

Chapter

Herbaceous Edible Oilseed-Bearing Plants: Origin, Botanical Insights, Constraints, and Recent Progress

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Abstract

Carbohydrates, lipids (mostly fats and oils), proteins, vitamins, minerals, and water are the six main classes of nutrients found in foods. After carbohydrates, oils are important source of major calories required in the human diet. Oils act as a vehicle for some of the important vitamins and possess a range of nutrients and bio-active compounds. These edible oil-yielding plants can be categorized into non-woody (herbaceous) and woody (non-herbaceous) oil-bearing plants. This chapter mainly focuses on important herbaceous edible oilseed (crop)plants such as pea(ground)nut (*Arachis hypogaea* L.), Indian mustard (*Brassica juncea* L. Czern. and Coss.), rapeseed (*Brassica campestris* L.) (syn. *B. rapa*), soybean (*Glycine max* L.), flaxseed (*Linum usitatissimum* L.), sunflower (*Helianthus annuus* L.), sesame (*Sesamum indicum* L.), safflower (*Carthamus tinctorius* L.), and niger (*Guizotia abyssinica* L.). It aims to (a) overview the key insights into the origin, botany and benefits of the mentioned herbaceous edible oilseed (crop)plants; (b) highlight the major constraints for their growth and productivity (quantitative-qualitative); (c) enlighten important mitigation-approaches for minimizing the constraints-accrued impacts; (d) briefly overview the major aims and achievements of important breeding programmes focused on these oilseed-bearing (crops)plants; and also to (e) briefly present important aspects least explored on the subject.

Keywords: edible oilseeds, edible oils, herbaceous edible oilseed-bearing plants, breeding oilseed crops, botanical insights, recent Progress

1. Introduction

1.1 Human, balanced diet, and plants

Plants and/or plant-based (food and non-food) resources fundamentally sustain and nourish almost all life-forms on the Earth. In particular context of human nutrition (and diet), carbohydrates, lipids (mostly fats and oils), proteins, vitamins,

minerals, and water are the six classes of nutrients found in foods. The first three components together constitute the bulk of the human diet. Notably, falling in the category of lipids, oils stand second to carbohydrates as an important source of major calories required in the human diet. Oils act as a vehicle for some of the important vitamins and also provide a range of nutrients and bio-active compounds with numerous metabolic functions and health benefits (**Figure 1**).

Interestingly, edible oils are obtained to varying extents from the seeds, pulps, fruits, and plumules of certain plants, which can be categorized into non-woody (herbaceous) and woody (non-herbaceous) oil-bearing plants. In particular, edible oils are extracted from oil-yielding edible seeds (edible oilseeds). The list of major non-woody edible oilseed-bearing herbaceous (crop) plants includes pea (ground) nut (*Arachis hypogaea* L.), Indian mustard (*Brassica juncea* L. Czern & Coss.), rapeseed (*Brassica campestris* L.) (syn. *B. rapa*) (toria, sarson, summer turnip rape or Polish rape), soybean (*Glycine max* L.), flaxseed (*Linum usitatissimum* L.), sunflower (*Helianthus annuus* L.), sesame (*Sesamum indicum* L.), safflower (*Carthamus tinctorius* L.), and niger (*Guizotia abyssinica* L.). The oils obtained from the mentioned oil-yielding edible oilseeds significantly vary in their fatty acid compositions (**Figure 2A**) [1]. In particular, edible oils obtained from *A. hypogaea* and *B. campestris* (syn. *B. rapa*), possess the highest (about 80%) unsaturated fatty acids. On the other hand, oil palm (*Elaeis guineensis* Jacq.), tea-oil tree (*Camellia oleifera* Abel.), olive (*Olea europaea* L.), and coconut (*Cocos nucifera* L.) are four well-known woody edible oil-bearing plants (trees) with high oil content. Other important woody edible oil-bearing plants are walnut (*Juglans regia* L.), pecan (*Carya cathayensis* Sarg.), shiny-leaved yellow-horn (*Xanthoceras sorbifolium* Bunge.), and hazelnut (*Corylus heterophylla* Fisch. ex Trautv.) (**Figure 2B**) [1]. Interestingly,

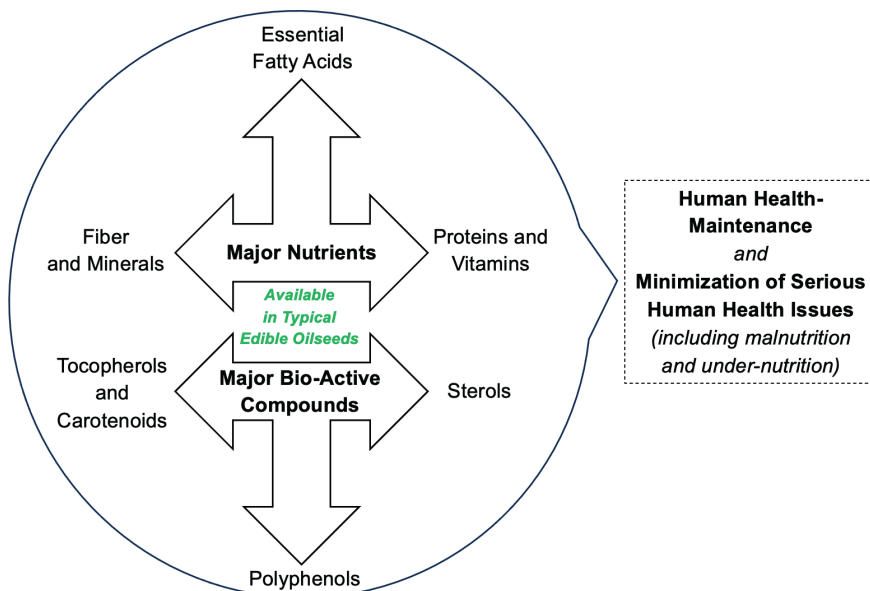


Figure 1. Schematic representation of the major nutrients and bio-active compounds available in typical edible oilseeds and their connection with human health.

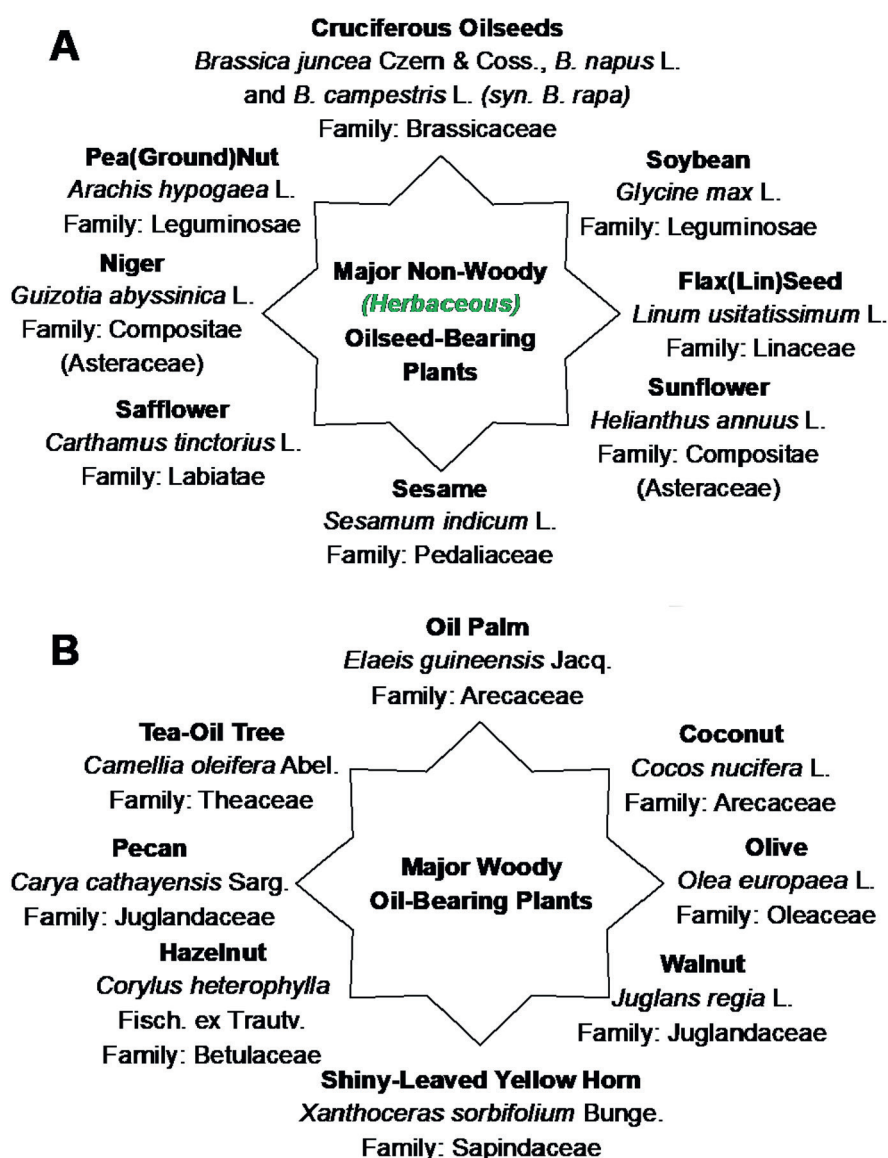


Figure 2.
 Schematic representation of the major non-woody (herbaceous) (A) and woody oil-bearing (B) plants [1].

human diet involving non-animal products (such as vegetable/rice, sugar, and nuts oils) minimizes the emission/relative footprints of greenhouse gases (heat-trapping gases in the Earth's atmosphere) [2]. There has been an increasing trend in the cultivation of oil-bearing (crop)plants on the globe. Unfortunately, edible oil-bearing (crop)plants are sensitive to most stress and extreme climatic factors. Most of these stresses or factors, in isolation or combination, varyingly impact the health of edible oil-bearing (crop)plants and thereby also limit their quantitative and qualitative productivity.

Taking into account major herbaceous edible oilseed (crop) plants (*A. hypogaea*, *B. juncea*, *B. campestris* (syn. *B. rapa*), *G. max*, *L. usitatissimum*, *H. annuus*, *S. indicum*, *C. tinctorius*, and *Guizotia abyssinica*), (i) their origin, key botanical insights, and the major health benefits are introduced; (ii) the major constraints and their impacts are provided and enlightens important mitigation strategies are overviewed; (iii) the major progress made in important breeding programmes for edible oilseed (crop) plants are highlighted; and also (iv) important aspects so far least or unexplored in the present context are mentioned as follows.

2. Origin, key botanical insights and benefits

2.1 Pea(ground)nut

Believed to have originated in the Southern Bolivia and Brazil to the northern Argentina region of South America, pea(ground)nut (*Arachis hypogaea* L.) (hypo-gaea = under the Earth) is a perennial, herbaceous, self-pollinated, monoecious (having both the male and female reproductive organs in the same plant), and a leguminous edible allotetraploid (AABB-type genome; $2n = 4x = 40$) oilseed crop and belongs to family Leguminosae (sub-family: Fabaceae). *A. hypogaea* usually attains 15-70 cm height, and its root system consists of a well-developed taproot with many lateral roots. Interestingly, *A. hypogaea* is a unique edible oilseed crop, which produces flowers above ground, and exhibits geocarpy, as it develops the fruits (pods containing edible oilseeds) below ground (earth). It is worldwide grown (as an annual crop) in the tropics and subtropics under rainfed conditions [3]. Moreover, *A. hypogaea* is grown mainly for the production of oil (seed-oil 43-55%), which is full of biologically active compounds with widely reported human health benefits (Figure 3). Given this, the consumption of *A. hypogaea*-based ‘ready-to-use therapeutic foods’ for community-based treatment of severe malnutrition has been encouraged by the World Health Organization of the United Nations [7].

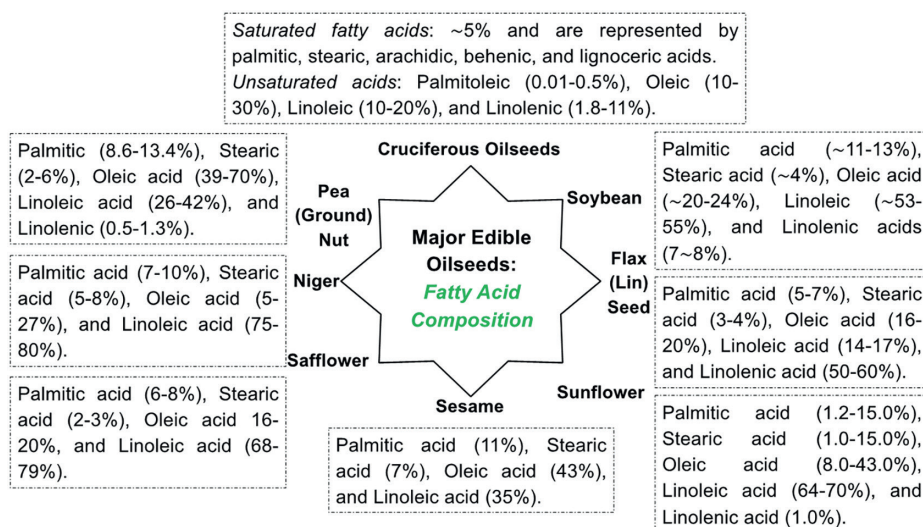


Figure 3. Schematic representation of a typical composition of fatty acids in major edible oilseed (crop) plants [4–6].

2.2 Cruciferous oilseeds

The cruciferous oilseeds (oilseed Brassicas) are herbaceous, self-pollinated, monoecious and annual economically important edible oilseed crops. Moreover, cruciferous oilseeds stand as the second largest oilseed crops after *Glycine max* in the world oilseed production [8]. The cruciferous oilseeds belong to a plant family Brassicaceae (Cruciferae), and are represented by a very complex genus Brassica. The genus Brassica possesses several taxonomic and classification problems because it has been entirely modified during its domestication by humans and contains many cultivated plants and wild species, entirely different from their ancestor(s). To his end, based mainly on the cytogenetic relationships, Nagaharu [9] attempted to systematically explain the major cultivated interrelated species of genus Brassica. Brassica species contain one or two of the three genome types A, B, and C. As per the relationships explained: *Brassica campestris* (syn. *B. rapa*) ($2n = 20$, with genome formula AA) of rapeseed and *B. nigra* ($2n = 16$, BB) and *B. oleracea* ($2n = 18$, CC) are the primary species. However, *B. napus* ($2n = 28$, AACC) and *B. carinata* ($2n = 34$, BBCC) of rapeseed and *B. juncea* ($2n = 36$, AABB) are the amphidiploids resulting from paired crossings between the primary species. A triangle of U [9] represents the botanical and genomic relationships between these six species.

The most widely distributed oilseed crop among the oilseed Brassicas, *B. campestris* (syn. *B. rapa*) is presently native to throughout Europe, Russia, Central Asia, and Near East; and has northern India (Himalayan region) as its primary centre of origin, and the European-Mediterranean area and Asia as its secondary centre of origin. Spring types of *B. campestris* are usually preferred and are largely grown in Sweden, Finland, some parts of Canada, and northwest China [10, 11]. Generally thought to have originated in the Middle East, *B. juncea* may also have arisen by independent hybridization at secondary centres in India, China, and Caucasus [12, 13]. *B. juncea* is the predominant Brassica in Asia and the Indian sub-continent. However, Canadian-grown Oriental mustard (golden yellow seed coat colored version of *B. juncea*) is used in Japan for about half of its edible oil-requirement [11]. Believed to be originated in India over 3000 years ago, rapeseed (*B. napus*) (also known as Argentine rape, Swede rape, and colza) was introduced into China and Japan, carried out to Europe in the nineteenth century, and was eventually introduced into Canada in 1936 by Polish travelers [14]. *B. napus* is of commercial value in Canada and Australia. In particular, Winter types of *B. napus* are largely grown under north European, Chinese, and Canadian conditions [8].

2.3 Soybean

Native to East Asia (central China) and recognized as the 'golden bean' or the 'miracle bean', soybean (*Glycine max* L.) is an erect, bushy, herbaceous, annual, self-pollinated, and diploid legume, which belongs to family Leguminosae (sub-family: Fabaceae). Morphological, cytogenetic, and molecular analyses have indicated the domestication of *G. max* from its wild relative (*G. soja*) in East Asia 6000-9000 years ago. Additionally, before its spread to huge *G. max* yield-producing America and Brazil (in the last 100 years), *G. max* was first introduced into Japan, Korea, and Southeast Asia [15, 16]. *G. max* seed-oil (18–20% of the dry weight of seed) is nutritionally very important as it possess five most abundant fatty acids (palmitic, stearic, oleic, linoleic, and linolenic acids) and exhibits arachidic acid (1–3%) and polyunsaturated/saturated ratio of 4:1. Lecithin (phosphatidylcholine), phospholipids,

tocopherols, and phytosterols also occur in *G. max* seed-oil. Given numerous human health benefits, *G. max* is in its high demand particularly in Northeast Asian countries including China, Japan, the Republic of Korea, and Russia [17].

2.4 Flax(lin)seed

An ancient annual herbaceous and a self-pollinated plant, linseed or flaxseed (*Linum usitatissimum* L.) belongs to Linaceae family and has its uncertain origin. However, east of the Mediterranean Sea toward India (having a very diverse forms of *L. usitatissimum*) is argued as the centre of its origin. *L. usitatissimum* has also been considered a native of West Asia and the Mediterranean coastal lands, Asia Minor, Egypt, Algeria, Tunis, Spain, Italy, and Greece, where fiber types (fiber type *L. usitatissimum*) of this plant were cultivated. On the other hand, seed-type *L. usitatissimum* for expressible oil was grown in Southwest Asia, including Turkestan, Afghanistan, and India [18]. *L. usitatissimum* attains 60-100 cm length, and has non-shattering capsules. The seed-type *L. usitatissimum* is shorter and more branched, when compared to slender and more branched fiber type *L. usitatissimum*. *L. usitatissimum* is widely distributed in the northern hemisphere (Canada, United States, Russia, China and India), where it is cultivated for its seed-oil (40% of its seed weight) and stem fiber (linen) [19]. Though *L. usitatissimum* seed-oil (linseed oil) components depend on seed cultivar, location, environmental condition, and methods of analysis, its seed-oil is enriched in nutritionally important omega-3 fatty acids including α -linolenic acid (an n-3 polyunsaturated fatty acid), and a good content of the important bioactive components (**Figure 4**). Linseed oil is particularly rich in total unsaturated fatty acids (87.8-89.8%). Hence, linseed oil is in its great demand as a dietary supplement and is also recognized as nutraceutical and functional food owing to numerous known and potential human health benefits of bioactive components therein [20, 21].

2.5 Sunflower

Originated from a Mexico native wild sunflower, *Helianthus lenticularis* Douglas (Greek term, *Helios* = sun; *Anthos*: a flower), sunflower (*Helianthus annuus* L.) is a

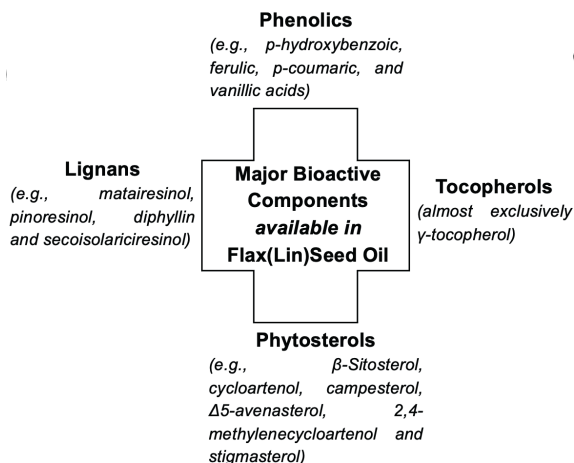


Figure 4. Schematic representation of the major bioactive components available in flax(lin)seed-oil [20, 21].

fast-growing diploid species ($2n = 2x = 34$) annual herb and is thought indigenous to central and eastern North America (and/or south-west United States-Mexico area and western Canada). Mainly commercialized in Russia, *H. annuus* is cultivated worldwide, extensively in sub-tropical and temperate regions, and its cultivation is spreading to tropical regions. A representative member of family Compositae (Asteraceae), *H. annuus*, is an erect, hardy, often unbranched, coarse, and stout-stemmed having a varying height up to 4.2 m and with a decorative flower head composed of disc florets in its centre and surrounded ray flowers [22, 23]. *H. annuus* seed-oil (22–55% of seed dry weight) is nutritionally valued for its high content of approximately 15% saturated and 85% unsaturated fatty acids. Its oil has multifaceted therapeutic benefits including attenuation of cardiovascular and inflammatory diseases, and antimicrobial, antioxidant, and antihypertensive benefits, among others [22].

2.6 Sesame

A native of Africa, China, and India, sesame (*Sesamum indicum* L.) is considered as the oldest known oilseed crop. It was domesticated nearly 3000 years ago and was the first known oil consumed by humans [24]. Domestication of *S. indicum* in South India has taken place about 1500 years ago [25]. It belongs to family Pedaliaceae and is recognized as the queen of oilseeds owing to its high value seed-oil quality and plethora of nutritive substances [26]. The genus *Sesamum* is one among the 13 genera of the family Pedaliaceae. In particular, *S. indicum*, together with *S. capense*, *S. malabaricum* and *S. schenckii*, has the somatic number $2n = 26$; *S. laciniatum*, $2n = 28$; *S. angolense* and *S. prostratum*, $2n = 32$; *S. occidentale*; and *S. radiatum*, $2n = 64$ [27]. *S. indicum* is an annual or biannual and self-pollinated herb with tall and branched (having an indeterminate growth habit) ridges bearing stems and mostly with solitary, axillary, shortly pedicellate, and zygomorphic flowers in white color (pink, purple, or various shades of purple-white flowers also occur). The fatty acid composition of *S. indicum* seed-oil comprises oleic acid (43%), linoleic acid (35%), palmitic acid (11%), and stearic acid (7%), which together contribute to 96% of total fatty acid content [4]. Given these, *S. indicum* seed-oil promotes health and also provides relief from hypertension, oxidative stress, and neurodegenerative diseases [28].

2.7 Safflower

An annual, erect, herbaceous, highly branched, spiny (leaves and bracts), thistle-like plant, safflower (*Carthamus tinctorius* L.) belongs to the family Asteraceae (Compositae), attains from 30 to 150 cm height, and has a chromosome number of $2n = 24$ [29]. A minor, underutilized, and xerophilous oilseed crop, *C. tinctorius* is the only cultivated representative of genus *Carthamus*. Based on the archaeological records, *C. tinctorius* was established in north-western India during the Chalcolithic culture, and thereafter, it was distributed to the other regions. Three major centres: Ethiopia, the Iran-Afghanistan area, and India were assumed by Nikolai Vavilov (1887-1943) as the centres of origin of *Carthamus* sp. [30]. Moreover seven centres of similarity: (i) The Far East (China and Korea), (ii) India-Pakistan, (iii) Middle East, (iv) Egypt, (v) Sudan, (vi) Ethiopia, and (vii) Europe were the regions, where the *Carthamus* spp. crop was mainly cultivated [31]. The hypothesis of these seven centres of similarity were also corroborated with molecular characterization of genetic diversity, population structure, and similarity centres for 131 *Carthamus* sp. accessions obtained from 28 countries using 12 Inter Simple Sequence Repeat markers [32].

In particular, *C. tinctorius* was domesticated from its putative wild ancestor, *C. palestinus*, about 4500 years ago. *C. tinctorius* is thought to be native to parts of Asia (northern China and India), the Middle East (Iran and Iraq), and Africa and Mediterranean basin and is grown in arid and semi-arid regions in the world [33]. Moreover, based on phylogenetic analysis, *C. tinctorius* has diverged from artichokes (*Cynara cardunculus*) and *Helianthus annuus*, approximately 30.7 and 60.5 million years ago, respectively [34]. *C. tinctorius* yields high quality 32-40% seed-oil, which is rich in bioactive components including polyunsaturated fatty acids (with linoleic acid being predominant at 70%), monounsaturated oleic acid (10%), small amounts of stearic acid, flavonoids, alkaloids, and poly-alkenes. These bioactive components are valued for human health reasons, and helps in significantly reducing blood cholesterol levels [35]. *C. tinctorius* seed-oil also helps in the management of coronary heart disease, hypertension, dysmenorrhoea, and amenorrhoea [35].

2.8 Niger

Another minor, neglected or underutilized crop, niger (*Guizotia abyssinica* L.) is native to the Ethiopian highlands [36]. The genus *Guizotia* has its centre of origin, distribution, and genetic diversity in Ethiopia, where *G. abyssinica* has been domesticated, and is only cultivated out of the six species in genus *Guizotia*. A stout, erect annual, and moderately to well-branched dicotyledonous herb, *G. abyssinica* belongs to the Compositae (Asteraceae) family and has soft, hairy, and hollow stem and a well-developed taproot system (with many lateral roots); grows up to 2 m tall; has hermaphroditic disk florets; and has a diploid genome constituting ($2n = 2x = 30$) chromosome number. *G. abyssinica* is mainly planted for its edible oil in India and Ethiopia. It is also cultivated at small scale in several other African and Asian countries [37]. As a good source of oil, *G. abyssinica* exhibits its oil-yielding capacity between 28 and 50%. The occurrence of a high amount of linoleic acid (C 18:2) as the main fatty acid in its oil makes *G. abyssinica* nutritionally valuable and attractive. Additionally, *G. abyssinica* seed-oil has been a good source of phytochemicals and antioxidants, known for busting many life-threatening diseases including cancer and cardiovascular ailments [38].

3. Major constraints, impacts, and mitigation

3.1 Pea(ground)nut

A. hypogaea seed yield and quality are mainly limited by both abiotic stresses (extreme temperatures, drought, and extreme soil factors) and biotic stresses (pod borers, aphids, mites as insect pests and leaf spots, rusts and toxin producing *Aspergillus* fungus among the diseases) [39]. Drought stress is known to impact stabilization and productivity of Fabaceae crops including *A. hypogaea* [40]. Improved growth, yields, quality, and economics were observed in summer *A. hypogaea*, employing agronomic management, which comprised irrigation scheduling, mulching and integrated nutrient management [41]. The supply of auxiliary combined applications of cobalt and chelated zinc to drought-stressed *A. hypogaea* increased the capacity of this crop for nutrient absorption and water-use-efficiency and eventually improved its yield [42]. Identifying the most sensitive growth stage to water stress and understanding its consequences were argued essential for developing

technologies aimed at enhancing the performance of crops (such as *A. hypogaea*) in water-limited environments [43]. Several genetic manipulations have been done in *A. hypogaea* for its improved tolerance to major abiotic stresses including drought [44, 45] and high salinity [46, 47]. Molecular genetic efforts have also been made to enhance to a great extent the resistance of *A. hypogaea* to the major biotic stresses such as pests/insects *Spodoptera litura* [48], and *Holotrichia parallela* larvae [49].

3.2 Cruciferous oilseeds

Abiotic stresses known impact the growth and productivity of Brassica oilseed crops including drought, temperature, and soil salinity [50, 51]. On the other hand, Brassica oilseed crop-health and productivity can also be impacted by biotic stresses such as fungal pathogens (*Alternaria brassicae*, which causes *Alternaria* leaf blight; *Albugo candida*, which causes white rust; *Sclerotinia sclerotiorum*, which causes *Sclerotinia* stem rot; *Erysiphe cruciferarum*, which causes powdery mildew; *Leptosphaeria maculans* and *L. biglobosa*, which cause blackleg disease; and *Hyaloperonospora parasitica*, which causes downy mildew), bacterial diseases (black rot, caused by *Xanthomonas campestris*, and leaf blight, caused by *Pseudomonas syringae*), and viral diseases (caused by Turnip yellows virus, cauliflower mosaic virus, and turnip mosaic virus) [50, 51]. Conventional breeding is difficult to develop varieties resistant to the mentioned fungal diseases due to unavailability of disease-resistant germplasm and also due to lack of sufficient innate resistance to these fungal diseases in most oilseed Brassicas such as *B. juncea*. Transgenic *B. juncea* cultivars produced by insertion of the *WRR4* gene, exhibited their broad-spectrum resistance to white rust [52]. Earlier, using a *B. juncea*-*B. napus* line and a *B. carinata*-*B. napus* line, possible genomic regions of interest for blackleg resistance genes were analyzed in the *B. juncea* genome [53]. *B. juncea*, *B. napus*, and *B. carinata* exhibited more tolerance to *Alternaria* blight when compared to *B. rapa* [54]. Overexpression of NPR1 (non-expressor of pathogen-related gene 1) in *B. juncea* was conferred the broad spectrum resistance of this oilseed crop to major fungal pathogens such as *Alternaria brassicae* and *Erysiphe cruciferarum* [50]. *Sclerotinia* stem rot (caused by a plant pathogenic fungus, *Sclerotinia sclerotiorum*) causes extensive yield losses world-wide in Brassica oilseed crops. To this end, marker trait associations for resistance against *Sclerotinia sclerotiorum* were detected in *B. juncea*-*Erucastrum cardaminoides* introgression lines [55]. An effective qualitative and quantitative resistance against the globally predominant *Xanthomonas campestris* races (such as R1 and R4) was observed in *B. juncea* [56, 57]. Resistance to Turnip Mosaic Virus was shown to be enhanced by *BjAOX1a* (an oxidase gene), which was cloned from *B. juncea* [58].

Drought stress was reported to cause significant yield losses in *B. juncea* [59]. The supply of methyl jasmonate and *Pseudomonas fluorescens* to drought stress-exposed *B. juncea* improved its drought tolerance by strengthening antioxidative defense mechanisms, elevating secondary metabolite production, and promoting osmolyte accumulation [59]. A differential regulation of certain genes and transcription factors was observed in drought-exposed *B. juncea* [60, 61]. The study also enlightened the coding transcripts, which, in turn, could be associated with drought tolerance traits in *B. juncea* [60, 61]. Salinity stress can also impact the growth, development, and productivity in oilseed Brassicas including *B. juncea* [62–64]. Nitrogen availability was found to regulate proline and ethylene production, which eventually alleviated salinity stress in *B. juncea* [62]. A salt-tolerant *Pseudomonas* species was found to ameliorate salinity stress and stimulate the growth of *B. juncea* [64]. In a recent study,

24-epibrassinolide-mediated alleviation of salinity stress in *B. juncea* involved 24-epibrassinolide-mediated regulation of functional components of nitric oxide (NO) signaling and antioxidant defense pathways [63]. Ectopic overexpression of cytosolic ascorbate peroxidase gene (*Apx1*) improved salinity stress tolerance in *B. juncea* by strengthening antioxidative defense mechanisms [65]. In *B. carinata*-derived *B. juncea* introgression lines, quantitative trait loci (QTL)-conferring drought tolerance was performed, and over 15 candidate genes related to biotic and abiotic stresses were reported in the genomic regions of identified QTLs [66].

Elevated temperature regimes (such as heat stress) were also reported to limit the growth and productivity of oilseed Brassica crops [67]. Differentially expressed genes and key pathways were analyzed in heat-stressed *B. napus* using bioinformatics tools [67]. Genome-Wide Association Studies (GWAS) have enlightened genomic regions and QTLs controlling various traits known to be affected by heat stress in *B. napus* [68] and *B. rapa* [69]. In particular, QTLs for heat stress tolerance in *B. rapa* were found distributed across the genome [69]. Moreover, the occurrence of QTL was also found in diverse genetic groups, flowering phenologies, and morphotypes [69]. Several transcription factors known to play regulatory roles in heat stress responses were also identified in *B. napus* [70, 71]. Additionally, major gene families involved in controlling different hormonal signaling networks during heat stress were also explored in *B. napus* [72]. Utilization of a number of crop wild relatives (CWRs) of *B. juncea* was recommended for biotic and abiotic stress management in *B. juncea* (Figure 5) [51, 73]. It was argued that these CWRs may serve as resourceful gene pools for introgression of stress resilience traits.

3.3 Soybean

The list of important abiotic stresses reported to impact the productivity and chemical composition of *Glycine max* oilseeds includes drought, temperature, and salinity. Drought stress decreased linoleic and linolenic acids; whereas, an elevated accumulation of oleic acid argued an adaptive mechanism for the maintenance of cell turgor in drought-stressed *G. max* [74]. Yield of seed and its oil and also the seed-oil fatty acid composition can be impacted by elevated soil salinity [75]. The major effects

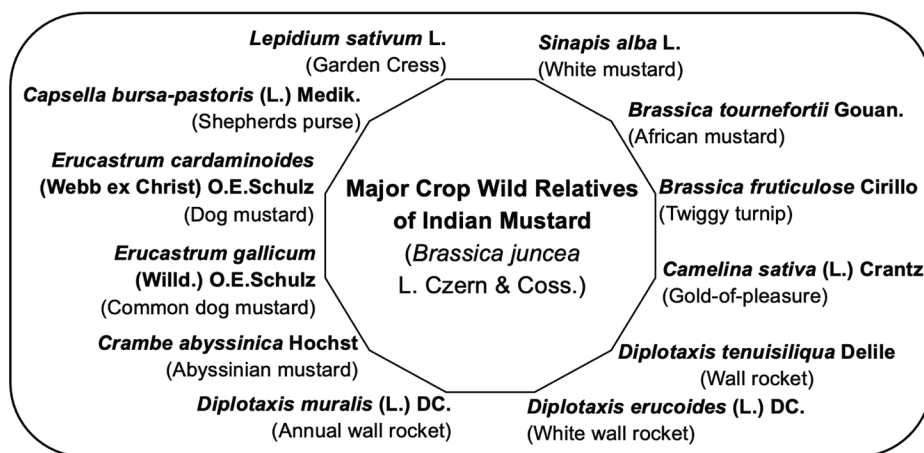


Figure 5. Representation of the major crop wild relatives of Indian mustard (*Brassica juncea* L. Czern & Coss.) [51, 73].

of drought and salinity were ascertained in *G. max* employing transcriptomics studies [76]. *Agrobacterium rhizogenes*-mediated hairy-root transformation was employed for *G. max* gene functional research [77]. Eventually, CRISPR/Cas9 system was extensively used in *G. max* gene functional study [78–80]. It was also employed in improving the major *G. max* traits, including abiotic stress (herbicide) tolerance and disease resistance [78–80]. Actin depolymerization factor (GmADF13) was functionally characterized in *G. max*, where GmADF13 was found responsible for drought stress resistance [81]. Recently, the major genetics underlying red crown rot disease-resistance was identified and dissected in a diverse *G. max* germplasm population [82].

3.4 Flax(lin)seed

In Asian countries (particularly India), oil-type *L. usitatissimum* mainly suffers from drought, salinity, and heat in addition to biotic stress factors such as *Fusarium oxysporum*, *Septoria linicola*, and *Melampsora lini*. Interestingly, due to its hardiness, *L. usitatissimum* is known to tolerate drought when compared to many other oil and food crops. However, two major reasons, namely, the occurrence of a shallow root system and the transpiration of a high amount of water owing to high transpiration coefficient (value of 787–1093), make this plant more susceptible to drought stress [83]. Drought stress (water scarcity) continues to be a significant impediment to *L. usitatissimum* production. To this end, understanding the ‘root system architecture’ can be pivotal in order to improve water-acquisition in *L. usitatissimum*. However, knowledge is still meager in *L. usitatissimum* [84, 85]. Research is also meager on the identification of drought-resilient genotypes and genome-wide analysis of drought-induced gene expression in *L. usitatissimum* [86, 87]. Soil salinity-alkalinity was reported to impact *L. usitatissimum* germination and emergence, seedling survival, growth, and productivity [88]. Identification of salinity-tolerant lines has been done in few studies [89, 90]. Additionally, important genes responsible for conferring salt tolerance were also identified [91].

Notably, *L. usitatissimum* is a cool season crop. The production and viability of pollen and seed set, and the quality and quantity of seed-oil in *L. usitatissimum* can be impacted by heat stress (40°C) [92, 93]. *Fusarium oxysporum* f. sp. *lini* was reported to cause wilt disease in *L. usitatissimum* and can cause 80–100% yield loss [94]. Genetic improvement and adaptive breeding for high temperature stress tolerance in *L. usitatissimum* can be accelerated with a comprehensive characterization of heat shock factor (HSF) candidate genes [95]. Genomic insights into HSFs were enlightened a candidate gene (*LusHSF*) for high temperature stress-adaptation and gene editing with minimal off-target effects in *L. usitatissimum* [95]. Drought-, salinity-, cold- and heat-associated NAC-domain transcription factor genes (*LuNACs*) were discovered and functionally characterized in *L. usitatissimum* [93]. A nuclear magnetic resonance-metabolomics-based tool was developed to select *L. usitatissimum* varieties with better nutrient profile [96]. The *de novo* genome of *L. usitatissimum*-rust pathogen *Melampsora lini* was sequenced, and putative protein coding genes were identified [97]. Important insights into the genetic architecture and genomic prediction of powdery mildew-resistance were enlightened in *L. usitatissimum* [98]. Drought and salinity impacts were ascertained in *L. usitatissimum* employing transcriptomics studies [99]. In order to efficiently exploit CRISPR-Cas9 technology in *L. usitatissimum*, a guideline was made available for designing *guide* RNA, assembling DNA fragments, and also for preparing a detailed protocol for protoplast isolation, transfection, and mutation detection [100].

3.5 Sunflower

Temperature and water regimes and exposure to soil salinity during the phenological development of *Helianthus annuus* plants were reported to impact its seed yield and also the seed-oil quality [101–103]. For its optimal growth and development, *H. annuus* plants require 15–35°C mean daily temperatures [101]. Unfortunately, *H. annuus* shows susceptibility to heat stress (elevated temperature). *H. annuus* exposed to elevated threshold temperature during its reproductive stage exhibited negative impacts on fertilization, grain-filling, embryo growth, seed number, seed growth, seed weight, and seed-oil characteristics [102]. A constant seven-day exposure of *H. annuus* to high temperatures of $\geq 35^{\circ}\text{C}$, during grain-filling, strongly modified seed-oil fatty acid composition [103]. *H. annuus* is considered a moderately drought-resistant oilseed crop and is adapted to low water-input regimes in warm to semi-arid zones, owing to its well-developed tap roots [104]. Water deficit reduced seed yield (16.3%), oil yield (22.5%), and linolenic and palmitic acid (29.8 and 28.5%, respectively) [35]. Soil salinity can cause over 55% reduction in *H. annuus* production worldwide [105, 106]. Enhanced growth and production were observed in salinity-exposed *H. annuus* supplied with *Pseudomonas aeruginosa* PF23 [105] and fluorescent *Pseudomonas* sp. PF17 [106]. Transcriptomics studies ascertained the effects of drought and salinity stresses in *H. annuus* [107]. Recently, the characterization of the genetic control of abiotic stress-related specialized metabolites was performed in *H. annuus* [108]. Putatively annotated 30 compounds were found to be associated to seven most likely candidate genes with varied functions [108]. An integrated omics approach (comprising genomics, epigenomics, transcriptomics, proteomics, metabolomics and phenomics) was recommended for efficient genetic improvement in *H. annuus* breeding [109].

Two major diseases, namely, downy mildew (caused by *Plasmopara halstedii*) and *H. annuus* rust (caused by *Puccinia helianthin*), and a holo-parasitic flowering plant species, broomrape (*Orobancha cumana*) cause significant damages to *H. annuus* growth and productivity [110–113]. In particular, downy mildew constitutes a significant risk factor during *H. annuus* production [111]. An integrated pest management approach against *H. annuus* downy mildew was recommended [111]. Moreover, among the downy mildew resistance inducers tested (azadirachtin, AZA; benzothiadiazole, BTH; *Trichoderma asperellum*) in *in vivo* experiments, BTH, *T. asperellum*, and the highest dose of AZA (0.2%) significantly reduced downy mildew symptoms in *H. annuus* [113]. *H. annuus* rust is another robust and economically important disease, which is known to cause significant damages and yield reductions in infected fields [110, 112]. Mutation and sequencing-based cloning and functional studies of a rust resistance gene were performed in *H. annuus* [112]. Most of the rust resistance genes (*R genes*), described so far, were found monogenic dominant. *Orobancha cumana* infects *H. annuus* roots in large areas of Europe and Asia, where it caused significant yield loss (up to 100%) [110, 114]. Seed pre-treatment with brassinosteroids was reported to stimulate *H. annuus* immunity against *O. cumana* infection [115].

3.6 Sesame

Due to changes in consumer lifestyle and health awareness programmes, the consumption of *S. indicum* is increasing globally, which is forecasted to be 100 million metric tonnes by 2030 [116]. However, a number of factors including: a narrow genetic base; the shattering of the seed-bearing capsule of *S. indicum* at harvest and

eventual unsuitability of this crop for mechanized harvesting; cultivation in marginal lands with poor management practices; and lack of production strategies has caused perceptible declines in both the global cultivated area of sesame and its yield potential [24, 117]. This list also includes exposure of sesame crops to many biotic and abiotic stresses; inefficient processing technology; and also the shifting in cultivation to other cash crops. The cultivated *S. indicum* is sensitive to salinity [118], drought [119], and waterlogging [120]. An elevated accumulation of an osmolyte proline (a good stabilizer of proteins and a regulator of cytosolic pH) was linked to a higher tolerance to salinity (50 and 100 mM NaCl) in *S. indicum* cv. Cumhuriyet [118]. Omics technologies have also differentially improved *S. indicum*-tolerance to major biotic and abiotic stresses [121, 122].

The growth and productivity of *S. indicum* may also be limited by phyllody (replacement of parts of a flower or the entire flower with leafy structures), which is associated with phloem-limiting phytoplasma, intracellular pathogens in Mollicutes class [24, 123]. *S. indicum* phyllody primarily spreads via leafhopper species, with *Orosius orientalis* as the major vector. Unfortunately, complete phytoplasma genome sequencing has not been undertaken yet [24]. Dry root rot (caused by a soil-borne Deuteromycetes fungus, *Macrophomina phaseolina*) is another widespread and destructive disease of *S. indicum* [24, 124]. Major disease-resistance mechanism against *M. phaseolina* involved 52 differentially expressed genes associated with different signaling pathways [125]. Earlier, *Fusarium* wilt-resistant genotype of *S. indicum* (Sanliurfa-63,189) was also identified [126]. Moreover, out of 28 *S. indicum* genotypes screened under field conditions, resistance of S2 and H4 cultivars of *S. indicum* to *Fusarium* wilt was reported [127].

Predicted through RNA-seq data analysis, a well-annotated data resource for transcriptomic signatures of abiotic and biotic stress responses, ‘Sesame Genomic Web Resource (SesameGWR)’ was recently developed in *S. indicum* [117]. SesameGWR is expected to boost the mining of various stress-associated genes and the molecular breeding of *S. indicum*. It will also help in developing climate-resilient *S. indicum* varieties and eventually in enhancing its growth and productivity (**Figure 6**) [117].

3.7 Safflower

Naturally gifted with a strong and deep tap root (which can grow to a depth of 2-3 m), *C. tinctorius* thrives under dry/xerophytic climates and marginal lands through extracting water from deeper soil layers (up to 5 feet). Mainly doing this, *C. tinctorius* satisfies its water requirements. Hence, *C. tinctorius* is considered a moderately tolerant oilseed crop to drought stress [128]. Despite this, varied abiotic stresses (including temperature and the soil moisture) were reported to severely impact *C. tinctorius* growth, development and the yield of oilseeds and seed-oil, and seed-oil quality. Exposure of *C. tinctorius* to drought stress during its flowering and seed filling stages was detrimental on its seed yield [129, 130]. Similarly, drought stress at the heading stage decreased seed and oil yields in *C. tinctorius* [131]. Moreover, drought stress was reported to decrease in *C. tinctorius* the yield of seed (9.4%) and oil (10.2%) and also linolenic acid (29.8%) and palmitic acids (28.5%) [35]. A higher proportion of oleic acid as compared to linoleic acid was observed in *C. tinctorius* exposed to a terminal heat stress [132]. The sowing dates, genotype characteristics, and the climate variability were also reported to significantly impact *C. tinctorius* yield, oil, and fatty acids [133, 134]. Several innovative approaches for genetic improvement of *C. tinctorius* stress resistance were also explored [135, 136].

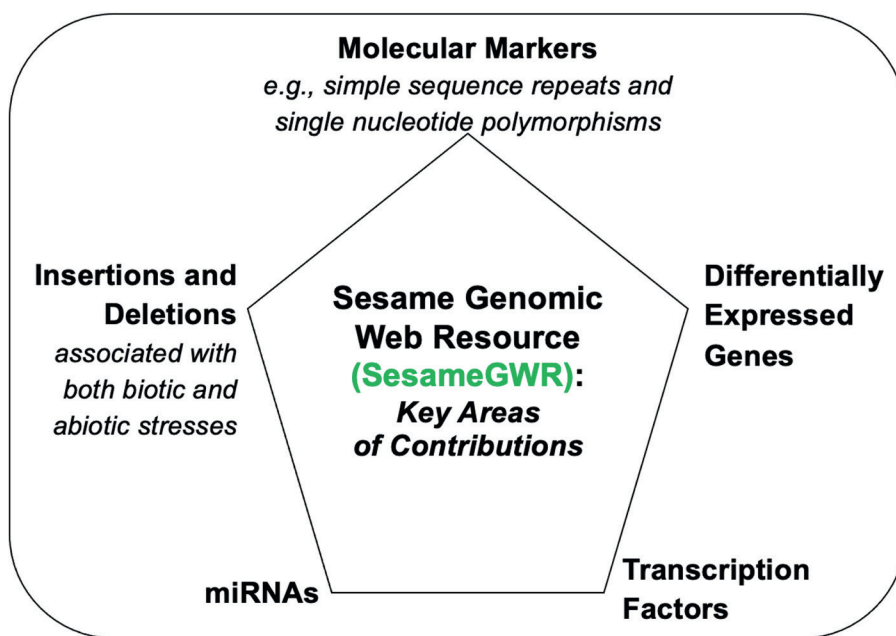


Figure 6.

Schematic representation of the key areas of contributions of Sesame Genomic Web Resource (SesameGWR), which is a well-annotated data resource for transcriptomic signatures of abiotic and biotic stress responses in sesame (*Sesamum indicum* L.) [117].

Important biotic stresses including leaf spot disease (caused by *Alternaria carthami*, *Cercospora carthami*, and *Ramularia carthami*), wilts (caused by *Fusarium oxysporum* and *Verticillium alboatrum*), powdery mildew (caused by *Leveillula taurica*), *Phytophthora* root rot (caused by several fungus-like organisms in the genus *Phytophthora*, including *P. cactorum* and *P. cryptogea*), and insects such as aphids and *C. tinctorius* fly are known to hamper *C. tinctorius* growth and productivity [137, 138]. Several insect pests also impact *C. tinctorius* health and productivity [139, 140]. To this end, *Acanthiophilus helianthi*, *Helicoverpa armigera*, and *Uroleucon carthami* were mainly found to diminish the productivity of *C. tinctorius* up to 35–80% [139]. Genetic mapping revealed two major QTLs (QUc-Ct3.1 and QUc-Ct5.1) associated with tolerance to the aphid, *Uroleucon compositae*, in *C. tinctorius* [140].

3.8 Niger

Major factors contributing to decreased growth and productivity in *G. abyssinica* include abiotic stresses, pathogens/diseases and parasitic weeds, low response to inputs, seed shattering due to indeterminate growth habit, lodging, insect pests, and diseases [36, 141–144]. Drought stress-caused differential growth and physiological alterations were observed in *G. abyssinica* cultivars [145]. Soil salinity is also a major constraint for the cultivation of *G. abyssinica* [141, 143]. Genomic identification of salt-induced microRNAs was done in *G. abyssinica*, which helped to get insights into the post-transcriptional regulatory aspect of the applied salt stress responses [143]. *G. abyssinica* is an outcrossing edible oilseed crop and has highly limited genomic

resources. To this end, RNA-Seq-based transcriptome sequencing of *G. abyssinica* genotypes provided novel genomic resources for this crop and also revealed micro-satellite frequency and distribution in its transcriptome [146]. The list of important diseases of *G. abyssinica* includes *Alternaria* blight (caused by *Alternaria porii* and *A. alternata*), leaf spot (caused by *Cercospora guizoticola*), seedling blight (caused by *Alternaria tenuis*), seed rot (caused by *Rhizoctonia bataticola*), rust (caused by *Puccinia guizotiae*), powdery mildew (caused by *Sphaerotheca* sp.), and root rot (caused by *Macrophomina phaseolina*) [142, 144]. Association of *Golovinomyces ambrosiae* and *Podosphaera xanthii* was investigated in causing powdery mildew disease of *G. abyssinica* in India [144].

4. Major breeding aims and progress

Edible seed-oils are preferred for domestic consumption due to their nutritional quality and numerous human health benefits. Edible seed-oil quality is largely based on the proportion of various fatty acids and other bioactive components. Recent breeding efforts in edible oilseed crops explored approaches for enhancing the quality of edible seed-oils through altering their major fatty acids and also other bioactive components. Major outcomes of the representative research done on improving the major seed traits (such as size, weight, yield, and oil quality) in specific edible oilseed crops under the umbrella of important breeding programmes are briefly highlighted hereunder.

4.1 Pea(ground)nut

A. hypogaea is a self-pollinated crop with cleistogamous flowers and exhibits limited genetic variation. To this end, gamma irradiation-mediated induced mutations was reported to develop *A. hypogaea* mutants (M1 generation) with improved morphological and quantitative characteristics and also with seeds having enhanced biochemical composition [147]. Moreover, a large number of mutant varieties (3402) (via gamma irradiation) was released through breeding in the world [148]. Induced biofortification of Fe and Zn metal ions in *A. hypogaea* oilseeds through a range of molecular-genetic and other approaches was also explored [149, 150]. Genetic, genomic, and breeding efforts have improved the *A. hypogaea* health and productivity and also the nutritional quality of its oilseeds [7]. Efforts have been made to address the major key challenges of *A. hypogaea* grain nutrient quality, minimizing carcinogenic and immunosuppressive aflatoxin contamination [151] and allergens [152], and improving oleic acid profile in its oil [153]. Quality traits (e.g., seed-oil and protein) were reported to have predominantly qualitative inheritance [154]. However, quantitative inheritances were also reported for seed-oil content and quality in *A. hypogaea* [155]. *A. hypogaea* has also been the focus of breeding programmes focused on developing its short duration and high-yielding varieties/hybrids [156, 157]. Fatty acid desaturase 2 (FAD2) enzymes are involved in the catalysis of the conversion of oleic acid to linoleic acid. At the same time, the oleic acid to linoleic acid conversion is argued as an important regulatory point linked both to improved abiotic stress responses, and the ratio of these two components decides the seed-oil quality [158]. Undertaking a CRISPR/Cas9-based site-specific genome modification approach, FAD2 cis-regulatory motifs were modified in *A. hypogaea* [158].

4.2 Cruciferous oilseeds

The development of cultivars with varied fatty acid composition to suit specific nutritional and industrial needs has been in focus of breeding programmes in cruciferous oilseeds. Notably, the pod-shattering trait has been reported to negatively affect the crop yield in oilseed *Brassicas* especially under dry conditions. Hence, identification of key genes and unraveling the pod-shattering mechanism thoroughly was argued which is very important for both understanding the trait better and also for cultivating higher resistance varieties [159]. Novel quantitative trait loci from an interspecific *B. rapa* derivative improved pod-shatter resistance in *B. napus* [160]. Moreover, major genes associated with senescence and polygalacturonase activity involved in pod shattering were unveiled in *B. napus* employing a comparative transcriptome and co-expression network analysis [160]. Expression divergence of FRUITFULL homeologs enhanced pod shatter resistance in *B. napus* [161]. Introgression of the *B. rapa* genome was exploited to expand the genetic variation of *B. juncea* [162]. Phenotypic variations for pod shattering, pod length and number of seeds per pod were investigated in large germplasm collections of *B. juncea* and its progenitor species, *B. rapa* and *B. nigra* [163].

Breeding programmes in cruciferous oilseeds are also focused on a very-long-chain monounsaturated fatty acid, erucic acid (C22:1, ω -9). An optimum level of erucic acid (low-erucic acid) (nationwide range: 2-5%) is important for health safety reasons. Low erucic acid *B. napus* seed-oil possess a large amount of unsaturated fatty acids (90%) and vitamin E. *B. napus* seed-oil has unique absorption rate by the human body (99%). Hence, the low erucic acid *B. napus* seed-oil is a nutritionally valuable edible oil and also occupies an important position in the food industry [164–166]. Low erucic acid *B. napus* seed-oil has also been granted Substances Generally Recognized as Safe status in the United States [164–166]. Notably, before the development of low erucic acid *B. napus* (with 0.36-3.0%), erucic acid content of *B. napus* seed-oil generally ranged from 45 to 50%. The loss-of-function mutations in the *FAE1* (*Fatty Acid Elongase 1*) gene and the *FAE2* (*Fatty Acid Elongase 2*) gene was revealed as the current selection for low erucic acid *B. napus* [166, 167]. A targeted mutation of the 845th base of *FAE1* resulted in a dramatic decrease in erucic acid content, which led to the development of world's first zero-erucic acid *B. napus* 'Oro' [168]. RNA interference (RNAi)-mediated inhibition of *FAE1* gene expression helped in decreasing erucic acid content of *B. napus* from 40% to less than 3% [169]. Intron-spliced hairpin RNA (ihpRNA)-mediated inhibition of *FAE1* gene expression decreased the erucic acid content of *B. napus* from 40% to 0.36% [170]. RNAi-mediated inhibition of *BnaFAE1* and *BnaFAD2* (*Brassica napus fatty acid* Δ 12-*desaturase 2*) expression decreased erucic acid content of low erucic acid *B. napus* from 0.87% to undetectable levels [171].

Since the first application of CRISPR/Cas9, *B. napus* genome editing was initiated, a critical mass of its genes were mutated [172, 173]. Eventually a valuable germplasm resource was generated for *B. napus* fundamental biological research and novel variety cultivation [172, 173]. For instance, CRISPR/Cas9 technology-assisted creation of targeted mutations on *BnaFAE1* (*BnaA08.FAE1* and *BnaC03.FAE1*) helped in the reduction of erucic acid content to nearly zero in *B. napus* [171]. Moreover, elevated seed-oil and protein content and altered fatty acid composition were obtained in *B. napus* mutants by knocking out the *BnTT8* gene mediated by CRISPR/Cas9 [172].

4.3 Soybean

The major breeding programmes for *G. max* aimed at improving the yield of its seed and seed-oil, protein and seed-oil composition and quality and also at its tolerance to the major biotic and abiotic stresses [174]. GWAS were performed for understanding insights into the modulators of seed-oil (and seed protein) *G. max* [175, 176]. A comprehensive GWAS identified QTLs for seed-oil contents and identified five genomic regions associated with seed-oil content [176]. A large portion of a selected region in the *G. max* genome was found occupied by overlapping QTL regions related to oil content [177]. *G. max* lines exhibiting stable oleic acid and linolenic acid across environments may be used as a source of germplasms with a desirable fatty acid composition [178]. *G. max* genetic transformation has become a valuable tool for the functional study of genes and the production of agronomically improved plants [77].

CRISPR/Cas9 system has enlightened *G. max* gene functions and has also improved important *G. max* traits, including yield, quality, and stress tolerance [78–80]. Based on the CRISPR/Cas9 system, stable male sterile lines were produced in *G. max* using the ABORTED MICROSPORES (AMS) homologs, where *GmAMS1* produced male sterile lines, whereas *GmAMS2* failed to produce [79]. Genetic regulatory networks of the *G. max* traits (seed size, oil and protein contents), and also the major strategies for improving the same, were also explored [179, 180]. GWAS and RNA-seq have identified *GmWRI1*-like transcription factor related to the seed weight in *G. max* [181]. Recently, GWAS was performed, and candidate gene mining of *G. max* seed size traits was done [182]. Major fatty acid desaturase genes were manipulated in *G. max* employing different molecular techniques such as induced mutagenesis [183], RNA interference [184], transcription activator-like effector nucleases genome editing [185], and CRISPR-cas9-mediated genome editing [186, 187]. *G. max* triacylglycerol lipase *GmSDP1* gene was reported to regulate the quality and quantity of seed-oil [188]. Transcription regulation of oil accumulation in *G. max* seeds was also enlightened [189, 190]. *G. max* WRINKLED1 transcription factor, *GmWRI1a* was found to positively regulate seed-oil accumulation [190]. Moreover, oil accumulation in *G. max* seeds was altered by modifying biosynthetic genes [191, 192]. A high-monounsaturated fatty acid *G. max* seed-oil was also successfully produced using *GmPDCTs* knockout via a CRISPR-Cas9 genome editing system [193].

4.4 Flax(lin)seed

The breeding programmes for *L. usitatissimum* largely aimed at improving yield of seed and oil and the quality of seed-oil [194–197]. Several QTLs for fatty acid composition and yield in *L. usitatissimum* were unveiled [195]. Three QTL each for oleic acid and stearic acid and two QTL each for linoleic acid and iodine value and one each for palmitic acid, linolenic acid, oil content were discovered [195]. These agronomic- and quality traits-associated QTLs may help in marker-assisted breeding as well as map-based cloning of key genes in *L. usitatissimum*. Earlier, GWAS have helped in the identification of single-nucleotide polymorphisms related to oil quality attributes [196, 197]. An association of seed color variation with yield and quality traits was observed in a diversity panel of *L. usitatissimum* [198]. Altered fatty acid content and composition (especially the increase of oleic acid content) were reported in *L. usitatissimum* employing the approaches based on RNA interference of *FAD2* gene encoding

the enzyme Fatty Acid Desaturase 2 [194]. Introduction of *Primula vialii*-sourced $\Delta 6$ -desaturase gene in *L. usitatissimum* increased therein the synthesis of ω -3 fatty acids [199]. Introduction of the *Solanum sogarandinum* glycosyltransferase (*SsGT1*) gene into *L. usitatissimum* genome elevated the accumulation of unsaturated fatty acids in *L. usitatissimum* seeds [200]. Significantly increased polyunsaturated fatty acids levels were observed in *L. usitatissimum* plants transformed with a chalcone synthase gene from *Petunia hybrida* [201]. The genetic diversity of stearoyl-ACP desaturase and fatty acid desaturase genes responsible for the fatty acid composition in *L. usitatissimum* cultivars and lines were investigated [202]. Heterosis for seed yield and its attributing traits in *L. usitatissimum* was also explored [203]. An apical meristem-targeted *in planta* transformation method can be promising for the successful development of transgenics in *L. usitatissimum* [204]. Genetic enhancement of major nutraceuticals was also attempted in *L. usitatissimum* [205].

4.5 Sunflower

The development of breeding *H. annuus* lines suitable for hybrid breeding, resistance to stresses (diseases, abiotic, biotic, and herbicides), and seed and oil yield and quality traits are mainly focused in *H. annuus* breeding [110, 206]. The fatty acid residue composition of the main oil lipids, triacylglycerides, and some of the minor lipids are the major determinants of the nutritional properties (and industrial use) of *H. annuus* seed-oil [207, 208]. QTLs controlling seed-oil content, oleic acid and linoleic acid content in *H. annuus* were mapped [209]. An F₂ mapping population from cytoplasmic male-sterile line COSF 7A (33-35% oleic acid) was developed. Additionally, high oleic acid inbred line HO 5-13 (88-90% oleic acid) was also phenotyped for oil content and oleic acid and linoleic acid content at the F₂ seed level [209]. The obtained QTLs may be useful in the marker-assisted selection breeding programme aimed at improving oil quality. Heterotic hybrids are required for the major improvements in *H. annuus*. These hybrids can be achieved by tapping combining ability of F₁ hybrids developed from crossing of two genetically diverse female lines with male testers [210]. Mutation breeding has also been argued rewarding for changed oil quality in *H. annuus* oilseeds [211]. Recommendation has also been made to employ 'pollen irradiation-mediated induction of haploid plants' for speeding-up breeding in *H. annuus* [212]. Combined high-resolution lipidome phenotyping and genome-wide genotyping has unveiled novel genetic determinants of seed-oil fatty acid content in inbred *H. annuus* lines [208]. Nutrigenomic approaches for understanding metabolic pathways of various quality traits in *H. annuus* was also explored [213].

4.6 Sesame

Over 27,000 genes and high genetic diversity in genes related to oil biosynthesis, resulting in variation in seed-oil content, were revealed through *de novo*-based assembly of the *S. indicum* genome [214]. Key genes associated with *S. indicum* seed-oil composition were identified in 705 accessions, where variation in seed-oil content was found associated with seed color [215]. GWAS have identified novel genes, *SiLTP3* and *SiACS8*, which were found related to seed yield traits, such as capsule length and number [214, 216]. The Ethiopian Institute of Agricultural Research (Addis Ababa, Ethiopia) developed and released a total of 32 improved *S. indicum* varieties through mass selection from among the local germplasm collections since 1976 [217]. Earlier, eight gamma ray (300-750 Gy)-induced closed capsule (indehiscent) mutants

were obtained from four different Turkish cultivars of *S. indicum* [218]. Moreover, hybridization has helped in a successful recovery of high-yielding *S. indicum* plants from a progeny of 103 crosses [219]. Important variants in *S. indicum* (with improved seed-oil yield, composition and quality) were generated employing genome editing technology [220]. Several favorable genes, QTLs, and genotypes were also discovered, which would act as a valuable genetic resource for *S. indicum* improvement [221]. CRISPR/Cas9 system and CRISPR/Cas9 coupled with hairy root transformation-mediated efficient targeted mutagenesis was efficiently created, and the major gene functions were assessed in *S. indicum* [222]. With the highlighted research progress, *S. indicum* has been transformed from an 'orphan crop' to a 'genomic resource-rich crop'.

4.7 Safflower

Unfortunately, the occurrence of low genetic diversity in *C. tinctorius*-breeding lines and cultivars restricts their utility in breeding programmes [223]. To overcome this issue, the prevalent genetic and phenotypic diversity among the global germplasm of *C. tinctorius* was extensively characterized. This has facilitated the identification of genetic determinants of trait variability and effective utilization of the prevalent diversity [224]. The genetic determinants of trait were also used in development of effective improvement programmes for *C. tinctorius* [224]. A scarcity of identified marker-trait associations is limiting the development of successful marker-assisted breeding programmes in *C. tinctorius*. To this end, a *C. tinctorius* panel (CartAP) comprising 124 accessions derived from two core collections was assayed for its suitability for association mapping [225]. The marker-trait associations were also identified, which are expected to facilitate marker-assisted breeding and identification of genetic determinants of trait variability in *C. tinctorius* [225]. Moreover, genetic variation among 131 *C. tinctorius* germplasm was argued to help in parental selection and the future breeding programmes for *C. tinctorius* [33]. Enhancements of γ -linolenic acid, α -linolenic acid, oleic acid, bioactive peptide, bioactive flavonoid, and stress resistance were also achieved [135, 136]. The miRNA expression pattern studied and novel miRNAs identified in developing seeds enlightened the role of miRNA in seed development and oil metabolism [226]. Genetic modification of *C. tinctorius* was also done for improved production of oils with distinct properties [227, 228]. The genetic origin and diversity of *FAD2-1* were identified and characterized in *C. tinctorius* [229]. This result could aid *C. tinctorius* breeders in reducing population size and generations required for the development of new high oleic acid varieties using perfect molecular marker-assisted selection [229].

4.8 Niger

G. abyssinica is known for its multiuse and numerous human health benefits. However, the average productivity of *G. abyssinica* in most world regions (including Ethiopia and Indian subcontinent) is very low. This may be due to the natural indeterminate growth habit, shattering lodging, and self-incompatibility (strict out-crossing nature) of *G. abyssinica* and/or due to its sensitivity to weeds, pests, diseases, and insects [230, 231]. *G. abyssinica* has been the focus of the major oilseed breeding programmes [232–234]. Mutation breeding was adopted for isolating mutants with desirable traits including seed yield and oil content [234, 235]. Individual and combined levels of gamma rays (24, 26, and 28 kR) and ethyl methane sulphonate (0.2 and 0.4% v/v) tested in *G. abyssinica* seeds (cultivar N-71) varying increased

grain yield and yield-related components [234]. *G. abyssinica* has a wide genetic basis, which may be used for the improvement of the species through conventional breeding and/or marker-assisted selection [230, 236]. Induced polyploidy has improved the major agronomic traits in economically important crop plants [237]. To this end, the tetraploidization in *G. abyssinica* plants (with larger capitula, larger seeds, and a greater number of seeds per capitula) was achieved by treating apical portion of *in vitro*-raised shoots with colchicine (0.02%) [233]. A highly efficient protocol for *in vitro* double haploid production was achieved employing anther culture, and Indian *G. abyssinica* varieties JNS 9 and JNS 28 were developed [238]. Moreover, double haploid was argued to develop inbred lines in a shorter time in problematic plants including *G. abyssinica*. Earlier, repeated selection and breeding increased oleic acid content from approximately 5-11% to 80-86% in *G. abyssinica* materials from Ethiopia [232]. Despite the highlighted above studies, *G. abyssinica* remained as an underutilized oilseed crop.

5. Conclusions and prospects

This chapter introduced the origin, key botanical insights, and the major health benefits of major herbaceous edible oilseed crops (*A. hypogaea*, *B. juncea*, *B. campestris* (syn. *B. rapa*), *G. max*, *L. usitatissimum*, *H. annuus*, *S. indicum*, *C. tinctorius*, and *G. abyssinica*) and overviewed the major constraints and their impacts on (and also enlightened important mitigation strategies adopted in) these major herbaceous edible oilseed crops. Additionally, it also highlighted the major aims and progress of important breeding programmes for the mentioned herbaceous edible oilseed crops (Table 1) (below).

Despite the nutritional and economic values of most edible oilseed crops, many constraints, and challenges limit their production and commercialization. The progressing worldwide climate changes are bound to cause elevations in temperatures, drought, and soil salinity, which are critical stress components in global edible oilseed crop cultivation. Efforts must be made to further improve the current cultivation and agronomic practices employed for the discussed edible oilseed crop (plants). Edible oilseeds-sourced oils are important commodity worldwide, and the quality of edible oils is largely decided by the proportion therein of fatty acids and other bioactive components. Genetic engineering for creating edible oilseeds with new properties and also with modified fatty acid composition may be achieved through intensifying research on overexpression, post-transcriptional gene silencing, and genome editing. Breeding efforts should also be made to employ advanced backcross QTL tools to further improve both the quality and quantity of edible oils produced. Efforts should be made to screen both the wild relatives of the edible oilseed crops and also the germplasms collected from various geographical locations and different stressful environments, and eventually these should be incorporated into edible oilseed crops-breeding programmes. Moreover, enhancements in yield and quality of edible oilseeds may also be made through getting major insights into the physiological responses and underlying genetics of stress tolerance in edible oilseed crops. The knowledge of how temperature and water regimes, and exposure to soil salinity during the phenological developmental stages (particularly during grain-filling) is important for selecting an environment or stable hybrids to produce grains (seeds) with the desired weight and oil and quality (oil fatty acid composition).

Concerted efforts should also focus minor, underutilized, or neglected edible oilseed crops, such as *G. abyssinica* and *C. tinctorius* (in addition to the major and

Herbaceous edible oilseed-bearing plants	Major breeding programme – outcomes	References
Pea(ground)nut (<i>Arachis hypogaea</i> L.)	Mutation (gamma irradiation-mediated) breeding-mediated release of mutant varieties with enhanced biochemical composition	[147, 148]
	Molecular-genetic and other approaches-mediated induction of biofortification of Fe and Zn metal ions in seeds	[149, 150]
	Grain nutrient quality, minimization of carcinogenic and immunosuppressive aflatoxin contamination and allergens, and improvement in seed-oil-oleic acid profile	[151–153]
	Developing its short duration and high yielding varieties/hybrids	[156, 157]
	CRISPR/Cas9-based site-specific genome modification approach-assisted unveiling of important insights into fatty acid desaturase 2 (FAD2) enzymes (involved in the catalysis of the conversion of oleic acid to linoleic acid)	[158]
Cruciferous oilseeds (<i>Brassica juncea</i> L. Czern. and Coss., and <i>Brassica campestris</i> L. syn. <i>B. rapa</i>)	Identification of key genes and unraveling the pod-shattering mechanism	[159–163]
	Long-chain monounsaturated fatty acid, erucic acid (C22:1, ω -9), and its optimum level	[164–171]
	CRISPR/Cas9-mediated genome editing for valuable germplasm resources, reduction of erucic acid content, elevated seed-oil and protein content, and altered fatty acid composition	[171–173]
Soybean (<i>Glycine max</i> L.)	Improving the yield of its seed and seed-oil protein and seed-oil composition and quality and its tolerance to the major biotic and abiotic stresses	[174]
	Understanding insights into the modulators of seed-oil (and seed protein)	[175, 176]
	CRISPR/Cas9 system-based production of stable male sterile lines	[79, 80]
	Identification of transcription factor related to the seed weight and size	[181, 182]
	Manipulation of major fatty acid desaturase genes	[183–187]
	Regulation of the quality and quantity of seed-oil	[188–190]
	CRISPR-Cas9 genome editing system-assisted production of a high-monounsaturated fatty acid seed-oil	[193]
Flax(lin)seed (<i>Linum usitatissimum</i> L.)	Unveiling important QTLs for fatty acid composition and yield	[195, 197]
	Insights into the association of seed color variation with yield and quality traits	[198]
	Alteration of fatty acid content and composition	[194, 199–202]
	Development of transgenics employing an apical meristem-targeted <i>in planta</i> transformation methods	[204]
	Genetic enhancement of major nutraceuticals	[205]

Herbaceous edible oilseed-bearing plants	Major breeding programme – outcomes	References
Sunflower (<i>Helianthus annuus</i> L.)	Development of breeding <i>H. annuus</i> lines suitable for hybrid breeding, resistance to stresses (diseases, abiotic, biotic, and herbicides) and seed and oil yield and quality traits	[110, 206]
	Insights into the modulation of seed-oil content and seed-oil-fatty acid composition (oleic acid and linoleic acid content)	[209–211]
	Pollen irradiation-mediated induction of haploid plants	[212]
	Combined high-resolution lipidome phenotyping and genome-wide genotyping-mediated unveiling of novel genetic determinants of seed-oil fatty acid content	[208]
	Nutragenomic approaches-assisted insights into the metabolic pathways of various quality traits	[213]
Sesame (<i>Sesamum indicum</i> L.)	Identification of key genes associated with seed-oil composition, seed color, and seed-oil content	[215]
	Identification of novel genes related to seed yield traits (such as capsule length and number)	[214, 216]
	Identification of closed capsule (indehiscent) mutants	[218]
	Hybridization-assisted recovery of high-yielding plants from progeny of large crosses	[219]
	Genome editing technology-mediated generation of the major variants (with improved seed-oil yield, composition, and quality)	[220–222]
Safflower (<i>Carthamus tinctorius</i> L.)	Extensive characterization-mediated identification of genetic determinants of trait variability and effective utilization of the prevalent diversity	[223, 224]
	Identification of marker-trait associations and identification of genetic determinants of trait variability	[225]
	Enhancements of γ -linolenic acid, α -linolenic acid, oleic acid, bioactive peptide, bioactive flavonoid, and stress resistance	[135, 136]
	Enlightening the role of miRNA in seed development and oil metabolism	[226]
	Identification and characterization of genetic origin and diversity of <i>FAD2-1</i>	[229]
Niger (<i>Guizotia abyssinica</i> L.)	Repeated selection and breeding-mediated increase in oleic acid content	[232]
	Tetraploidization-assisted achievement of cultivars with larger capitula, larger seeds, and a greater number of seeds per capitula	[233]
	Mutation breeding-mediated isolation of mutants with desirable traits including seed yield and oil content	[234, 235]
	Another culture-mediated production of <i>in vitro</i> double haploids	[238]

Table 1.
Summary of important outcomes of the major breeding programmes on the herbaceous edible oilseed-bearing plants (discussed in the current chapter).

dominating edible oilseed crops), and increase their production and utilization. In order to implement genetic transformation on *G. abyssinica*, *C. tinctorius*, and other dominating edible oilseed crops, an establishment of a reproducible transformation protocol should be a priority task. Immense genetic potential of crop wild relatives (CWRs) (CWR mutant and over-expression lines) may be exploited for producing edible oilseed crops with both improved resistance against various (a)biotic stresses and enhanced seed-oil and fatty acid composition and quality. Extensive research on this aspect in edible oilseed crops would yield promising results. Efforts should be made to focus also on omics profiling tools (such as genomics, epigenomics, transcriptomics, proteomics, metabolomics, and phenomics), which may make the genetic improvement of discussed above major edible oilseed crops easy, feasible, and successful. Moreover, in the pursuit of the genetic improvement of the major/dominating, and also minor (underutilized, or neglected) edible oilseed crops, there is urgent need to adopt the use of genome editing technology based mainly on Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR).

A trend of using the major oilseed crops as a sustainable alternative for energy generation is rapidly increasing. However, this could threaten both the nutritious food availability and also the food security particularly in developing countries. Hence, the use of either of the major and minor edible oilseed crops as an alternative for biodiesel etc., could only be profitable when these crops are produced on a large scale.

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