed oil and protein content) associations in six environments (Liu et al. 2015b). To date, many QTLs associated with OC have been identified, among which major cottonseed OC loci have been mapped to chromosomes, such as At11 (3 QTLs), At12 (4 QTLs), Dt5 (4 QTLs), Dt9 (4 QTLs), and Dt11 (5 QTLs) (Yu et al. 2012; Shang et al. 2016). Based on the orthologs in other organisms, several genes associated with oil synthesis, such as *AtGh13LPAAT5*, *GhPEPC2*, *GhACCase*, and *GhWRI1a*, have been identified in upland cotton (Cui et al. 2017; Wang et al. 2017a, b). Unfortunately, few candidate genes related to oil accumulation have been mined according to QTLs in cotton. Therefore, detecting and mining more QTLs associated with cottonseed oil and fatty acids is important in cotton breeding programs. The detected QTLs for seed quality traits (cottonseed oil, important fatty acids, and the seed index) are useful for developing cotton varieties with improved cottonseed nutrient quality.

Genetic engineering to improve oil content in cotton

Genetic engineering, a quick and direct breeding approach, can be exploited to develop oils with the desired fatty acid profile depending upon consumer and industrial demand. The oleic acid percentage in cottonseed oil could be increased by suppressing the endogenous enzyme fatty acid desaturase 2 (*FAD2*), which converts oleic acid into linoleic acid. Therefore, transgenic cotton plants were developed via *Agrobacterium* transformation by inserting a previously designed binary vector to suppress *FAD2*, resulting in an increase in oleic acid in cottonseed oil from 21% to 30% in primary transformants and 47% in progeny (Chapman et al. 2001).

The stearic acid content increased from 2%–3% to 40% via gene silencing of *ghSAD-1*, whereas the oleic acid content increased from 15% to 77%, with downregulation of the *ghFAD2-1* gene and a significant decrease in the palmitic acid percentage (Table 3). Therefore, the silencing of both genes may be helpful for developing cultivars with varying percentages of oleic, linoleic, stearic, and palmitic acids in cotton (Liu et al. 2002). These genotypes may be utilized to satisfy consumer demands for improved nutritional value of cottonseed oil. Recently, there was an increasing approvals and safety certificates for gene edited crops in various countries including US and China. China has accelerated gene-editing works on the improvement of cottonseed fatty acids profile. They reported successful edits and expression studies with measurable shifts in seed fatty acids composition. Gene-editing shortens the path from field trial to commercial use and opens the opportunities for deploying CRISPR-derived cotton varieties in those countries. However, the gene-edited lines could still

Table 3 Genes used to improve cottonseed oil in genetically engineered cotton

Gene	Transgenic event	Major result	References
<i>GhACCase</i>	Overexpression, Gh	An increase of 17%–21% in cottonseed oil content	Cui et al. (2017)
<i>GhFATB</i> , <i>GhFAD2-1</i>	RNAi, Gh	Increase oleic acid content by 156.96%, decreased palmitic acid content by 21.28%, decreased linoleic acid by 33.92%	Liu et al. (2002)
<i>GhPEPEC2</i>	RNAi, Gh	Seed oil increased by 7.3%	Zhao et al. (2018a)
<i>GhWRII-7</i>	Mutant Arabidopsis	Lipid content reduced by three times	Zang et al. (2018)
<i>GhWRI1</i>	Arabidopsis	An increase of 19.85%–25.25% in cottonseed oil content	Zhao et al. (2018b)
<i>GhCIPK6</i>	Insertion, Gh	Oil content reduced to 25.4%–32.7% from 33.6%	Cui et al. (2020)
<i>GhDGAT1</i>	Overexpression, Gh	An increase of 4.7%–13.9% in cottonseed oil content	Wu et al. (2021)
<i>GhFAD2-1A/D</i>	CRISPR/Cas9, Gh	Up to 77.72% increase in oleic acid, accompanied by a concomitant decrease in linoleic acid from 58.62% to 6.85%	Chen et al. (2021)

be developed within pre-commercial breeding and processing trials where regulatory or market acceptance is slow.

The RNAi technique was exploited for the development of high-oil-containing genotypes by downregulating the phosphoenolpyruvate carboxylase 1 (*GhPEPC1*) gene to increase the oil content to 16.7% without drastically affecting the phenotype (Xu et al. 2016). Furthermore, RNAi upregulated lipid synthesis-related genes by downregulating *PEPC2*, resulting in a 7.3% increase in cottonseed oil content (Zhao et al. 2018a). Incorporating the natural mutant allele of *FAD21D* found in *G. barbadense* (Shockey et al. 2017) into *G. hirsutum* doubled the oleic acid content in cottonseed oil (Dowd et al. 2020). Moreover, Chen et al. (2021) confirmed that knockout mutants

of the *GhFAD2* genes in upland cotton via CRISPR/Cas9 editing increased the oleic acid level to 77.7%, with concomitant decreases in linoleic acid (from 58.6% to 6.9%) and palmitic acid (from 23.95% to 13.18%) contents (Tables 3 and 4). Additionally, the overexpression of lysophosphatidic acid acyltransferase (*LPAAT*) genes, which catalyze phosphatidic acid synthesis, especially *Gh13LPAAT5*, within *G. hirsutum* could increase fatty acid production in cottonseed oil through biotechnology (Wang et al. 2017a, b).

The adoption of high-oil cotton varieties in developing countries faces several structural and market-related challenges. Farmers predominantly prioritize cotton varieties with superior lint yield and fiber quality, as lint remains their primary source of income. Consequently, the economic potential of cottonseed

Table 4 Advantages and disadvantages of different genetic and biotechnological strategies to enhance oil content

Strategies	Advantages	Disadvantages	References
Conventional breeding	• Expands genetic variation • Low cost • Ensures adoption in local agro-ecosystems	• Limited genetic gain • Slow progress • Varying heterosis effects across environments	Rodrigues et al. (2016) Kurt et al. (2025)
Mutagenesis breeding	• Creates novel variation • No regulatory barriers	• Random mutation may introduce undesirable traits • Requires large mutant populations • Labor-intensive screening	Skoric et al. (2008) Gao et al. (2025)
Marker-assisted selection (MAS)	• Targets specific loci • Faster than conventional • Maintains genetic diversity • Low cost • Applicable to non-transgenic varieties	• Requires well-characterized maps • Marker-trait associations • Linkage may break	Spasibionek et al. (2020) Dimitrijevic et al. (2018)
Genomic selection (GS)	• Higher prediction accuracy • Accelerates breeding cycles (3–4 generations faster than MAS) • Higher prediction accuracy	• Less effective for traits with low heritability • Requires large training population • Computationally intensive	Janila et al. (2016) Ma et al. (2019)
Transgenic approach	• Stable heritability • Direct genetic improvement	• Regulatory challenges • Public acceptance issues	Zhang et al. (2018) Wang et al. (2017a, b)
Gene editing	• Precise editing • No foreign DNA	• Regulatory restrictions in many regions • Off-target effects • High technical cost for multiplex editing	Liao et al. (2025) Cai et al. (2024)

oil is often overlooked due to limited awareness and a lack of targeted extension efforts. Moreover, breeding programs focused on enhancing oil content in cottonseed are relatively scarce, and seed companies tend to prioritize traits related to lint performance over oil yield. This imbalance in research and development further constrains the availability of high-oil varieties in the market. Another significant barrier is the underdeveloped cottonseed oil value chain, including inadequate processing infrastructure and limited market access, which limits the commercialization of cottonseed oil. Cottonseed oil markets are strongly influenced by crushing capacity, ginning practices, and competition from lower-cost oils such as soybeans and palms. Additionally, the absence of differentiated pricing for oil-rich seeds provides little economic incentive for farmers to adopt these varieties.

Despite these challenges, there is a considerable market potential for high-oil cotton varieties. This potential can be unlocked through strategic investments in processing facilities, the introduction of premium pricing mechanisms for oil-rich seeds, and efforts to meet the growing local demand for edible oils. Mechanization and better post-harvest handling reduce seed damage, improving oil recovery and making high-oil cotton more viable. Premium seed pricing and partnerships with crushers benefit farmers, while a steady supply of value-added cottonseed strengthens processors' advantage. High-oleic cottonseed oil offers desirable traits—superior oxidative stability, heart-health benefits, and longer shelf life—similar to high-oleic sunflower and canola oils. Developing high-oleic cotton varieties can boost consumer acceptance of cottonseed oil. Finally, raising farmer awareness and reinforcing the value chain are critical to driving adoption of these dual-purpose cotton varieties.

Prospective

Cottonseed, a by-product of cotton production, serves multiple purposes, including food, feed, and fuel. Although cotton is primarily cultivated for fiber, utilizing cottonseed can enhance the economic returns for producers without additional land or investment. Increasing domestic cottonseed oil production could reduce edible oil imports and support national self-sufficiency goals in many developing countries. Currently, cottonseed accounts for approximately 15%–20% of farm-gate value. Improving cottonseed quality through conventional breeding and advanced genomic approaches offers significant potential to enhance nutrient composition. However, integration of omics technologies to identify genes regulating oil and fatty acid profiles, combined with machine learning, can accelerate the development of high-oil cotton varieties.

From a market perspective, future strategies should include national programs promoting cottonseed oil as part of edible oil self-sufficiency initiatives and subsidies for processing technologies. Furthermore, gene-edited, seed-specific low-gossypol cotton could improve consumer acceptance by linking breeding progress to safety and nutritional quality. In conclusion, developing dual-purpose cotton varieties that deliver high lint and seed value will be critical for widespread adoption of high-oil cotton.

Abbreviations

ACP	Acyl carrier protein
DAG	Diacylglycerol
HDL	High-density lipoprotein
LDL	Low-density lipoprotein
MUFAs	Monounsaturated fatty acids
OC	Oil content
PUFAs	Polyunsaturated fatty acids
SFAs	Saturated fatty acids
TAG	Triacylglycerol
TFs	Transcription factors
USD	United States Dollar
USFAs	Unsaturated fatty acids

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