Chapter 1
Breeding Major Oilseed Crops: Prospects and Future Research Needs

A. L. Rathnakumar and M. Sujatha

Abstract Oils obtained from plants have been used primarily for edible purposes and to a greater level in industries. Edible plant oils (EPOs) are extracted mainly from 11 plant sources: 2 are of tree origin, namely, oil palm and coconut; 9 are from annuals like soybean, groundnut, rapeseed-mustard, sunflower, safflower, sesame, cotton seed, and maize and rice (bran); and 2 crops, castor and linseed, are exclusively used for industrial purposes. Although several other sources of oils are also available, their production and use are limited to specific regions. The major objectives in oilseed crop improvement are enhancement of seed and oil yield, quality of oil for edible and industrial purposes, and development of varieties to suit different cropping systems having inbuilt resistance or tolerance to major biotic and abiotic stresses. Achievements in varietal breeding programs of nine annual oil crops and future research needs have been discussed. This chapter also summarizes developments in genomics and other biotechnological tools in seven edible oil crops, namely, *Brassica*, soybean, groundnut, sunflower, sesame, niger, and safflower, and in two industrial crops, viz., castor and linseed, with special emphasis on the prospects of molecular markers in genetic improvement of these crops. Molecular markers reported for genetic diversity assessment and mapping and tagging genes/QTLs for different oil quality traits and their use in marker-assisted selection have also been presented.

Keywords Molecular marker-assisted selection · Genetic resources · Oil quality · Trait breeding · Metabolic engineering

1.1 Introduction

Oils of plant origin have been used since ancient times and have been used in many ways. Predominantly, oils are used for edible purposes. Oils are also used in medicines and pharmaceuticals, industries, biodiesel, and pet foods and as components

---

A. L. Rathnakumar · M. Sujatha (✉)
ICAR-Indian Institute of Oilseeds Research, Hyderabad, India
e-mail: a.rathnakumar@icar.gov.in

S. S. Gosal, S. H. Wani (eds.), *Accelerated Plant Breeding, Volume 4*,
https://doi.org/10.1007/978-3-030-81107-5_1

of many other products. During the last three decades, the oil crop production in the world has increased to 240%, while the increase in area and in yield was to the tune of 82% and 48%, respectively (El-Hamidi and Zaher 2018). Over the last few decades, the adoption of these crops has been growing up significantly, cultivated in about 324 million hectares in 2019 worldwide (www.FAOSTAT.org). The prime reason for this phenomenal growth is seed oils are not only a demand for various industries and also for the possibility to use their subproducts (metabolites) in biofuel development (Yadava et al. 2012).

Oilseed crops are very diverse in the plant kingdom and belong to several families, and oils are extracted mainly from their seeds, germs, and/or fruits. About 13 each of herbaceous and woody crops are reported to be important sources of oil (Zhou et al. 2020), but 10 herbaceous and 2 woody (coconut, oil palm) sources are considered important on the basis of their global production and use. Among the different oil-yielding crops, soybean (*Glycine max* L. Merr.), rapeseed/canola (*Brassica rapa* L. var. yellow sarson/brown sarson/toria; *Brassica napus* L.ssp. *oleifera* DC var. *annua* L.; *Eruca sativa* Mill.), mustard (*Brassica juncea* (L.) Czern. & Coss; *Brassica nigra* L. Koch; *Brassica carinata* A. Braun), palm (*Elaeis guineensis* Jacq.), sunflower (*Helianthus annuus* L.), cottonseed (*Gossypium hirsutum* L.), peanut or groundnut (*Arachis hypogaea* L.), sesame (*Sesamum indicum* L.), niger (*Guizotia abyssinica* (Lf). Cass.), and camelina (*Camelina sativa* (L.) Crantz) are commonly used oils, while castor bean (*Ricinus communis* L.), *Jatropha* (*Jatropha curcas* L.), tung tree (*Aleurites fordii* Hemsl.), jojoba (*Simmondsia chinensis* (Link) C. K. Schneid.), *Sachainchi* (*Plukenetia volubilis* L.), and others are used for industrial purposes. Although linseed or flax (*Linum usitatissimum* L.) oil is predominantly used for industrial applications such as oil paint, linoleum, and varnishes, in few pockets seeds of linseed and oil are used for edible purpose. Details of distribution, oil content, and fatty acid composition of important oil crops, chromosome number, genome size, and genomic resources of major oil crops have been provided (Table 1.1).

Analyses of the data of the past three decades on area, production, and productivity (www.FAOSTAT.org) of the eight annual oil crops (soybean, rapeseed-mustard, groundnut, sunflower, sesame, safflower, and linseed) except for niger revealed (Fig. 1.1) that soybean exhibited a phenomenal growth in area over the past three decades from 54.9 million ha in 1991 to more than its double (125.85 million ha) in 2017; production tripled from 102.8 million tons during the year 1991 to 359.5 million tons during 2017. The yield levels of soybean gradually increased from 1873 kg/ha in 1991 to 2857 kg/ha in 2017 with a coefficient of variation of just 11% indicating a slow and steady growth in yield.

In rapeseed-mustard, area, production, and yield witnessed a steady growth. Area increased from 17.6 million ha (1990) to 36.9 million ha (2018) with an average of 28.2 million ha over the three decades. Production varied from 24.4 million tons (1990) to as high as 76.6 million tons (2017), whereas the productivity ranged from 1308 kg/ha (1994) to 2142 kg/ha (2017).

Same is the trend for groundnut which exhibited a steady growth in area from 19.8 million ha (1990) to 29.7 million ha (2018) with an average of 24.3 million ha

Table 1.1 Basic information on family, chromosome number, genome size, distribution, mode of pollination, oil content, and fatty acid composition of important oil crops

No.	Common name	Species	Family	Chromosome number	Genome size (Mb)	Pollination mechanism	Main producing area	Oil content (%)	Saturated FA (%)	Oleic acid (%)	Linoleic acid (%)	Linolenic acid (%)
1	Soybean	*Glycine max* (Linn.) Merr.	Leguminosae	2n = 4x = 40	1115	Self-pollination	The USA, Brazil, Argentina, China, India, Paraguay, Canada	18–24	15.1	15.0–36.0	42.8–58.1	2.0–14.0
2	Rapeseed	*Brassica napus* L.	Brassicaceae	2n = 4x = 38	1187	Cross-pollination	All over the world	37–46	6.3	56.0–72.0	13.8–24.6	4.3–11.3
3	Sunflower seed	*Helianthus annuus* L.	Asteraceae	2n = 2x = 34	3000	Cross-pollination	All over the world	46–50	12.2	16.4–27.6	60.2–72.1	0.07–1.8
4	Peanut/groundnut	*Arachis hypogaea* L.	Leguminosae	2n = 4x = 40	2800	Self-pollination	Asia, Africa, America	46–57	14.8	37.0–55.6	25.3–39.7	0.40–3.2
5	Sesame	*Sesamum indicum*	Pedaliaceae	2n = 2x = 26	948	Often-cross-pollination	Tropical and temperate regions	43–61	12.4–14.4	36.7–42.0	43.2–48.6	0.2–0.95
6	Linseed/flax	*Linum usitatissimum* L.	Linaceae	2n = 2x = 30	686	Self-pollination	Mediterranean region, Euro-Asian	26–45	9.5	19.9	15.9	52.7

(continued)

Table 1.1 (continued)

No.	Common name	Species	Family	Chromosome number	Genome size (Mb)	Pollination mechanism	Main producing area	Oil content (%)	Saturated FA (%)	Oleic acid (%)	Linoleic acid (%)	Linolenic acid (%)
7	Safflower	*Carthamus tinctorius* L.	Asteraceae	2n = 2x = 24	1350	Predominantly self-pollination; extent of cross-pollination depends on bee activities	India, the USA, Ethiopia China, Russia, Japan, North Korea, Iran	27–25	9.0	13.1	77.7	–
8	Cotton	*Gossypium* spp.	Malvaceae	2n = 2x-52	2200	Often cross-pollination	China, the USA, India, Uzbekistan, Egypt	15–40	27.9	17.6	53.3	0.3
9	Corn	*Zea mays* L.	Gramineae	2n = 2x = 20	2355	Cross-pollination	Tropical and temperate regions of the world	4.5–4.8	14.4	27.5	57.0	0.9
10	Rice	*Oryza sativa* L.	Poaceae	2n = 2x = 24	430	Self-pollination	Almost everywhere, expect Antarctica.	15–23	19.6	43.8	34.0	1.2
11	Hemp	*Cannabis sativa* L. subsp. sativa	Moraceae	2n = 2x = 20	800–900	Cross-pollination	All over the world	25–35	19.0	59.6	3.4	18.0
12	Grape	*Vitis vinifera* L.	Vitaceae	2n = 2x = 38	500	Cross-pollination	All over the world	10–20	10.4	14.3	74.7	0.15

No.	Common name	Species	Family	Chromosome number	Genome size (Mb)	Pollination mechanism	Main producing area	Oil content (%)	Saturated FA (%)	Oleic acid (%)	Linoleic acid (%)	Linolenic acid (%)
13	Perilla	*Perilla frutescens* (L.) Britt.	Labiatae	2n = 2x = 40	--	Self-pollination	India, Myanmar, Japan, Korea, Indonesia	40–50	17.0	11.0	17.0	55.0
14	Coconut	*Cocos nucifera* L.	Palmae	2n = 2x = 32	2478	Cross-pollination	Indonesia, Philippines, India, Sri Lanka, Brazil, Vietnam, Papua New Guinea	60–64	91.4	6.5	1.5	–
15	Oil palm	*Elaeis guineensis* Jacq.	Palmae	2n = 2x = 32	1800	Cross-pollination	Indonesia, Malaysia, Thailand, Columbia, Niger, Ecuador	50–56	43.8–54.2	37.4–44.1	8.7–12.5	0–0.6
16	Castor	*Ricinus communis* L.	Euphorbiaceae	2n = 2x = 20	320	Cross-pollination	India, China, Brazil, Mozambique, Paraguay, Thailand	40–55	3.0	4.0 (88)[a]	4.0	–
17	Niger	*Guizotia abyssinica* Cass	Asteraceae	2n = 2x = 30	978	Cross-pollination	Africa, Ethiopia, India, West Indies, Bangladesh, Bhutan	30–40	14.0	10.0	76.0	–

[a] In castor, predominant fatty acid is ricinoleic acid (hydroxyl-oleic acid) and constitutes about 88% of the total fatty acids

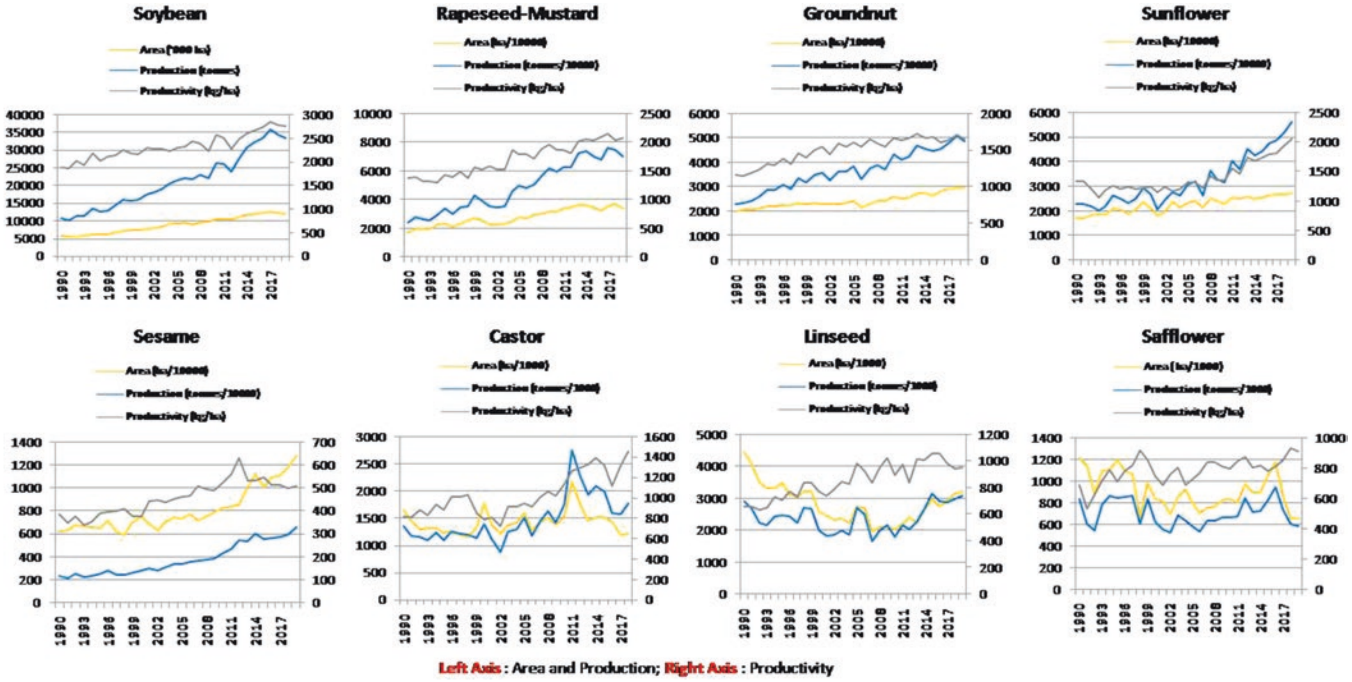

Fig. 1.1 Trends of area, production, and yield of major oil crops (1990–2019)

over the three decades; production increases from 23.0 million tons (1990) to 50.8 million tons (2018); and yields dwindled from 1151 kg ha in the year 1991 to 1722 kg in 2013 and 1713 kg per ha in 2018. The coefficients of variation for both area and yield over the three decades remained very low (11%) indicating a slow growth both in area and yields especially in India and Africa.

Sunflower area was not dramatic during the last three decades, and it varied from 17.03 million ha (1990) to 26.80 million ha (2017). Production dwindled between from 20.02 million tons in 1993 to 51.90 million tons in 2018. The yield levels varied from 1066 kg/ha in 1993 to 1937 kg/ha in 2018.

Sesame area increase was just lower than double its value over 1990, i.e., from 6.13 million ha in 1990 to 11.8 million ha in 2018 despite the demand. Rise in production was from 2.2 million tons during 1991 to 5.9 million tons in 2018, and the increase is mainly registered through increase in area. However, the yield levels ranged from 348 kg/ha in 1990 and reached an all-time high of 633 kg/ha in 2013 and dropped down further to 502 kg/ha in 2018. The increase in yields of sesame over three decades is only 30%.

However, in case of both safflower and linseed, there was a steep decline in area. Safflower area was 1.2 million ha in 1990 and reduced to 0.65 million ha in 2018; production also exhibited a decreasing trend (0.84 million tons in 1990 to 0.61 million tons in 2018), but productivity showed a slight increase (from 690 kg in 1990 to 929 kg in 2018) of about 390 kg/ha over the last three decades. Meanwhile, linseed area declined from 4.4 million ha in 1990 to 3.2 million ha in 2018, but production and yield showed a marginal increase (production: 2.9 million tons in 1990 to 3.1 million tons in 2018; productivity: 658 kg/ha in 1990 to 944 kg/ha in 2018).

Over three decades, average castor area remained at about 1.41 million ha although the area reached an all-time high of 17.4 million ha in the year 2012. Castor productivity witnessed a gradual increase from 800 kg/ha to 1300 kg/ha, the lowest yield being 781 kg/ha in the year 2000 to as high as 1452 kg/ha in the year 2018. Year-to-year and regional variations were not uncommon for area, production, and productivity in all the oilseed crops.

During the last triennium (2016–2019), the extraction of oils from the major sources around the world was 66.18 million tons of palm oil, 7.17 million tons of palm kernel oil, 55.05 million tons of soybean oil, and 24.40 million tons of rapeseed oil. Together these four oils contributed to 88% of total edible oil production of the world. The rest are groundnut or peanut oil (5.59 million tons), cotton seed oil (4.37 million tons), olive oil (3.39 million tons), maize oil (3.15 million tons), coconut oil (3.07million tons), rice bran oil (1.60million tons), sesame oil (1.10 million tons), linseed oil (0.76 million tons), and safflower oil (0.09 million tons) (www.FAOSTAT.org).

1.2 Genetic Resources and International Institutions

Availability of diverse germplasm with heritable variations is very important for continued success in any breeding program. Most of the oil crops currently grown across the globe are spread far away from their primary centers of origin and resulted in adaptation to specific environments/regions where they are being presently cultivated leading to narrow genetic base in these crop species (Jones 1983; Wang et al. 2017). Therefore, the oil crop germplasm of any country would comprise only few accessions from the origin, primary and secondary centers of diversity and more of breeding materials and cultivars developed using these sources, thus further reducing the genetic variation that could be exploited in crop improvement programs.

There are now (by 2019) more than 1750 individual gene banks worldwide, holding a total of around 7.4 million accessions of germplasm, in which about 130 of them hold more than 10,000 accessions each (www.CGIAR.org; https://www.cgiar.org/news-vents/news/guardians-of-diversity-the-network-of-genebanks-helping-to-feed-the-world).

Genebanks are located in all continents, but these are relatively fewer in Africa compared with the rest of the world. Substantial ex situ collections in botanical gardens (2500 around the world) of various plant species are also being maintained. The data of 290 gene banks of different countries, regions, and CGIAR centers indicate that among the different crop species conserved ex situ, oil crops constitute only 3% (FAO 2010), clearly indicating the priority for the oil crop genetic resources in terms of collection, multiplication, evaluation, and conservation has been very low globally. Moreover, these crops have gained economic importance only a couple of decades before, and few of them as secondary sources of oil (rice bran, corn, cotton seed oils) are being exploited only of late. Among the oil crops, only in groundnut and soybean over 15,000 accessions each are currently being maintained by two centers, viz., ICRISAT Asia Centre, Patancheru, India, and SINGER (System-wide Information Network for Genetic Resources) network, respectively. Among the 15,000 groundnut accessions maintained at ICRISAT, only 453 are wild forms and the rest are cultivated forms which exhibit limited morphological variability except for their growth forms (Dwivedi et al. 2007). In case of soybean, most of the accessions maintained by SINGER network are vegetable types. The European Plant Genetic Resources gene banks, the largest network of gene banks numbering 441 (43 national inventories and 398 individual holding institutions), the total number of accessions maintained in the two major oil crops of Europe was only 4879 in case of oil rape and 4444 in case of sunflower against a total collection of 20.19 million accessions of ten important crop species (Vollmann and Rajcan 2009; ECPGR 2019). Notwithstanding these facts, the conservative estimates of FAO indicate that out of about 7.4 million accessions which are currently being maintained in different countries, between 25 and 30 percent of the total holdings (1.9–2.2 million accessions) are only distinct, and the rest are duplicates held either in the same or, more frequently, a different collection (Jaramillo and Baena 2002). Hence, there is an urgent need to augment and enhance the collection of the valuable genetic resources and evaluate for specific/target traits, and incorporating them in breeding programs remains the foremost activity in genetic enhancement of the oil crops.

1.2.1 Gene Pools

Harlan and de Wet (1971) proposed a three-gene pool concept, primary (GP-1), secondary (GP-2), and tertiary (GP-3), for effective utilization of germplasm resources in crop improvement programs. Genetic resources are identified or developed through multidisciplinary approaches by plant exploration, taxonomy, genetics, cytogenetics, plant breeding, microbiology, plant pathology, entomology, agronomy, physiology, wide hybridization, and molecular biology, including cell and tissue culture, DNA analyses, and genetic transformation. These efforts have produced superior oilseed cultivars with resistance to abiotic and biotic stresses and improved oil quality and quantity. The concept of primary, secondary, and tertiary gene pools and genetic transformation has played a key role in improving oilseed crops.

1.2.2 Primary Gene Pool

The primary gene pool (GP-1), consisting of landraces and biological species, has been identified for most of the oilseed crop species. Wild progenitors of cultivated oilseed crops are identified, postulated, and proposed based on geographical distribution, classical taxonomy, cytogenetics, and molecular methods. For example, the GP-1 for soybean ($2n = 40$) is only its wild annual progenitor *Glycine soja* Sieb. and Zucc. ($2n = 40$) (Chung and Singh 2008). Castor belongs to the monotypic genus *Ricinus* of the *Euphorbiaceae*. Although several authors have classified *R. communis* into different species and subspecies on the basis of morphological traits and geographical distribution, none of them are accepted as true species or subspecies and they represent merely the local types or ecotypes adapted to different environmental conditions or human selection (Weiss 2000). For rapeseed, six species depicted in the famous U triangle, viz., *Brassica carinata* (Ethiopian mustard; $2n = 34$), *Brassica juncea* (Indian mustard, brown mustard; $2n = 36$), *Brassica napus* ssp. *napus* (oilseed rape, fodder rape: $2n = 38$), *B. napus* ssp. *napobrassica* (Swede; $2n = 38$), and *B. napus* ssp. *napus* var. *pabularia* (leaf rape, kale; $2n = 38$), constitute the primary gene pool (Morinaga 1934; U., N 1935). Groundnut is an allotetraploid species ($2n = 4x = 40$) that evolved from natural doubling of a cross between two diploid progenitors (*A. duranensis* Krapov. and W.C. Gregory and *A. ipaënsis* Krapov. and W.C. Gregory) (Bertioli et al. 2016; Stalker 2017; Levinson et al. 2020). Four *Arachis* gene pools contain 80 species, distributed among 9 sections, and are native to 5 countries of South America. The primary gene pool consists of landraces and traditional cultivars of groundnut from primary and secondary centers of genetic diversity in South America and other groundnut-growing countries, and one tetraploid wild species *A. monticola* found in northwest Argentina has crossability success with *A. hypogaea* producing normal segregants (Singh and Simpson 1994; Singh and Nigam 2016).

The genus *Helianthus* comprises 53 species within the tribe *Heliantheae* of the family *Asteraceae*, and the cultivated sunflower (*Helianthus annuus* var. *macrocarpus*) has been derived from a widely branched annual plant with many flower heads otherwise called the common sunflower (*H.annuus var. annuus*) (Heiser Jr. 1955). The primary gene pool of the sunflower consists of both cultivated and wild varieties of *Helianthus annuus*, as well as winter's sunflower (*Helianthus winteri* J.C. Stebbins), a perennial species found in the southern Sierra Nevada foothills of California.

Wild species of sesame vary in their habitat, morphological features, and ploidy levels, the latter of which is represented by three chromosome groups: 26, 32, and 64 (Joshi 1961). The progenitor species of cultivated sesame are unknown as no wild species except for *S. malabaricum*, which produces fertile hybrids with *S. indicum*, are known (Weiss 2000). These two species form the primary gene pool of sesame.

The genus *Carthamus* consists of 25 species, distributed worldwide. Among the 25 safflower species, the cultivated safflower grown around the world is only *Carthamus tinctorius* L., containing 12 pairs of chromosomes (Patel and Narayana 1935; Richharia and Kotval 1940). Based upon the chromosome numbers, the genus was categorized into four sections, and the three closely related annual species *C. tinctorius*, *C. palaestinus*, and *C. oxyacantha* together with cultivated types sharing the same chromosome number (2n = 24) are placed in section I. Among these three species, *C. oxyacantha* is proposed to be the wild ancestor of cultivated safflower (Bamber 1916; Ashri and Knowles 1960). Recent DNA sequence-based analyses in four species of safflower revealed that the progenitor species of safflower is most likely *C. palaestinus* which is a self-compatible species native to southern Israel to western Iraq (Chapman and Burke 2007a, b).

Chromosome pairing indicated that cultivated niger, *Guizotia abyssinica* and *G. scabra* subsp. *schimperi*, are morphologically very similar, both annuals, and are attacked by the same pests and diseases. Both species have 2n = 30 chromosomes with a similar karyotype. The hybrid between *G. abyssinica* and *G. scabra* subsp. *schimperi* is fertile and forms 15 bivalents in 95% of the pollen mother cells indicating that *G. scabra* subsp. *schimperi* are the probable progenitor species of niger (Murthy et al. 1993). In both safflower and niger, cytomorphological and molecular phylogeny analyses will throw more light for exploitation of diversity and genetic enhancement in these crop species.

The flax or linseed genus, *Linum*, is a large group with ~230 species (Heywood 1993). The genus is divided into five sections, *Linum*, *Linastrum*, *Cathartolinum*, *Dasylinum*, and *Syllinum*, based on chromosome number, floral morphology, and interspecific compatibility (Gill 1987). Cultivated flax, *L. usitatissimum*, is placed in the section *Linum* and has 30 diploid chromosomes (Tammes 1928). The other species, *L. angustifolium*, also known as pale flax, is closely related to flax, found mainly in Mediterranean Sea, Iran, and the Canary Islands, and has a similarity to cultivated flax (Diederichsen and Hammer 1995). Both cultivated and pale flax are homostylous, inbreeding species and share similarity in chromosome number (Gill 1987; Tammes 1925). The genetically similar behavior of *L. angustifolium* and *L. usitatissimum* and the ease of hybridization with each other in any direction (male or female) resulting in infertile hybrids (Gill 1966) suggest that *L. angustifolium* is the wild progenitor of flax (Dillman and Goar 1937) and thus form the primary gene pool of flax.

1.2.3 Secondary, Tertiary, and Quaternary Gene Pools

The secondary gene pool (GP-2) includes all species that can be hybridized with GP-1 with at least some fertility in F_1s resulting in gene transfer (Harlan and de Wet 1971). *Glycine max* and castor (*R. communis*) do not have GP-2. The GP-2 for *Brassica* oilseeds includes *B.nigra*, *B.oleracea* (includes crop varieties, *B.alboglabra*, *B. bourgeaui*, *B.cretica*, *B.hilarionis*, *B.incana*, *B.insularis*, *B. macrocarpa*, *B.montana*, *B.rupestris*, *B.villosa* and *B.rapa* (includes wild and cultivated varieties). In case of groundnut, the secondary gene pool consists of diploid species from section *Arachis* which are cross-compatible with cultivated groundnut and produce sterile to partially fertile hybrids despite ploidy differences (Singh and Simpson 1994; Singh and Nigam 2016). Two sesame species namely, *S. alatum* and *S. prostratum*, have been placed under gene pool-2 due to barriers in hybridization with *S. indicum* (Raghavan and Krishnamurthy 1947; Rajeswari and Ramaswamy 2004) although in few reports no seed set has been observed for *S. alatum* during hybridization (Lee et al. 1991;Rajeswari and Ramaswamy 2004).

The tertiary gene pool of soybean comprises 26 wild perennial species of the subgenus *Glycine*. These species are indigenous to Australia and are geographically isolated from *G. max* and *G. soja* (Newell and Hymowitz 1983; Singh 2019). Species that belong to the sections *Procumbentes*, *Erectoides*, and *Rhizomatosae* which are partially cross-compatible with species of section *Arachis* and *A. hypogaea* are grouped under tertiary gene pool in groundnut. The rest of the species of five sections (*Caulorhizae*, *Heteranthae*, *Extranervosae*, *Triseminatae*, *Trierectoides*) of groundnut that are cross-incompatible or very weakly cross-compatible to species of section *Arachis*, form the quaternary gene pool. The gene flow among different gene pools and between different sections and within tertiary and quaternary gene pools is generally limited (Gregory and Gregory 1979; Singh and Nigam 2016). One species of sesame, namely, *S. radiatum*, is placed in gene pool-3 of sesame due to lack of capsule formation, no seed set, and use of embryo rescue methods (Singh et al. 2016) upon hybridization.

1.2.4 Utilization of Genetic Resources in Oil Crops

Despite availability of vast germplasm resources in the oil crops, the genetic base of different cultivars developed in each of these crops is very narrow (Hyten et al. 2016; Holbrook et al. 2014; Wang et al. 2017; Khedikar et al. 2020). For example, in soybean, it has been reported that for northern and southern North America breeding pools, there were only 19 ancestors with 17 of them common to both regions of the USA. The 19 ancestors contributed to 85% of the genes to each region (Gizlice et al. 1994; Hyten et al. 2016; Cober et al. 2009). The same is true for oilseed rape as well, and the major reason can be attributed to geographical constraints, selection bottle necks during origin of species, and subsequent domestication. More specifically, the modern canola varieties with zero erucic acid and low glucosinolate originate from only two varieties: “Liho” and “Bronowski” (Hasan et al. 2006; Friedt and Snowdon 2009). Of the canola varieties released in Australia from 1995 to 2002, 11 ancestral varieties contributed 98.7% of the pedigree composition, and 2 ancestors (Canadian low erucic spring variety “Zephyr” and Polish low glucosinolate spring variety “Bronowski”) were present in the pedigrees of every variety (Cowling 2007).

In groundnut, although large number of accessions have been evaluated for desirable traits either at USDA or ICRISAT, relatively few accessions only have been utilized in breeding programs for cultivar development in the USA and ICRISAT (Isleib et al. 2001; Dwivedi et al. 2007) leading to narrow genetic base of the cultivars. In spite of the large number of cultivars available to growers, the US groundnut crop has been characterized as being genetically vulnerable to diseases and insect pests (Hammons 1972; Hammons 1976; Knauft and Gorbet 1989). This has been due to the commercial success of specific cultivars grown in particular production areas. For example, in the three major production regions of North America, the runner-type cultivar ‘Florunner’ dominated the southeastern US. (Georgia, Florida, and Alabama which produces approximately 65 percent of all USA-grown groundnut) from 1972 to 1993 and in the Virginia-Carolina (VC) production area (which accounts for nearly 13 percent of all USA-grown groundnut),the most dominant cultivar over 40 years in the VC areawas ‘Florigiant’. Even in India, a single variety, “GG 20” (released and notified in 1992), developed by Gujarat State Agricultural University is grown in almost 60–70% of area (about 1.2 million ha) under groundnut in the state and has become popular in other states as well. The narrow genetic base of cultivars in castor and coconut owing to their monotypic species nature is also an impediment for further genetic improvement in these crops.

One of the ways that plant breeders can increase the genetic diversity of a crop is to incorporate diverse germplasm into the breeding populations from which thousands of accessions and cultivars can be derived. Besides the variability available in primary gene pool of different oil crop species, introgression of useful genes from wild species into the cultivated species has attracted the oil crop breeders because of their resistance to diseases and insect pests for which the genetic variation in primary gene pool is limited. The most accessible variability of primary and secondary gene pools has been successfully utilized in few crop species like soybean and groundnut. Further success in introgression of the novel genes like resistance to major insect pests and diseases and drought and cold and heat tolerance into the cultivated background has been limited due to poor understanding of genome relationships, cross-incompatibility, and nonavailability of true progenitor species. The exploitation of tertiary and quaternary gene pools awaits advancement in the biotechnological techniques/interventions and policy decision with regard to release of transgenic varieties and genome edited lines at global level (Singh and Nigam 2016).

1.3 Mode of Pollination and Breeding Behavior in Oil Crops

Many of the edible oil crops exhibit a wide range of pollination mode/mechanism(s) like self- and cross-fertilization, self-incompatibility, etc. notably seed cotton, coconut, sunflower, rapeseed, and niger. Sunflowers have one of the two pollination systems; in most oil-producing cultivars, the flower switches between the male and female phases, whereas in hybrid production, specifically bred male and female lines are planted within the same field. Both benefit from insect visitation to optimize pollen transfer to female plants (Free 1993). Rapeseed and canola are highly self-compatible and readily set pods with wind and self-pollination; further, their high nectar concentration makes them attractive to insects which can increase pollen transfer and increase the total yield by 20% (Bommarco et al. 2012; FAO 2018). In seed cotton, biotic pollination resulted in a 20% increase in seed weight and a 16% increase in lint production (Rhodes 2002; Potts et al. 2014).

Some edible oil crops gain very little benefit from pollination, such as soybean, groundnut, and linseed (Williams 1991; Palmer et al. 2001a, b), whereas olive is entirely wind pollinated (Klein et al. 2007). Safflower and sesame are basically self-pollinated but certain degree of cross-pollination does occur in sesame (Ashri and Knowles 1960; Andrade et al. 2014) due to bee activities, while bees, butterflies, and other flies aid in cross-pollination in safflower.

In oil palm, male and female inflorescences are borne in the same tree separated by time and space. Cross-pollination through the weevil, *Elaeidobius kamerunicus* Faust (*Curculionidae*), is predominant (Syed et al. 1982; Abrol and Shankar 2012). Coconut is monoecious with protandrous staminate flowers, and hence, it is highly cross-pollinated aided by bees.

Although the breeding systems of the oilseed crops together with inheritance of the targeted trait(s) primarily decide the breeding method to be adopted, it has been observed that in self-fertilized oil seed crops like soybean, groundnut, and flax, yield improvement per se remains restricted in comparison with the cross-fertilized oil crops.

1.4 Major Goals of Oil Crop Breeding, Achievements and Strategies

Different breeding methodologies have been adopted in oil crops depending upon their breeding systems. Pollination mode in oilseed crops ranges from highly self-pollinated (soybean, groundnut, linseed) to often cross-pollinated (cotton, sunflower, safflower, *Brassica*, sesame, coconut) plants. Hybrid sunflower, safflower, and rapeseed are also produced using cytoplasmic male sterility. Conventional breeding methods (selection, pedigree, bulk, backcross, single-seed descent) have produced oilseed crops with high seed yield, oil content, and quality coupled with resistance or tolerance to major biotic and abiotic stresses. As it would be beyond the scope of this chapter to discuss the genetic enhancement accomplished in each of these traits, the discussions will be restricted to improvement made in seed yield, oil content, seed oil quality, and anti-nutritional factors.

1.4.1 High Seed Yield

To improve productivity of any crop plant, it is essential to increase seed yields. However, the agricultural area worldwide has been flat for over 40 years (FAO 2017). Therefore, improving seed yield per plant has become increasingly important. Since increasing seed yield is one of the major issues in plant science, effective strategies for increasing yield have been explored by many oil crop breeders.

Soybean began its transition from a forage crop to a valuable source of protein and oil with the establishment of the US Regional Soybean Industrial Products Lab at Urbana in 1936. Breeding soybean largely remained with the public sector breeders until the passage of the Plant Variety Protection Act (PVP) in 1970. Government protection of intellectual property in the form of cultivars encouraged private industry to heavily invest in soybean breeding, and today the bulk of research is conducted by industry rather than public institutions. However, public sector breeders still play an important role in soybean breeding and release of improved cultivars.

The main reason for the slow phase of increase in soybean yield is mainly due to stagnation in productivity in Asian continent mainly comprising China (remained at 1.8 tons/ha) and India (remained at 1.1 tons/ha). In India, production of soybean is confined to the states of Maharashtra and Madhya Pradesh which contribute 89% of the total production, while Rajasthan, Andhra Pradesh, Karnataka, Chhattisgarh, and Gujarat contribute the remaining 11% production, mostly grown as a rainfed crop. Soybean is highly sensitive to environment, most importantly to moisture stress, thus restricting the productivity in these regions.

Soybean yield potential has been increased by increasing the number of pods per plant, which has been achieved by increasing the number of nodes per plant while decreasing internode length to prevent lodging due to excessive height. In addition, number of seeds per plant and seed weight also contributed to yield improvement

(Sharma et al. 2016; Xu et al. 2020). Large number of cultivars in China (651), the USA (258), Brazil (69), and India (107) have been developed and released for cultivation.

In an effort to discover the genetic variability for seed yield in soybean, a genome wide association study (GWAS) was performed on 451 diverse lines from the USDA core collection for height, internode length, and the number of nodes. The QTL signifying Dt1 was found correlating to height and number of nodes, but no significant QTLs for internode length were uncovered. This suggests that genomic selection for variation in plant height is feasible (Moreira et al. 2019). Further improvement should come from identification of traits associated with yield, understanding the genetic mechanisms underlying their inheritance in addition to developing photo-thermo-insensitive cultivars and other stress-tolerant cultivars.

Genetic improvement of seed yield of rapeseed and mustard in the Indian subcontinent is the primary breeding objective, while in western world breeding for quality assumed priority. In case of Europe and Canada, breeding for oil for human consumption and oil cake (meal) quality for animal nutrition received the top priority than the other countries (Gupta 2012). In case of winter oilseed rape, the increase in cultivated area is responsible for only a 20% rise in global crop biomass production, whereas the intensification of the production process, mainly through breeding, accounts for the remaining 80% increase in seed yield (Swiecicki et al. 2011). The morphological traits responsible for superior performance of oilseed rape can be considerably modified by breeders. Intensive breeding efforts conducted in the 1960s have contributed to the economic significance of this species (low levels of erucic acid and glucosinolates). The yield limiting factors identified were number of siliques per unit area, number of seeds per silique, and the 1000-seed weight (Diepenbrock 2000) which can form a suitable selection criterion for increasing seed yield. Dry matter accumulation at rosette stage and leaf area index (LAI) have also been reported to be associated with seed yield (Olsson 1990). Hybrid breeding by exploiting the heterosis through the two sources, viz., male sterility Lembke of Germany (MSL; genic male sterile system) in *B. napus* and Ogura CMS system of France from radish, should further help in increasing seed yields of oil rapeseed.

In India, rapeseed-mustard is the second most important source of edible oil. Under the umbrella of All India Coordinated Research Project on Rapeseed Mustard (AICRP-RM), a total of 248 varieties of rapeseed-mustard have been released till 2018, and out of them, 185 varieties released and notified comprise of Indian mustard, 113; toria, 25; yellow sarson, 17; gobhi sarson, 11; brown sarson, 5; karan rai, 5; taramira, 8; and black mustard, 1. These include six hybrids and varieties having tolerance to biotic (white rust, *Alternaria* blight, powdery mildew) and abiotic stresses (salinity, high temperature) and quality traits and have been recommended for specific growing conditions. In 2019, three more hybrids, “Kesari Gold (31J3403),” “Kesari 5111 (PCJ03-401),” and one private sector’s hybrid “Bayer Mustard 5222 (Pro 5222),” have also been released and notified for cultivation in India. However, lack of stable fertility restorers for different male sterile systems has hampered the exploitation of these CMS systems for producing commercial hybrid seed.

Groundnut being largely a rain-dependent crop, wide variations in production and productivity, across and within the regions/countries around the world, are quite frequent. The crop is grown in two distinct production systems – low- and high-input production systems. Low-input production system, predominant in Asia and Africa, is characterized by rainfed cultivation and, with little inputs, manual labor and low yields (700–1000 kg/ha). However, in high-input production system coupled with mechanization, as prevalent in the USA, Australia, Argentina, Brazil, China, and South Africa, the groundnut yields are as high as 2.0–4.0 tons/ha. High pod and seed yields are the ultimate goals of a groundnut breeder. In *kharif*, yield levels up to 3.0 tons/ha and in *rabi*-summer up to 9.0 tons/ha have been reported under farm conditions in specific locations even in India (Rathnakumar et al. 2015). However, the average yields in India hover around 1.0 to 1.5 tons/ha depending on rainfall (quantum and distribution) in *kharif* and during *rabi*-summer,1.5 to 2.0 tons/ha. Thus, there exists a wide gap between the potential and realized yields. In addition, few biotic factors reduce yield of groundnut in *kharif* season. Therefore, any further increase in yield of *kharif* groundnut should be possible by developing stress-tolerant varieties which respond to low inputs. For *rabi*-summer cultivation, the varieties should respond to high nutrient and management conditions with high water use efficiency as the crop is raised totally under irrigated conditions.

The important yield components of groundnut are pod number, seed mass (weight of 100 kernels), and shelling outturn. However, it appears that yield improvement in most groundnut-growing states in India was brought about through a progressive improvement in pod size of the new varieties (Reddy 1988) and number of pods, size of pods, and seed size (Nigam et al. 1991; Janila et al. 2013, 2016). However, shelling outturn could not be improved substantially in the modern-day cultivars which ranges from 68% to 70% (Rathnakumar et al. 2010). For example, the pod weight increased from 68 g in PG-1 (1953) to 100 g in c-501 (1961), to 120 g in M-13 (1972), and to 119 g in M-37 (1982) in Punjab; from 76 g in RS-1 (1953) to 103g in RSB-87 (1961) in Rajasthan; from 80 g in T-28 (1960) to 118 g in Chandra (1977) in Uttar Pradesh; from 72 g in AK-12-24 (1940) to 75 g in SB-XI (1965), to 119 g in JL-24 (1978), to 120 g in TG-17 (1982), and to 127g in UF-70-103 (1984) in Maharashtra; from 52 g in Kadiri-71-1 (1971) to 91 g in Kadiri-2 (1978) and Kadiri-3 in Andhra Pradesh; from 77 g in s 206 (1969) to 88 g in Dh-3-30 (1975) in Karnataka; and from 76 g in TMV-2 (1940) to 91 g in TMV-7 (1967) and 92 g in TMV-9 (1970) in Tamil Nadu (Reddy 1988).

Over the years, 220 public bred varieties have been released as of 2020 in India, and in these varieties the yield improvement has also been achieved through progressive increase in seed size. For example, during 1940–1950, the varieties had small seeds in the range of 29.4 g/100 seeds (AK-12-24) to 36.6 g/100 seeds (TMV 3 and TMV 4). However, after four decades, the average seed size of the varieties was medium (44.8 g/100 seeds) with a range of 27 g/100 seeds (Pragathi) to 90 g/100 seeds (B-95). During the previous decade (2001–2010), the average seed size of the varieties remained medium (47.9 g/100 seeds) (Rathnakumar et al. 2013).

Further improvement in this crop can be achieved through inter subspecific crosses between Virginia types with more fruiting nodes, and large seeds with

Spanish bunch types with early maturity may simultaneously increase the number of pods and seed mass. Most of the high yielding groundnut varieties released globally have resulted from the higher harvest index brought about by reduction in the total biomass. Breeding for high biomass coupled with high harvest index can be one of the strategies to further increase yield in many groundnut-growing countries.

Sunflower was used by the American Indians around 3000 BC. The native Americans were the first “sunflower breeders” to improve and select types that varied widely for length of growing season, degree of branching, and the size and color of achenes. Later it was introduced into Europe during the sixteenth century, gradually spreading to Russia where it became widely recognized as an oilseed crop. Breeding and selection to improve sunflower at experimental stations was initiated in Russia as early as 1910 in Kharkov station and at Kruglik and Saratov stations in 1912 and 1913, respectively. Major objectives in sunflower breeding include improved seed yield, early maturity, shorter plant height, uniformity of plant type, and resistance to major diseases and insect pests. The introduction of hybrid cultivars exploiting the heterosis created a major breakthrough in increasing the seed yield of sunflower by around 25% across different growing regions (Fernández-Martínez et al. 2009). Further significant improvement in grain yield has not been reported on a large scale before or after this point (Lopez Pereira et al. 2008). However, several studies have identified specific traits associated with seed yield improvement in sunflower, namely, head size and number of seeds per head, seed weight (Miller et al. 1982; Connor and Hall 1997), and indirect and adaptive traits like improving the combining ability of parental lines, shorter plant stature in areas associated with lodging risk (Schneiter 1992), high degree of fertility in regions with limited or nil pollinator populations (Miller et al. 1992), or pronounced head inclination in high temperature and intense sunlight or high risk of bird predation areas (Hanzel 1992; Linz and Hanzel 2015) and disease resistance in case of hybrid sunflowers. However, almost all the sunflower hybrids currently cultivated are derived from a single CMS source, i.e., *H. petiolaris* (PET1), and hence, diversification of CMS sources and fertility restorers under agronomically superior genetic backgrounds will further enhance yields.

Although almost all the oil crops are grown under marginal and submarginal lands having poor soil fertility in developing nations including India, sesame, niger, and safflower are almost neglected crops grown purely under rainfed conditions and under input starved conditions. In case of sesame, seed yield failed to show any marked increase for over five to six decades across the world, although sesame oil is used largely in Asia and Africa. Previous studies of various sesame breeders indicated that plant height, number of branches per plant, capsules per plant, seeds per capsules, and 1000-seed weight are the traits which have shown significant and positive correlations with yield (Ashri 1998; Singh et al. 2016). The capsules per plant had highest direct effect on seed yield followed by 1000-seed weight. Hence, these traits may be used as selection criteria in breeding programs for the improvement of seed yield of sesame (Mustafa et al. 2015). In addition to the above, the physiological attributes such as harvest index and crop growth rate (CGR) which exhibit positive relationship with seed yield (Chauhan et al. 1996; Ruchi 2008) should be included in the selection criteria for breeding high yielding varieties of sesame. Early senescence of lower leaves, seed shattering from lower and matured capsules, and indeterminate growth habit resulting in differential maturity of capsules and seeds are the major bottlenecks in the improvement of seed yield in sesame (Rao et al. 2002; Cagirgan 2006). Breeding for improved/ideal plant types for different production regions, determinate habit, and non-shattering types would increase further the seed yield in sesame.

In safflower, studies on development of the sequential traits of seed yield (heads/plant, seeds/head, and seed weight) indicated that genotype had a large effect on seed weight and smaller effects on seeds/head and heads/plant. Location effects were generally highly significant for each trait. The sequential traits showed independence in a correlation analysis. Together the traits accounted for 97% of the variation in yield, with head numbers and seeds in the head accounting for most of the variation (Golkar et al. 2011). Seed weight accounted for most of the variation in yield, followed by seeds/head and head numbers. Regression analyses indicate that for selection, one should give more weight to head numbers and seeds/head when all these traits are considered simultaneously and to head numbers when one trait is considered at a time. In general, head numbers or seeds/head or both traits could be responsible for high yielding lines. Seed weight was generally inflexible in different environments, but heads/plants and seeds/head were more flexible (Abel and Driscoll 1976; Arslan 2007). Though the crop has tremendous potential to be grown under varied conditions and to be exploited for various purposes, the area under safflower around the world is limited largely due to the lack of information on its crop management and product development (Singh and Nimbkar 2007). It has remained as a neglected crop due to its low seed oil content (28–36%), spininess (in some genotypes), and vulnerability to number of diseases and pests (Sujatha 2008). However, further investigations on physiological traits associated with yield components and their manipulations through breeding can increase safflower seed yield.

In niger, number of branches, capitulum/plant, seeds/capitulum, and 1000-seed weight are the major yield contributing traits. For niger to be competitive with other oilseed crops, its seed yield must be significantly improved. To achieve this objective, single-headed, dwarf types must be developed with uniform maturity resulting in reduced shattering losses. The Ethiopian germplasm collection contains short-stature plants which could be used for the development of dwarf types. Genetic variation exists for number of heads per plant that could be utilized in breeding programs to select single headed types (Getinet and Sharma 1996). The presently used normal-height niger accessions have many leaves and a low harvest index (Belayneh et al. 1986). Reducing plant height would decrease the number of leaves per plant and result in a better harvest index. Shorter plants would be capable of utilizing fertilizer more efficiently in that seed yields could be increased through the application of fertilizers. Standard niger types respond to fertilizer application by increasing vegetative growth, which promotes lodging of the crop and decreases seed yield.

Seed yield is a quantitative trait that is the most important in an oilseed flax breeding program. The number of improved cultivars has been released in different countries, but the yields remained low in many developing countries. Although numerous crop characteristics and environmental factors have been reported to influence seed yield, little is published on basic crop characteristics of flax that affect yield, such as canopy expansion and light interception, dry matter production, and partitioning. During the reproductive phase, light use efficiency and harvest index are correlated with grain production under favorable growing conditions (D'Antuono and Rossini 1995). The factor which increased the amount of dry matter was reported to be the air temperature during the period of plant emergence – budding and large amount of rainfall during vegetative stage reduce average seed yield by about 40%. Hence, breeding for improved seed yield of flax needs to consider these physiological traits before formulation of suitable breeding strategies.

The world castor productivity has increased 146% in the last five decades with 4.0% compound growth rate (Anjani 2014). The tremendous improvement in castor productivity was mainly because of development of number of high-yielding hybrids, especially in India. In the world, the castor production and productivity are high in India (more than 80% of the worldwide production) along with Mozambique, China, Brazil, Myanmar, Ethiopia, Paraguay, and Vietnam. The development and popularization of castor hybrids led to rapid increase in productivity and production in India. Prior to cultivation of castor hybrids, castor production was less than 300 kg/ha, which has now escalated to 1593 kg/ha in 2018–2019 (https://eands.dacnet.nic.in). In Brazil, seed yields averaged around 667 kg/ha over the last 10 years, and yields of up to 1600 kg/ha under better soil fertility and agronomic practices have also been reported (Anjani 2014). Presently the main objectives of the breeding programs around the world are earliness of seed maturation, plant architecture amenable for mechanized harvest, and disease resistance (root not and gray mold). These should be combined with superior productivity of cultivars and at least of 48% oil content of seed. Most breeding programs target genotypes/hybrids with short height (less than 1.5 m), height of primary raceme between 20 and 40 cm, less than 150 days for harvesting, erect plant, and non-shattering fruits (Milani and Nóbrega 2013; Lavanya et al. 2018). Using genome-wide association analysis, candidate genes associated with nine agronomically important traits including the candidate genes encoding a glycosyltransferase related to cellulose and lignin biosynthesis have been associated with both capsule dehiscence and endocarp thickness. It has been hypothesized that the abundance of cellulose or lignin in endocarp is an important factor for capsule dehiscence (Fan et al. 2019). This finding can provide a lead for castor breeding and genetic study, especially in preventing capsule dehiscence and thereby preventing yield losses.

1.4.2 Increasing Seed Oil Content

Since oils of plant origin are commercially important, improving oil content in several crop species has long been a major focus by the breeders of several countries. Planned breeding efforts have led to the improvement of oil content in several crops.

The oil content of the seeds of modern cultivars is significantly higher than those of wild species (Škorić 1992; Zheng et al. 2008) barring few exceptions. The oil content in the most prevalent oil crops ranges from 20% in soybean to more than 60% in candlenut, sesame, *Oiticica* and *Ucuhuba* (Murphy 1996). Therefore, there is a potential to increase oil content in other oil crops.

Increasing oil content in the seeds has been a major objective in soybean breeding programs across the globe. Domestication of soybean from land races with low oil and high protein content has resulted in an adaptive balance of these two maxima. Relationship between oil concentration and seed yield and between oil and protein content is more intrinsic and negative (Brim and Burton 1979; Burton 1987), and hence, breeding for high oil concentration results in lower seed yield and protein contents. A balanced approach for modest gain in oil concentration and yield needs to be targeted without compromising seed protein content (Cober et al. 2009). Through mutagenesis, Bhatnagar et al. (1992) were able to break this negative association and obtained stable genotypes with high protein and oil content. Oil content in soybean has been reported to be maternally influenced (Brim et al. 1968) with additive gene action (Singh and Hadley 1968; Raut et al. 2000). The QTLs associated with seed oil and fatty acids in soybean have been extensively investigated, and more than 322 oil QTLs and 228 fatty acid QTLs have been reported in all 20 chromosomes in the SoyBase database. However, most of these identified QTLs have low selection accuracy and have not been effectively used in marker-assisted selection (MAS) in soybean for seed oil due to insufficient linkage disequilibrium with desirable QTL alleles and the genetic complexity of the trait (Yao et al. 2020).

Some predictions state that the oil content of rapeseed, which is currently 45–48% in Canada and around 42% in China and Australia, might even reach 65% (Wang et al. 2010a, b; Seberry et al. 2011; Wang et al. 2018). Recently, a ultrahigh oil content rapeseed line, "YN171," with 64.8% oil content in *B. napus* has been developed, and the structural analysis of its seeds indicated a high positive correlation between the oil body organelles to seed ratio and oil content of the seed, and it has been estimated that rapeseed oil content could even reach 75% through breeding (Hu et al. 2013).

Wide variation exists for oil content in groundnut germplasm. It ranges from 46.5% to 63.1% in cultivated types, while the range observed in wild species was from 43.6% to 55.5% (Norden et al. 1987). In few wild *Arachis* species, oil content up to 60% has also been reported (Wang et al. 2010a, b). Oil content and yield has been reported to be independent, thus suggesting possibilities of breeding varieties with high yield and oil content. Narrow-sense heritability has been worked out to be high (Martin 1967) for oil content. Inheritance of oil is governed by two pair of alleles with nonadditive genetic component being predominant (Basu et al. 1988). Hence, selection should be postponed to later generations to eliminate the undesirable recombinants. Following hybridization and wide-scale screening efforts, several high oil lines (>50%) were identified, but the stability for the trait could not be obtained. However, extensive multilocation testing identified four high oil-yielding lines ICGV 05155, ICGV 06420, ICGV 03042, and ICGV 03043 for release in India (Janila et al.2016).

Sunflower is mainly grown for its oil; crushing factories offer premium price for types with more than 40% oil. The ornamental value of sunflower was turned to an important oil source, and over a span of two to three decades, oil content has been enhanced from 30–33% to 43–46% and even up to 50% in certain cases in Russia following Pustovoit method of reserves (Fick and Miller 1997a, b). The kernel to hull ratio is one of the main features that decides the oil content in sunflower. This ratio varies between 10 and 60% in sunflower germplasm (Fick and Miller 1997a, b), and it has been reported that two-thirds of enhancement in oil content came through the reduction in hull content while one-third came from actual increase in oil content (Alexander 1966). However, there exists a negative correlation between husk content and between seed yield and oil content (Kaya et al. 2007), and hence, the breeding strategies should be balanced to achieve higher values for yield and oil content while reducing the hull content. Thus, ease of hulling or its removal automatically forms a criterion while selection. Genetics of hull content has also been worked out which indicates that the trait is controlled by polygenes with minor effects but acting on additive manner with a high heritability (Kovacik and Skaloud 1990) whereas oil content per se has been reported to be sporophytically controlled (Pawlowski 1964).

Sesame has a relatively superior oil quantity and quality than major oil crops. The oil content ranges from 34.4% to 59.8% but is mostly around 50% (Ashri 1998; Dossa et al. 2017), and values up to 69.8% have also been reported in some cultivars (Baydar et al. 1999). Both genetic and environmental factors affect oil content in sesame. Late maturing cultivars have been reported to have higher oil content than early maturing ones. Indeterminate cultivars have also been observed to possess higher oil content than the semi- or partially determinate types. Variations also occur between the capsules located at different positions of the same plant such that seeds obtained from basal capsules of the main stem possess higher oil content than those located toward the apex and on side branches (Mosjidis and Yermanos 1985). Black seeded cultivars were also found to have lower oil content than brown and white seeded types, thus complicating the breeding and selection scheme for improving the oil content. However, phenotypic correlation between oil content and seed yield is also reported to be weak suggesting that it would be possible to develop sesame varieties with both high yield and high oil content. A recent study on GWAS in sesame identified 46 candidate causative genes, including genes related to oil content, fatty acid biosynthesis, and yield. Several of the candidate genes reported in the study for oil content encode enzymes involved in oil metabolism. Two major genes were also found to be associated with lignification and black pigmentation in the seed coat and were also observed to be associated with large variation in oil content. The genes identified in sesame for oil production and quality probably play important roles in other closely related oilseed species (e.g., sunflower) as well, offering the opportunity to look for genes with common function (Wei et al. 2015).

Over the decades, one of the major breeding goals in safflower has been and continues to be to increase seed oil content. Safflower seeds are usually white or creamy in color, and their typical composition is 55–65% kernel and 33–45% hull (Singh and Nimbkar 2007). In normal hull types, the whole seed contains 25–37%

(Weiss 2000), but in very thin hull types, this ratio increases to 46–47% (Golkar 2014). Number of seed coat phenotypes with their genetic control have been identified: partial hull (*par par*), which is recessive to normal hull, inherited independently of thin hull (*th th)* and striped hull *(stp stp)* (Urie 1981), grey-striped hull (*stp2*) (Abel and Lorance 1975) and reduced hull (*rh rh)* (small dark blotches on the seed*)*. Partial hull plants produce achenes which are predominantly dark with high oil and protein levels, and the partial hull character is recessive to reduced hull (Urie 1986). In California, genetic variations for hull content have been developed with a resultant increase in oil content of 42–50%, and hence seed/hull ratio assumes importance. With its simple inheritance, this ratio can be modulated through suitable breeding schemes for increasing oil content in safflower seeds. The same holds good for niger as well. The oil content of niger seed varied from 30% to 50% (Seegeler 1983). The oil, protein, and crude fiber contents of niger are affected by the hull thickness, and thick-hulled seeds tend to have less oil and protein and more crude fiber. In Ethiopia, where the crop is mainly used for edible oil purpose, medium to late maturing types were found to possess high oil content (Abat) types. With the available genetic variations in niger germplasm, oil content can be increased by 5% through selection of genotypes with less hull content (Getinet and Teklewold 1995; Getinet and Sharma 1996).

Oil content in seeds of castor germplasm ranges from 42% to 58% with conflicting reports of its inheritance: polygenic control (Zimmerman 1958), additive gene action (Rojas-Barros 2001), dominance gene action (Okha et al. 2007), and under sporophytic control (Rojas-Barros 2001). Similar to sunflower, safflower, and niger, there exists a negative correlation between seed oil and hull content, with the low hull content reported to be partially recessive over normal hull (Moshkin and Dvoryadkina 1986). It has been demonstrated recently that recurrent selection through screening single seed is an effective method to improve oil content in castor (Grace et al. 2016). Two cycles of recurrent selection increased the mean oil content from 50.33% to 54.47%. Consequently seed weight also increased after two selection cycles, thus establishing a positive relationship between seed oil content and seed weight which allows further improvement of oil content by screening for larger seeds in a population (Grace et al. 2016). However, the role of environment needs to be ascertained in confirming the results obtained in other castor growing regions of the world.

Unfortunately, some studies reported an inverse relationship between oil and protein accumulation in the seeds of some species, such as rapeseed and soybean (Chung et al., 2003; Cober and Voldeng 2000; Hu et al. 2013). Additionally, Vollmann and Rajcan (2009) noted other growth traits also correlated with oil content, such as time to flowering, seed weight, and fatty acid concentrations, which complicate the process of breeding for oil. Recent studies using quantitative trait loci analyses revealed that seed oil contents are controlled by many genes with additive effects (Li et al. 2011; Jiang et al. 2014) indicating that it would be a challenge for the crop breeders to improve oil content through conventional/traditional breeding methods. Biotechnological interventions, genomic tools, and gene editing techniques may be useful in obtaining desired levels of oil content in these crops.

1.4.3 Breeding for Improvement of Quality Traits in Oil Crops

The quality traits in oil crops include both physical and chemical attributes. Nutritional traits include oil, protein, sugar, iron and zinc content, fatty acid profile, and freedom from toxins, while the other quality parameters include visual and sensory attributes (consumer and trader preferred traits) and traits desirable in food/oil processing industries. Similarly, desirable traits for confectionery uses fetch higher price in the market because of its export value which includes seed traits like uniformity of seed shape, intact testa and its color, flavor components, high sugar and protein contents, low oil, and freedom from toxic principles like phytic acid or allergens as in case of groundnut. Depending on the nature of use, low oil and high protein contents (for food use), high oil content (for oil use), and high-oleic/high-linoleic fatty acid ratio (for longer shelf life) are important targeted traits in oil crop breeding programs. The other important quality consideration in assessing the utility of the produce of oil crops includes the quality meal or cake which remains after extraction of oil. Protein and fiber contents and their digestibility and freedom from toxic substances determine their value. Covering all the aspects of quality of each of the oil crop is beyond the scope of this chapter, and hence, functional and nutritional quality improvements are dealt here. For a better understanding of the subject, few earlier reviews on this subject may be consulted (Fernández-Martínez et al. 2004; Yadava et al. 2012; Vollmann and Rajcan 2009; Singh and Nimbkar 2007; Golkar 2014).

1.4.3.1 Genetic Improvement of Fatty Acid Composition

Initially, focus was in increasing oil content, but efforts of the present day are directed toward modification of fatty acid composition of seed oil for food and non-food purposes which has gained much attention during the last decade mainly due to the identification of sources and molecular markers associated with the fatty acids whose composition decides the quality and functionality of oils. Most of the edible oils are rich (>65%) in polyunsaturated fatty acids mainly linoleic and linolenic fatty acids which are unstable oxidatively resulting in rapid spoilage of oil and the food. Hence, to improve the oil quality in crops, lowering the levels of poly unsaturation and increasing the contents of monounsaturated fatty acid, i.e., oleic acid which has relatively higher oxidative stability and higher shelf life, have been aimed, thereby increasing the functional use of the oils.

In soybean, three genes, *fan*1, *fan*2, and *fan*3, were identified that individually reduce the linolenic acid to 2.9–4.9% and in combination were able to reduce it to 1% from different germplasm accessions (Hammond and Fehr 1983; Ross et al. 2000). Using these genes, breeders have successfully developed high yielding lines and cultivars with more than 80% high-oleic acid (HO) soybeans which occupy most of the soybean areas in the USA. These research efforts lasted over 40 years employing conventional pedigree breeding and backcrossing followed by selection and fatty acid profiling. Targeted perturbation of fatty acid desaturase-2 (FAD2) alleles not only resulted in HO (75–80%) soybeans but concomitantly reduced palmitic acid by 7–8%, which is 20% reduction over original palmitic acid content (Kinney and Knowlton 1997).

In rapeseed and mustard, identification of naturally occurring zero erucic acid mutants in both *B. napus* and *B. rapa* marked a new era of oil quality improvement through mutagenesis in any crop (Downey and Craig 1964). The first low erucic acid spontaneous mutant was obtained from the German spring rapeseed "Liho" and released for cultivation in the 1970s. The Polish spring rapeseed variety "Bronowski" was identified in 1969 as a low glucosinolate type, and these two varieties formed the basis for developing high yielding "00" types (low erucic acid and low glucosinolate or canola) internationally through backcross breeding approach. The first "00" canola variety "Tower" was released in 1974, and thus canola became the most important oil crop of the temperate region of the world (Friedt and Snowdon 2009). Further, the variety "Splendor" or "Nexera" having "high-oleic and low linoleic (HOLL or HOLLi)" with more than 75% oleic acid and 3% linolenic acid has been developed through experimental mutagenesis followed by selection. These varieties fetch premium price in the international market both for human consumption (low erucic acid and high-oleic acid types) and animal feed (low glucosinolates types) (Friedt and Snowdon 2009).

Indian rapeseed-mustard breeding program was also reoriented to accommodate quality parameters and lay emphasis to develop "canola" varieties. Initial efforts concentrated on the development of genetic stocks for low erucic acid in the indigenous background using exotic sources. Sustained efforts at Punjab Agricultural University (PAU), Ludhiana; Tata Energy Research Institute (TERI), New Delhi; Indian Agricultural Research Institute (IARI), New Delhi; G.B. Govind Ballabh Pant University of Agriculture and Technology (GBPUA& T), Pantnagar; and Indian Council of Agricultural Research-Directorate of Rapeseed and Mustard Research (ICAR-DRMR), Bharatpur have resulted in the development of zero erucic mustard lines (LEB 15, LES 39 CRL 1359–19, YSRL 9-18-2, TERI (OE) M 9901, TERI (OE) M 9902, PRQ 9701, BPR6-205-10 and BPR 91–6). Several "0"/"00" strains of rapeseed-mustard have been registered with the National Bureau of Plant Genetic Resources (ICAR-NBPGR) New Delhi, viz., INGR 98001 (0), INGR 98002 (0), INGR 98005 (0), INGR 99007 (00), INGR 99008 (00) (Chauhan et al. 2002). Work is in progress and efforts have been underway to improve the agronomic base of low yielding zero erucic lines and to recombine low erucic acid and low glucosinolate to develop "00" varieties.

Oil quality in groundnut refers to oil content, fatty acid composition, iodine value, ratio of oleic to linoleic acid (O/L), and stability or shelf life. Genetic manipulation of fatty acid composition has been reported by few workers. The Virginia types generally have higher oleic acid content while Spanish-Valencia's have higher linoleic acid. This results in a lower iodine value for oil of Virginia types and indicates that these types will become rancid through autoxidation more slowly than the Spanish-Valencia's. The groundnut breeder is faced with a paradox when breeding for oil quality. Consumers prefer to have oils both with low iodine (long shelf life) and high iodine value (to have high level of unsaturation from the health point of view). Crosses between all the four habit groups have shown that a wide range of iodine values can be obtained through recombination of genes from different parents and that the iodine value in groundnuts is highly heritable (Bovi 1982).

The oleic/linoleic (O:L) acid ratio, which is an indicator of oil stability and shelf life of groundnut products, varied between 1 and 3 in different cultivars. However, in two Florida breeding lines in the USA, O:L ratio of 40 was reported (Norden et al. 1987). Moore and Knauft (1989) followed up this work further and reported that the high O:L ratio in these lines was governed by two recessive genes. Genomics-assisted breeding (GAB) approaches including marker-assisted selection (MAS) and marker-assisted backcross (MABC) breeding schemes were used successfully in the development of high-oleic cultivars (Janila et al. 2016). Initially linked markers for mutant FAD2 alleles were deployed for improving the nematode-resistant variety “Tifguard” by transferring mutant alleles using MABC, leading to the development of the improved breeding line ‘Tifguard’ high O/L (Chu et al. 2011). Subsequently, these linked markers were used in MABC and MAS approaches for converting three elite varieties, ICGV 06110, ICGV 06142, and ICGV 06420, into high-oleic lines. These high-oleic lines contained up to 80% oleic and reduced palmitic and linoleic acid, a perfect combination for industry and cooking oil use. Recently, two high-oleic varieties, namely, ICGV 15083 (Girnar 4) and ICGV 15090 (Girnar 5), derived from the cultivar ICGV 05141 using MAS were released for the first time in India after multilocational validation of their performance for yield and stability of high-oleic acid. Substantial progress has also been obtained in developing foliar disease (rust and LLS) resistant cultivars under high-oleic background (Janila et al. 2016; Bera et al. 2018; Shasidhar et al. 2020).

As in other oil crops, high-oleic trait has been explored in sunflower. Monogenic (designated as “ol”) dominance of the gene controlling this trait with several modifiers has been reported (Miller et al. 1987; Fernández-Martínez et al. 2009; Pérez-Vich et al. 2002). Three recessive alleles each, P1, P2, P3, for high palmitic acid and three (Es 1, Es2, Es3) for high stearic acid have been reported (Pérez-Vich et al. 2006) and determined by the genotype of the developing embryo, thereby complicating the selection scheme. All the alleles for the target trait need to be introgressed into both the parents in case of hybrid development (Fernández-Martínez et al. 2004).

Sesame is primarily grown for its oil-bearing seed in different countries. Beside the high oil content, sesame seeds contain almost 18% protein, and among the fatty acids, oleic acid (39.6%) and linoleic acid (46%) are the two main components with the ideal ratio of almost 1:1 (Anilakumar et al. 2010). Until 2013, the molecular mechanisms of the high oil content and quality in sesame seeds were unclear. An association mapping of oil and protein contents and oleic and linoleic acid concentrations based on multi-environment trials was conducted using 79 simple sequence repeats (SSR), sequence-related amplified polymorphism (SRAP), and amplified fragment length polymorphism (AFLP) markers in 216 Chinese sesame accessions (Wei et al. 2013). Only one associated marker (M15E10-3) was identified for oil content in two environments suggesting inadequate molecular markers and/or germplasm resources. On the basis of reference genome sequence, the sesame genome was found to harbor low copy of lipid-related genes (708) compared to soybean (1298). In a comprehensive GWAS for oil and quality traits in 705 sesame accessions under 4 environments, 13 significant associations were unraveled for oil, protein, sesamin, sesamolin, saturated fatty acids (SFA), unsaturated fatty acid (USFA), and their ratio SFA/USFA (Wei et al. 2013). Several causative genes were uncovered for oil content, sesamin, and sesamolin, but none were identified for oil quality indicating that still some more studies are required to unravel the genetic control of these valuable traits.

Safflower has remained as a neglected crop due to its low seed oil content (28–36%). The nutritional value of safflower oil is related to its high level of polyunsaturated oils (Weiss 2000). Safflower oil contains about 75% linoleic acid that is essential for human nutrition (Weiss 2000). Knowles (1968) registered the first safflower accession UC-1 (PI 572434) having high-oleic acid (78%). Safflower cultivars with high-oleic acid content (>70%) have been developed and commercially successful and, two lines, CR-50 with high palmitic acid and CR-13 with high stearic acid, were developed (Hamdan et al. 2009). Incorporation of the high-oleic trait through conventional breeding techniques has been a slow process due to recessive inheritance and difficulties associated with phenotyping by biochemical methods. DNA-based marker-assisted selection (MAS) for high-oleic trait would accelerate the breeding efforts in safflower. A recent study with a set of high-oleic varieties were found to carry the same mutation in the fatty acid desaturase 2-1 gene, CtFAD2-1, which is presumed to be the "ol" allele associated with high-oleic acid content in safflower. Genotypic assays, namely, Kompetitive Allele Specific PCR (KASP) and the Amplifluor™ SNPs Genotyping System (Amplifluor®), were designed for the prediction of high-oleic trait based on the mutation in the CtFAD2–1. The assays were thoroughly validated in segregating populations derived from crosses between low- and high-oleic parents. Through marker-assisted backcrossing scheme, the high-oleic allele, "ol" from the exotic variety, Montola-2000 was incorporated into the background of popular Indian linoleic type variety, "Bhima," and a set of promising high-oleic lines (75.2–81.8%) were developed (Kadirvel et al. 2020). These MAS-derived lines showed consistent expression of high-oleic acid content over seasons and comparable seed and oil yield performance with the local check varieties. The genotypic assays reported in this study were robust, nondestructive, and codominant and accurately predicted the high-oleic trait in segregating populations, thus recommending for fast-track breeding of high-oleic cultivars in safflower.

In niger, the fatty acid composition of oil from the accessions characterized at Ghinchi, Ethiopia, was analyzed using gas chromatography. Linoleic acid ranged from 74.8% to 79.1% with a mean of 76.6%. Contents of other fatty acids were palmitic acid (7.8–8.7%), stearic acid (5.8–7.4%), and oleic acid (trace amounts, 0.5–1.5%). Further evaluation of germplasm to identify genes for high-oleic traits as observed in other oil crops would help furtherance of oil quality for both consumption and industrial purposes in niger (Getinet and Sharma 1996).

Castor seed contains about 50% oil which is composed of 80–90% ricinoleic acid. This hydroxyl fatty acid is unique and cannot be synthesized outside of the castor seed. A number of chemicals and polymers are synthesized and used in bio-based fuels and industrial products from castor oil. Reduction of ricinoleic acid in castor oil will reduce the importance of this oil functionally, but its high viscosity reduces its use as a biofuel. A mutant USDA accession (PI 179729) has been identified in which conversion of oleic to ricinoleic acid has been partially blocked resulting in HO types (78% oleic acid against the normal of 4%). The trait is controlled by two independent major genes (ol Ml) exhibiting dominant-recessive epistasis (Rojas Barros et al. 2005). Understanding further the genetic regulation of this trait through molecular tools can help in developing suitable varieties.

Dry seed of linseed contains 35–45% oil and around 60% of linolenic acid. Due to its high iodine value, linseed oil has been used primarily for industrial purposes, such as linoleum floor covering, with a high level of unsaturated fatty acids making the oil very reactive and resulting in a short shelf life. Mutation breeding in flax led to the development of a new type of edible flax seed oil that has nearly eliminated the α-linolenic acid (ALA) (Green and Marshall 1984; Rowland 1991). The deficient ALA trait is known to be controlled by two recessive genes (ln1 and ln2) at independent loci (Green and Marshall 1984; Rowland 1991; Ntiamoah and Rowland 1997). Low linolenic acid cultivars have introduced linseed to the edible food market. In 1994, the Flax Council of Canada developed the term “Solin” to describe linseed with less than 5% linolenic acid. The original hybridization work was carried out by CSIRO in Australia with the release of two Linola cultivars in 1992 under the Plant Varieties Rights Scheme. “Linola 947” was the first Solin cultivar registered in Canada. Solin cv. “Linola™ 989” has been reported to have 46% oil (dry basis) and 34% protein. Few more varieties (“Linola™ 1084,” “Linola™ 2047,” “Linola™ 2090,” “Linola™ 2126,” “Linola™ 2149”) have also been developed (with <5% linolenic acid) and released subsequently in Canada (Dribnenki and Green 1995; Dribneki et al. 2007), and in India “TL 99” (an induced mutant with <5% linolenic acid) has also been released during 2018–2019.

1.4.4 Genetic Engineering in Oil Crops and Identification of Genes for Novel Traits

The oil crops are usually grown under rain-dependent production systems in developing countries mainly in Asia and Africa, while in countries like the USA and in Europe, they are grown under well-managed growing conditions. The oil crops grown under these situations are challenged by both biotic and abiotic stresses and further complicated by the recent climate change scenario. Although advances in oil crop breeding and management have resulted in substantial improvement in seed yield and oil content and quality, for further improving the seed yield, oil content, nutritional quality, and industrial needs, newer techniques like genetic engineering through exploitation of the available plant genetic resources in combination with modern molecular tools for genome-wide association studies (GWAS) and application of genomic selection are very much essential.

In soybean, 809 worldwide accessions were assembled and phenotyped for 2 years at 3 locations for 84 agronomic traits. Genome-wide association studies identified 245 significant genetic loci, among which 95 genetically interacted with other loci. It has been determined that 14 oil synthesis-related genes are responsible for fatty acid accumulation in soybean and function in line with an additive model (Fang et al. 2017). Genome-wide association studies conducted on 249 soybean accessions from China, the USA, Japan, and South Korea for 15 seed amino acid contents by following genotype by sequencing (GBS) indicated presence of genetic variation for amino acids among the accessions. Among the 231 single nucleotide polymorphisms (SNPs) significantly associated with variations in amino acid contents, 15 SNPs were localized near 14 candidate genes involved in amino acid metabolism. Twenty-five SNP markers were observed to associate with multiple amino acids which can be used to simultaneously improve multi-amino acid concentration in soybean. Genomic selection analysis of amino acid concentration showed that selection efficiency of amino acids based on the markers significantly associated with all 15 amino acids was higher than that based on random markers or markers only associated with individual amino acid. The identified markers could facilitate selection of soybean varieties with improved protein quality (Qin et al. 2019).

GWAS was performed for three seed-quality traits, including erucic acid content (EAC), glucosinolate content (GSC), and seed oil content (SOC) using 3.82 million polymorphisms in an association panel in rapeseed-mustard. Six, 49, and 17 loci were found associated with EAC, GSC, and SOC in multiple environments, respectively. The mean total contribution of these loci in each environment was 94.1% for EAC, 87.9% for GSC, and 40.1% for SOC. A high correlation was observed between phenotypic variance and number of favorable alleles for associated loci, which will contribute to breeding improvement by pyramiding these loci. Four novel candidate genes were detected by correlation between GSC and SOC and sequence variations. The study also validated detection of well-characterized *FAE1* genes at each of two major loci for EAC on chromosomes A8 and C3, along with *MYB28* genes at each of three major loci for GSC on chromosomes A9, C2, and C9 which would be useful for genetic improvement of *B. napus* (Wang et al. 2018). In a similar genome-wide association study (GWAS), using an association panel comprising 92 diverse genotypes, GBS identified 66,835 loci, covering 18 chromosomes in Indian mustard (*Brassica juncea*). Different loci (16, 23, and 27) were found associated with oil (16), protein (23), and glucosinolates (27), respectively, including common SNPs for oil and protein contents. Annotation of the genomic region around the identified SNPs led to the prediction of 21 orthologs of the functional candidate genes related to the biosynthesis of oil, protein, and glucosinolates. The identified loci will be very useful for marker-aided breeding for seed-quality modifications in *B. juncea* (Javed et al. 2020).

In groundnut, a genome-wide association study was conducted to investigate the genetics basis of oil, protein, 8 fatty acid concentrations, and O/L ratio using a diverse panel of 120 accessions of the US mini core collection with 13,382 single nucleotide polymorphisms (SNPs) grown over 2 years. A total of 178 significant quantitative trait loci (QTLs) associated with seed composition traits were identified. RNA-Seq analysis identified 282 DEGs (differentially expressed genes) within the 1 Mb of the significant QTLs for seed composition traits. Among those 282 genes, 16 candidate genes for seed fatty acid metabolism and protein synthesis were screened according to the gene functions. Quantitative trait locus (QTL) analysis using genotyping and phenotyping data identified 8 QTLs for oil content including 2 major (QTLs, qOc-A10, and qOc-A02) ones and 21 QTLs for 7 different fatty acids (Zhang et al. 2021). The QTLs identified in this study could be further dissected for candidate gene discovery, and development of diagnostic markers for breeding improved groundnut varieties with high oil content and desirable oil quality.

In sunflower, commercial hybrid seed production currently relies on a single cytoplasmic male sterility (CMS) source, PET1, and the major fertility restoration gene, Rf1, leaving the crop genetically vulnerable to various pests and diseases. A new fertility restoration gene, *Rf7*, which is tightly linked to a new downy mildew (DM) resistance gene, *Pl34*, in the USDA sunflower inbred line, RHA 428, was identified. To identify markers associated with the fertility restoration trait in a panel of 333 sunflower lines, 8723 SNP markers were used for genotyping. Twenty-four SNP markers were significantly associated with the trait, and these markers were validated in a world collection panel of 548 sunflower lines and observed to be associated with the Rf1 gene (Talukder et al. 2019). The SNP and SSR markers tightly flank the *Rf7* gene, and the *Pl34* gene would benefit the sunflower breeders in facilitating marker-assisted selection (MAS) of *Rf* and *Pl* genes.

GWAS was performed on 705 diverse sesame varieties for 56 agronomic traits in 4 environments, and 549 associated loci were identified. Examination of the major loci resulted in identification of 46 candidate causative genes, including genes related to oil content, fatty acid biosynthesis, and yield. Two major genes associated with lignification and black pigmentation in the seed coat were also observed to be associated with large variation in oil content which may accelerate selection efficiency in sesame breeding and to formulate improvement strategies for a broad range of oilseed crops (Wei et al. 2015). Yet another study on GWAS in sesame for 39 seed yield-related traits including capsule size, capsule number, and seed size at 3 different environments using 705 diverse lines identified novel candidate genes, such as *SiLPT3* and *SiACS8*, which may control capsule length and capsule number traits, thus forming the basis for research on genetics and functional genomics toward seed yield improvement in sesame (Zhou et al. 2018).

1.5 Future Research Strategies

Oil crops are grown mainly in the USA, Europe, Russian Federation, Australia, Africa, China, India, Malaysia, Indonesia, Canada, Argentina, Brazil, Paraguay, and Uruguay apart from Middle Eastern regions. The growing conditions vary in each of these countries mainly of irrigated, high input, and well-managed situations, and in countries like China, India, and Africa, cultivation of oil crops is restricted to rain-dependent, low input, and management conditions. Hence, oil crop breeding is dichotomous suiting to these two situations although the major breeding goal is to improve seed yield, oil, and protein contents. Hence, clear-cut breeding strategies should be worked out on cropping system perspective suiting to the above needs rather than improving the yield per se of the individual crops.

Most of the oil crops especially in Asian and African continent are grown in marginal lands under rainfed conditions. Frequent drought spells varying in intensity and duration coupled with attack by various biotic and abiotic stresses impede with the genetic enhancement of these crops. Hence, development of stress-tolerant varieties with higher seed and oil yield is the need of the hour.

Seeds are the basic unit of crop production, human nutrition, and food security in any crop. A key trait which determines the performance of seeds is the seedling vigour which is a complex trait but very essential especially in rain-dependent production regions of the world where soil moisture availability immediately after the rains will be for a limited period of time, and hence seed/seedling vigour and rapid and uniform establishment and nutrient use efficiency using the available soil moisture are critical for crop productivity. Improving seedling vigour to enhance the critical and yield defining stage of crop establishment remains a primary objective of the agricultural industry and the seed/breeding companies that support it (Finch-Savage and Bassel 2015). Knowledge of the regulation of seed germination has developed greatly in recent times, yet understanding the basis of variation in vigour and therefore seed performance during the establishment of crops remains limited. Hence, understanding of seed vigour at ecophysiological, molecular, and biomechanical level is paramount in these crops. Alongside, seed viability during storage of oil crops especially in orphan crops like safflower, niger, and sesame is an important researchable issue as the seeds of these crops are stored by the resource-poor farmers under poor or suboptimal storage conditions. Soybean crop needs special attention in this area as its seed contains higher concentrations of protein and oil than cereal crop seeds, and oxidation of these biomolecules significantly reduces seed longevity and decreases germination ability in addition to its greater sensitivity to environment, and hence, seeds easily get deteriorated. Generally, soybean seed vigor can be maintained for less than a year and, hence, needs to be multiplied every year. Varieties with good seed vigor are essential for maintaining optimum plant population and stable high yields. Hence, along with seed size, viability of seeds needs to be addressed for maintaining plant population as well as stable yield. Certain landraces of China exhibited better seed vigor than cultivars (Hao et al.

2020), and hence, a fresh relook into the available genetic resources for these two traits is very important for increasing the yields and seed quality in oil crops.

In case of groundnut, fresh seed dormancy is an important trait as the pods are subterranean, and unseasonal rains at crop harvest stage will spoil the produce leading to huge economic loss of the resource-poor semiarid farmers especially in India where more than 70% groundnut area is occupied by erect-type cultivars where fresh seed dormancy is absent. Hence, assembling the vast genetic resources available in these regions and evaluation for yield and other related traits including the resistance/tolerance to prevailing major biotic and abiotic stress factors at diverse environments and utilizing them in breeding programs would further enhance the genetic potentials of this crop. In orphan crops like sesame, safflower, linseed, and niger, there is a reduction in area under cultivation in different countries including India mainly due to the stringent competition from other economically profitable crops and cropping systems. Hence, high yielding and short duration varieties suiting to the profitable cropping pattern/systems need to be developed. One area where most of the oil crops suffer is due to lack of clear-cut studies on management strategies for irrigation water and nutrient use efficiencies. Although genetic variation for nutrient and water use efficiency has been reported in few crops, traits associated with these parameters further need to be addressed.

Oil crops are rich in energy but have C_3 mode of photosynthesis and, hence, are photosynthetically less efficient in partitioning of assimilates when compared with C_4 plants. Since large amount of biomass is still locked up in the vegetative parts of the plants, remobilization of photosynthates from vegetative parts to their respective reproductive parts also improves HI and, thus, seed yield. Although several studies are available on biomass accumulation, the physio- and biochemical mechanisms regulating assimilate partitioning and their genetics are yet to be elucidated in detail. The target traits include expanding and optimizing light capture by the leaf canopy, inducing a more rapid relaxation of non-photochemical quenching at photosystem II, increasing the carboxylation capacity of the Rubisco enzyme as well as minimizing oxygenation and photorespiration, enhancing the regenerative capacity of the carbon reduction cycle, optimizing the electron transport chain, and adding components of cyanobacterial or algal systems to pump CO_2 or compartmentalize Rubisco (Bailey-Serres et al. 2019).

Improving photosynthetic efficiency is neither a new nor a universally accepted idea. Some have argued that the selection pressures endured by photosynthesis render it unamenable to improvement. Despite decades of research, the challenge of engineering Rubisco for improved specificity and carboxylation rate remains unmet. However, some recent successes in engineering photosynthetic enzymes and introducing novel pathways into chloroplasts may lead to substantial gains in crop performance including oil crops.

The current trajectory for crop yields is insufficient to nourish the world's population by 2050. Greater and more consistent crop production must be achieved against a backdrop of climatic stress that limits yields, owing to shifts in pests and pathogens, precipitation, heat waves, and other weather extremes. Above all temperature extremes, frequent floods and drought may increase consequently. Genetic variations available in the reservoirs of germplasm resources in each of the crops need to be captured for use in future breeding programs.

The increasing demand for proteins worldwide as human nutrition and animal feed leads to a growing interest on other protein sources. Moreover, with increasing urbanization and income rise in many developing countries, per capita consumption of animal products would rise, and consequently the demand for feed grains would increase by 3% annually in these countries (FAO 2017). The oil meal or cake which remains after extraction of oil from the seed is a good source of protein both for ruminant and nonruminant animals. However, certain toxic compounds like phytate, erucic acid, glucosinolates, aflatoxins, etc. need to be eliminated/reduced through recent genetic and genomic tools and gene editing techniques.

Among the oil crops, groundnut crop has the unique advantage of a good source of fodder especially in Asian countries. About 40% is the underground pod biomass, while the aerial vegetative portion contributes 60% of the total biomass. They are rich in protein (14–21%) even at harvest stage, and hence any improvement in nitrogen content of the haulms would qualitatively improve the animal performance in terms of meat and milk yields. Only very few reports (Omokanye et al. 2001; Nigam and Blümmel 2010) are available on genetic variation for fodder quality traits like nitrogen/protein content, in vitro dry matter digestibility (IVDMD), metabolizable energy values, lignin, and fiber fractions. However, inheritance and strategies and selection schemes for evaluation of these important fodder quality traits in segregation generations are missing in the literature which is an important grey area in groundnut research.

Seeds of oil crops like sunflower, groundnut, and sesame are also used in confectioneries, and hence, high protein and sugar contents and low oil along with flavor compounds need to be addressed. Although there are few reports on these areas, further studies on flavor compounds and their genetic control, molecular and biochemical mechanisms regulating these compounds, and breeding strategies to exploit them need to be designed.

Studies on oil QTLs and candidate genes for oil content and oil quality traits through molecular approaches including GWAS are being accumulated in the literature during the last decade, and their validation in different genetic resources and breeding populations need immediate attention for genetic improvement of the oil crops.

References

Abel GH, Driscoll MF (1976) Sequential trait development and breeding for high yields in safflower. Crop Sci 16(2):213–216

Abel GH, Lorance DG (1975) Registration of dart safflower. Crop Sci 15:100

Abrol DP, Shankar U (2012) Pollination in oil crops: recent advances and future strategies. In: Gupta SK (ed) Technological innovations in major world oil crops, vol 2 Perspectives, pp 221–267

Alexander DE (1966) The 'Lysenko' method of increasing the oil content of the sunflower. Crop Sci 2:279–280

Andrade PB, Freitas BM, Rocha EEM, Lima JA, Rufino LL (2014) Floral biology and pollination requirements of sesame (*Sesamum indicum L.*). Acta Sci Anim Sci 36:93–99

Anilakumar KR, Pal A, Khanum F, Bawas AS (2010) Nutritional, medicinal and industrial uses of sesame (*Sesamum indicum* L.) seeds. Agric Conspec Sci 75:159–168

Anjani K (2014) A re-evaluation of castor (*Ricinus communis* L.) as a crop plant. CAB Rev 9(038):1–21

Arslan B (2007) Path analysis of yield and its components in safflower (*Carthamus tinctorius* L.). J Biol Sci 7(4):668–672

Ashri A (1998) Sesame breeding. Pl Breed Rev 16:179–228

Ashri A, Knowles PF (1960) Cytogenetics of safflower (*Carthamus* L.) species and their hybrids. Agron J 52:11–17

Bailey-Serres J, Jane E, Parker JE, Elizabeth AA, Giles ED, Oldroyd GED, Julian I, Schroeder JI (2019) Genetic strategies for improving crop yields. Nature 575:109–118

Bamber CJ (1916) Plants of the Punjab. Superintendent Government Printing, Lahore, pp 372–373

Basu MS, Nagaraj G, Reddy PS (1988) Genetic of oil and other major biochemicalcomponents in groundnut (*Arachis hypogaea*L.). Int J Trop Agric 6(1–2):106–110

Baydar H, Turgut L, Turgut K (1999) Variation of certain characters and line selection for yield, oil, oleic and linoleic acids in the Turkish sesame (*Sesamum indicum* L.) populations. Turk J Agric For 23:431–441

Belayneh H, Riley KW, Tadesse N, N. (1986) The effect of sowing date, seed rate and fertilizer on seed yield of niger in central highland of Ethiopia. J Oilseeds Res 3:216–222

Bera SK, Kamdar JH, Kasundra SV, Dash P, Maurya AK, Jasani MD, Chandrasekhar AB, Manivannan N, Vasanthi RP, Dobariya KL, Pandey MK, Janila P, Radhakrishnan T, Varshney RK (2018) Improving oil quality by altering levels of fatty acids through marker assisted selection of ahfad2 alleles in peanut (*Arachis hypogaea* L.). Euphytica 214:162

Bertioli DJ, Cannon SB, Froenicke L, Huang G, Farmer AD, Cannon EK, Liu X, Gao D, Clevenger J, Dash S, Ren L, Moretzsohn MC, Shirasawa K, Huang W, Vidigal B, Abernathy B, Chu Y, Niederhuth CE, Umale P, Araújo AC, Kozik A, Kim KD, Burow MD, Varshney RK, Wang X, Zhang X, Barkley N, Guimarães PM, Isobe S, Guo B, Liao B, Stalker HT, Schmitz RJ, Scheffler BE, Leal-Bertioli SC, Xun X, Jackson SA, Michelmore R, Ozias-Akins P (2016) The genome sequences of *Arachis duranensis* and *Arachisipaensis*, the diploid ancestors of cultivated peanut. Nat. Genet 48(4):438–446. https://doi.org/10.1038/ng.3517. Epub 2016 Feb 22. PMID: 26901068

Bhatnagar PS, Tiwari SP, Singh C (1992) Disrupting the negative association between oil andprotein content in soybean seeds through mutagenesis. Mut Breed Newsl 39:7

Bommarco P, Lorenzo Marini L, Vaissière BE (2012) Insect pollination enhances seed yield, quality, and market value in oilseed rape. Oecologia 169:1025–1032

Bovi MLA (1982) Genotypic and environmental effect on fatty acid composition, iodine value and oil content of peanut (*Arachis hypogea* L.). Ph.D. thesis submitted to the University of Florida, p 119

Brim CA, Burton JW (1979) Recurrent selection in soybeans. II selection for increased percent protein in seeds. Crop Sci 19:494–498

Brim CA, Schutz WM, Collins FI (1968) Maternal effect on fatty acid composition and oil contentof soybean, *Glycine max* (L) Merrill. *Crop Sci* 8:517–518

Burton JW (1987) Quantitative genetics: results relevant to soybean breeding. In: Wilcox JR (ed) oybeans: improvement, production, and uses, 2nd edn. ASA, CSSA, and SSSA, Madison, pp 211–242

Cagirgan I (2006) Selection and morphological characterization of induced determinate mutants in sesame. Field Crop Res 96:19–24

Chapman MA, Burke JM (2007a) Genetic divergence and hybrid speciation. Evolution 61-7:1773–1780

Chapman MA, Burke JM (2007b) DNA sequence diversity and the origin of cultivated safflower (*Carthamus tinctorius* L.; Asteraceae). BMC Plant Biol 7:60

Chauhan JS, Singh CV, Singh RK (1996) Analysis of growth parameters and yield in sesame (*Sesamum indicum* L.). Indian J Agric Sci 66(1):55–58

Chauhan JS, Tyagi MK, Kumar PR, Tyagi P, Maharaj Singh M, Kumar S (2002) Breeding for oil and seed meal quality in rapeseed-mustard in India – a review. Agric Rev 23(2):71–92

Chu C, Wu L, Holbrook CC, Tillman BL, Person G, Ozias-Akins P (2011) Marker-assisted selection to pyramid nematode resistance and the high oleic trait in peanut. Plant Genome 4:110–117

Chung J, Babka HL, Graef GL, Staswick PE, Lee DJ, Cregan PB, Shoemaker RC, Specht JE (2003). The Seed Protein, Oil, and Yield QTL on Soybean Linkage Group I. Crop Sci. 43:1053–1067

Chung G, Singh RJ (2008) Broadening the genetic base of soybean: a Multidisciplinary Approach. Crit Rev Plant Sci 27:295–341

Cober E, Voldeng HD (2000) Developing high-protein, high-yield soybean populations and lines. Crop Sci 40(1). https://doi.org/10.2135/cropsci2000.40139x

Cober E, Cianzio Silvia RC, Pantalone V, Rajcan I (2009) Soybean. In: Vollmann J, Rajkan IT (eds) Oil crops. Hand book plant breeding, vol 4. Springer, pp 57–90

Connor DJ, Hall AJ (1997) Sunflower physiology. In: Schneiter AA (ed) Sunflower technology and production. ASA, CSSA, SSSA, Wisconsin, pp 113–182

Cowling W (2007) Genetic diversity in Australian canola and implications for crop breeding for changing future environments. Field Crop Res 104(1–3):103–111

D'Antuono LF, Rossini F (1995) Experimental estimation of flax (*Linum usitatissimum* L.) crop parameters. Ind Crops Prod 3:261–271

Diederichsen A, Hammer K (1995) Variation of cultivated flax (*Linum usitatissimum* L. subsp. *usitatissimum*) and its wild progenitor pale flax (subsp. *angustifolium* (Huds.) Thell.). Genet Resour Crop Evol 42:263–272. https://doi.org/10.1007/BF02431261

Diepenbrock W (2000) Yield analysis of winter oilseed rape (*Brassica napus* L.): a review. Field Crops Res 67:35–49

Dillman AC, Goar LG (1937) Flaxseed production in the Far Western States. U.S. Department of Agriculture. University of Illinois at Urbana-Champaign, p 22

Dossa K, Diouf D, Wang L, Wei X, Zhang Y, Niang M, Fonceka D, Yu J, Mmadi MA, Yehouessi LW, Liao B, Zhang X, Cisse N (2017) The emerging oilseed crop *Sesamum indicum*enters the "Omics" era. Front Plant Sci 8:1154

Downey RK, Craig BM (1964) Genetic control of fatty acid biosynthesis in rapeseed (*Brassica napus* L.). J Am Oil Chem Soc 41(7):475–478

Dribneki JCK, Mceachern SH, Chen Y, Green AG, Rashid KY (2007) 2149 solin (low linoleic acid flax). Can J Plant Sci 87:297–299

Dribnenki JCP, Green AG (1995) Linola'947' low linolenic flax. Can J Plant Sci 75:201–202

Dwivedi SL, Bertioli DJ, Crouch JH, Valls JF, Upadhyaya HD, Fávero M, Paterson AH (2007) Peanut. In: Kole C (ed) Genome mapping and molecular breeding in plants, Volume 2 Oilseeds. Springer, Berlin/Heidelberg, pp 115–151

El-Hamidi M, Zaher FA (2018) Production of vegetable oils in the world and in Egypt: an overview. Bull Natl Res Centre 42:19. https://doi.org/10.1186/s42269-018-0019-0

European Cooperative Programme for Plant Genetic Resources (ECPGR) (2019) Phase X (2019–2023), Annual Progress Report (January–December), 2019, p 22

Fan W, Lu J, Pan C, Tan M, Lin Q, Liu W, Li D, Wang L, Hu L, Wang L, Chen C, Wu A, Yu J, Hu S, Yan X, Lu S, Cui P (2019) Sequencing of Chinese castor lines reveals genetic signatures of selection and yield-associated loci. Nat Commun 10:3418. https://doi.org/10.1038/s41467-019-11,228-3

Fang C, Ma Y, Wu S et al (2017) Genome-wide association studies dissect the genetic networks underlying agronomical traits in soybean. Genome Biol 18:161. https://doi.org/10.1186/s13059-017-1289-9

FAO (2010) The second report on the state of the world's plant genetic resources for food and agriculture. Food and Agriculture Organization of the United Nations, Rome, pp 55–94

FAO (2017) The future of food and agriculture – trends and challenges. Food and Agriculture Organization of the United Nations, Rome, pp 1–180

FAO (2018) The pollination of cultivated plants a compendium for practitioners. In: Roubik DW (ed) . Food and Agriculture Organization of the United Nations, Rome, pp 1–289

Fernández-Martínez JM, Velasco L, Pérez-Vich B (2004) Progress in genetic modification of sunflower oil quality. In: Proceedings of 16th Intl. Sunflower Conf. Fargo, ND, USA, pp 1–14

Fernández-Martínez JM, Pérez-Vich B, Velasco L (2009) Sunflower. In: Vollmann J, Rajcan I (eds) Oil crops. Springer, New York, pp 155–232

Fick GN, Miller JF (1997a) Sunflower breeding. In: Schneiter AA (ed) Sunflower technology and production. American Society of Agronomy, Inc, Madison/Wisconsin, pp 395–433

Fick GN, Miller JF (1997b) Sunflower breeding. In: Schneiter AA (ed) Sunflower science and technology, Agronomy Monograph, vol 35. ASA-CSSA-SSSA, Madison, pp 253–258

Finch-Savage WE, Bassel GW (2015) Seed vigour and crop establishment: extending performance beyond adaptation. J Exp Bot 67(3):567–591

Free JB (1993) Insect pollination of crops, 2nd edn. Academic. Harcourt Brace Jovanovich Publishing, London, p 684

Friedt W, Snowdon R (2009) Oilseed rape. In: Oil crops, Hand book of Plant Breeding, vol 4. Springer, pp 91–126

Getinet A, Sharma SM (1996) Niger. *Guizotia abyssinica* (L. f.) Cass. Promotingthe conservation and use of underutilized and neglected crops, vol 5. Institute of PlantGenetics and Crop Plant Research/International Plant Genetic Resources Institute, Gatersleben/Rome, p 108

Getinet A, Teklewold A (1995) An agronomic and seed-quality evaluation of niger (*Guizotia abyssinica* Cass.) germplasm grown in Ethiopia. Plant Breed 114:375–376

Gill KS (1966) Evolutionary relationship among *Linum* Species (Ph.D.). University of California, Riverside, CA, USA, p 260

Gill KS (1987) Flax. Indian Council of Agricultural Research, New Delhi, 386 p

Gizlice Z, Carter TE, Burton JW (1994) Genetic base for North American public soybean cultivars released between 1947 and 1988. Crop Sci 34:1143–1151

Golkar P (2014) Breeding improvements in safflower (*Carthamus tinctorius* L.): a review. Australian J Crop Sci 8(7):1079–1085. ISSN:1835-2707

Golkar P, Arzani A, Rezai AM (2011) Determining relationships among seed yield, yield components and morpho-phenological traits using multivariate analyses in safflower (*Carthamus tinctorious* L.). Ann Biol Res 2(3):162–169

Grace Q, Chen KJ, Eva Morales E, Mackey B, Lin JT (2016) Rapid development of a castor cultivar with increased oil content. Ind Crop Prod 94:586–588

Green AG, Marshall DR (1984) Isolation of induced mutants in flax (*Linum usitatissimum*) having reduced linolenic acid content. Euphytica 33:321–328

Gregory WC, Gregory MP (1979) Exotic germplasm of *Arachis* L. interspecific hybrids. J Hered 70:185–193

Gupta SK (2012) Brassicas. Technological innovations in major world oil crops. 1:53–83. https://doi.org/10.1007/978-1-4614-0356-2

Hamdan YAS, Pérez-Vich B, Fernández-Martínez JM, Velasco L (2009) Novel safflower germplasm with increased saturated fatty acid content. Crop Sci 49:127–132

Hammond EG, Fehr WR (1983) Registration of A5 germplasm line of soybean. Crop Sci 23:192

Hammons RO (1972) Peanuts. In: Genetic vulnerability of major crop plants. NAS-NRC Agric. Board, Washington, DC, pp 217–223, 252

Hammons RO (1976) Peanuts: genetic vulnerability and breeding strategy. Crop Sci 16:527–530

Hanzel JJ (1992) Proceedings of the 13th International Sunflower Conference. Development of bird-resistant sunflower, vol 2, Pisa, Italy, pp 1059e1064

Hao Q, Yang Y, Guo C, Liu X, Chen H, Yang Z, Zhang C, Chen L, Yuan S, Chen S, Cao D, Guo W, Qiu D, Zhang X, Shan Z, Zhou X (2020) Evaluation of seed vigor in soybean germplasms from different eco-regions. Oil Crop Sci 5:22–25

Harlan RR, de Wet JMJ (1971) Toward a rational classification of cultivated plants. Taxon 20:509–517

Hasan MF, Seyis AG, Badani J, Pons-Kuhnemann, Friedt W, Luhs W, Snowdon RJ (2006) Analysis of genetic diversity in the *Brassicanapus* L. gene pool using SSR markers. Genet Resour Crop Evol 53:793–802

Heiser CB Jr (1955) The origin and development of the cultivated sunflower. Am Biol Teach 17(5):161–167

Heywood VH (1993) Flowering plants of the world. Oxford University Press, Oxford, pp 207–208

Holbrook CC, Brenneman TB, Stalker HT, Johnson WC, Ozias-Akins P, Chu Y, Vellidis G, Mc Clusky D (2014) Peanut. In: Smith S, Diers B, Specht J, Carver B (eds) Yield gains in major U.S. field crops. ASA-CSSA-SSSA, Madison, pp 173–194

Hu Z, Hua W, Zhang L, Deng L, Wang X, Liu G, Hao W, Wang H (2013) Seed structure characteristics to form ultrahigh oil content in rapeseed. PLoS One 8(4):e62099. https://doi.org/10.1371/journal.pone.0062099

Hyten DL, Song Q, Zhu Y, Choi IY, Nelson RL, Costa JM, Specht JE, Shoemaker RC, Cregan PB (2016) Impacts of genetic bottlenecks on soybean genome diversity. Proc Natl Acad Sci USA 103:16666–16671. https://doi.org/10.1073/pnas.0604379103

Isleib G, Holbrook CC, Gorbet DW (2001) Use of plant introductions in peanut cultivar development. Peanut Sci 28:96–113

Janila P, Nigam SN, Manish K, Pandey MK, Nagesh P, Varshney RK (2013) Groundnut improvement: use of genetic and genomic tools. Front Plant Sci 4(3):1–16

Janila P, Murali TV, Manish K, Pandey MK, Haile Desmae H, Babu N, Motagi BN, Okori P, Surendra S, Manohar SS, Rathnakumar AL, Radhakrishnan T, Liao B, Varshney RK (2016) Genomic tools in groundnut breeding program: status and perspectives. Front Plant Sci 7:1–15

Jaramillo S, Baena M (2002) Ex situ conservation of plant genetic resources: training module. International Plant Genetic Resources Institute, Cali, p 229

Javed A, Mohini Prabha S, Anju S, Harjeevan K, Navneet K, Sanjula S, Baudh B, Sardana VK, Surinder BS (2020) Association Mapping of seed quality traits under varying conditions of nitrogen application in *Brassica juncea* L. Czern & Coss. Front Genet 11:744. https://doi.org/10.3389/fgene.2020.00744

Jiang CC, Shi JQ, Li RY, Long Y, Wang H, Li DR, Zhao JY, Meng JL (2014) Quantitative trait loci that control the oil content variation of rapeseed (*Brassica napus* L.). Theor Appl Genet 127:957–968. https://doi.org/10.1007/s00122-014-2271-5

Jones Q (1983) Germplasm needs of oilseed crops. Econ Bot 37(4):418–422

Joshi AB (1961) Sesamum. A monograph. Indian Central Oil Seeds Committee, Hyderabad. (now Ind. Council of Agric. Res., New Delhi, India), p 109

Kadirvel P, Cheelam Veerraju C, Senapathy Senthilvel S, Yadav P, Usha Kiran B, Shaik Shaw R, Velu Mani S, Rushwanth Reddy V, Darpan Mohanrao M, Mukta N (2020) Marker-assisted selection for fast-track breeding of high oleic lines in safflower (*Carthamus tinctorious* L.). Ind Crops Prod 158:112983. https://doi.org/10.1016/j.indcrop

Kaya Y, Evci G, Durak S, Peckan V, Gucer T (2007) Determining the relationships between yield and yield attributes in sunflower. Turk J Agric For 31:237–244

Khedikar Y, Wayne E, Clarke WE, Lifeng Chen L, Erin E, Higgins EE, Kagale S, Koh CS, Rick Bennett R, Parkin IAP (2020) Narrow genetic base shapes population structure and linkage disequilibrium in an industrial oilseed crop, *Brassica carinata* A. Braun. Sci Rep 10:12629. https://doi.org/10.1038/s41598-020-69255-w

Kinney AJ, Knowlton S (1997) Designer oils: the high oleic soybean. In: Harander S, Roller S (eds) Genetic engineering for food industry: a strategy for food quality improvement. Blackie Academic, London, pp 193–213

Klein AM, Vassiere BE, Cane J, Steffan-Dewenter I, Cunningham S, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. Proc Royal Soc 274:303–313

Knauft DA, Gorbet DW (1989) Genetic diversity among peanutcultivars. Crop Sci 29:1417–1422

Knowles PP (1968) Registration of UC-1 safflower. Crop Sci 8:641

Kovacik AV, Skaloud – RostlinnaVyroba-UVTIZ (Czechoslovakia) (1990) The yield results of pilot trials with sunflower hybrids. agris.fao.org

Lavanya C, Vishnuvardhan Reddy A, Dutta B, Bandopadhyay R (2018) Classical genetics, cytogenetics and traditional breeding in castor bean. In: Kole C, Rabinowicz P (eds) The castor bean genome, Compendium of plant genomes. Springer, Cham, pp 33–65

Lee JI, Lee BH, Seong NS, Kang CW (1991) Studies on interspecific hybridization in sesame. I Characteristics and cross affinity of wild sesame. Korean J Breed 22:356–360

Levinson CM, Marasigan KM, Chu Y, Stalker HT, Holbrook CC, Ni X, Williams WP, Ozias-Akins P (2020) Resistance to fall armyworm (*Lepidoptera*: Noctuidae) feeding identified in nascent allotetraploids cross-compatible to cultivated peanut (*Arachis hypogaea* L.). Peanut Sci 47(3):123–134. https://doi.org/10.3146/PS20-13.1

Li HW, Zhao TJ, Wang YF, Yu DY, Chen SY, Zhou RB, Gai JY (2011) Genetic structure composed of additive QTL, epistatic QTL pairs and collective unmapped minor QTL conferring oil content and fatty acid components of soybeans. Euphytica 182:117–132. https://doi.org/10.1007/s10681-011-0524-9

Linz GM, Hanzel JJ (2015) Sunflower bird pests. In: Martinez-Force E, Dunford NT, Salas JJ (eds) Sunflower chemistry, production, processing, and utilization. AOCS Press, Urbana, in association with USDA APHIS Wildlife Services NWRC, pp 175–186

Lopez Pereira M, Berney A, Hall AJ, Trapan IN (2008) Contribution of pre-anthesis photoassimilates to grain yield: its relationship with yield in Argentine sunflower cultivars released between 1930 and 1995. Field Crop Res 105:88–96

Martin JP (1967) A contribution to the study of certain hereditary characters of agronomicimportance in the groundnut. *Oleagineux* 22:673–376

Milani M, Nóbrega MBM (2013) Castor breeding. https://www.intechopen.com/books/plant-breeding-from-laboratories-to-fields/castor-breeding

Miller JF, Fick GN, Roath WW (1982) Relationships among traits of inbreds and hybrids sunflower. In: Proceedings of 10th International Sunflower Conference Surfers Paradise, Australia, pp 238–240

Miller JF, Zimmerman DC, Vick BA (1987) Genetic control of high oleic acid content in sunflower oil. Crop Sci 27(5):923–926

Miller JF, Seiler GJ, Jan CC (1992) Introduced germplasm use in sunflower inbred and hybrid development. In: Shands HL, Weisner LE (eds) Use of Plant Introductions in Cultivar Development Part 2, Volume 20. CSSA Special Publications Inc, pp 151–166. https://doi.org/10.2135/cssaspecpub20.c7

Moore KM, Knauft DA (1989) The Inheritance of high oleic acid in peanut. J Hered 80(3):252–253

Moreira FF, Hearst AA, Cherkauer KA, Rainey KM (2019) Improving the efficiency of soybean breeding with high-throughput canopy phenotyping. Plant Methods 15:139

Morinaga T (1934) Interspecific hybridization in *Brassica*. VI. The cytology of F1 hybrids of *Brassica juncea* and *B. nigra*. Cytologia 6:62–67

Moshkin VA, Dvoryadkina AG (1986) Cytology and genetics of qualitative characters. In: Moshkin VA (ed) Castor. Amerind, New Delhi, pp 93–102

Mosjidis JA, Yermanos DM (1985) Plant position effect on seed weight, oil content, and oil composition in sesame (*Sesamum indicum*). Euphytica 34:193–200

Murphy DJ (1996) Engineering oil production in rapeseed and other oil crops. Trends Biotechnol 14:206–213

Murthy HN, Hiremath SC, Salimath SS (1993) Origin, evolution and genome differentiation in *Guizotia abyssinica* and its wild species. Theor Appl Genet 87:587–592

Mustafa BHS, Ejaz-ul-Hasan, Anwar AM, Aftab M, Mahmood T (2015) Selection criteria for improvement in sesame (*Sesamum indicum* L.). Am J Exp Agric 9(4):1–13

Newell CA, Hymowitz T (1983) Hybridization in the genus *Glycine* subgenus *Glycine* Willd (*Leguminosae*, Papilionoideae). Am J Bot 70:334–348

Nigam SN, Blümmel M (2010) Cultivar-dependent variation in food-feed-traits in groundnut (*Arachis hypogaea* L.). Anim Nutr Feed Technol 10S:39–48

Nigam SN, Dwivedi SL, Gibbons RW (1991) Groundnut breeding: constraints, achievements and future possibilities. Plant Breed Abstr 61:1127–1136

Norden AJ, Gorbet DW, Knauft DA, Young CT (1987) Variability in oil quality among peanut genotypes in the Florida breeding program. Peanut Sci 14:7–11

Ntiamoah C, Rowland GG (1997) Inheritance and characterization of two low linolenic acidEMS-induced McGregor mutant flax (*Linum usitatissimum*). Can J Plant Sci 77:353–358

Okha JO, Ojo AA, Vange T (2007) Combining ability and heterosis of oil content in in six accessions of castor at Makurdi. Nat Sci 5:18–23

Olsson G (1990) Rape yield Production components *Svenskn Frotidning*. 59:168–169

Omokanye AT, Onifade OS, Olorunju PE, Adamu AM, Tanko RJ, Balogun RO (2001) The evaluation of dual-purpose groundnut (*Arachis hypogaea*) varieties for fodder and seed production in Shika. Nigeria J Agric Sci 136:75–79

Palmer RG, Gai J, Sun H, Burton JW (2001a) Production and evaluation of hybrid soybean. Plant Breed Rev 21:263–307

Palmer RG, Gai J, Sun H, Burton JW (2001b) Production and evaluation of hybrid soybean. Plant Breed Rev 21:263–308

Patel JS, Narayana GV (1935) Chromosome numbers in safflower. Curr Sci 4:412

Pawlowski SH (1964) Seed genotype and oil percentage relationship between seeds of a sunflower. Can J Genet Cytol 6(3):293–297

Pérez-Vich B, Fernández-Martínez JM, Grondona M, Knapp SJ, Berry ST (2002) Stearoyl-ACP and oleoyl-PC desaturase genes cosegregate with quantitative trait loci underlying high stearic and high oleic acid mutant phenotypes in sunflower. Theor Appl Genet 104:338–349

Pérez-Vich B, Leon AJ, Grondona M, Velasco L, Fernández-Martínez JM (2006) Molecular analysis of the high stearic acid content in sunflower mutant CAS-14. Theor Appl Genet 112:867–875

Potts SG, Breeze T, Gemmill-Herren B (2014) Crop pollination. In: Van Alfen NK (ed) Encyclopedia of agriculture and food systems. Academic, pp 408–418

Qin J, Shi A, Song Q, Li S, Wang F, Cao Y, Ravelombola W, Song Q, Yang C, Zhang M (2019) Genome wide association study and genomic selection of amino acid concentrations in soybean seeds. Front Plant Sci 10:1445. https://doi.org/10.3389/fpls.2019.01445

Raghavan TS, Krishnamurthy KV (1947) Cytogenetical studies in *Sesamum*. Part 1. Cytology of the parents, *Sesamum orientale* Linn., and *Sesamum prostratum* Retz. and the cytology of the sterile hybrid between them and of the fertile amphidiploid. Proc Indian Acad Sci B 26(6):236–275

Rajeswari S, Ramaswamy NM (2004) Effect of growth regulators on retention of floral pedicelsand capsules in sesame. Sesame Safflower Newsl 19:1137–1617

Rao KR, Kishor PB, Vaidyanath K (2002) Biotechnology of sesame – an oil seed crop. Plant Cell Biotechnol Mol Biol 3:101–110

Rathnakumar AL, Singh R, Parmar DL, Misra JB (2013) Groundnut a crop profile and compendium of notified varieties of India. Directorate of Groundnut Research, Junagadh, p 118

Rathnakumar AL, Nigam SN, Muralidharan V, Misra JB (2015) Groundnut at a cross-road in India. Indian Oil Producers and Exporters Association of India, Mumbai, pp 1–103

Ratnakumar AL, Hariprasanna K, Lalwani HB (2010) Genetic improvement in Spanish type groundnut, *Arachis hypogaea* L varieties in India over the years. J Oilseeds Res 27:1–7

Raut VM, Tawari SP, Halvankar GB (2000) Gene effects for some quantitative characters insoybean (*Glycinemax*) crosses. Indian J Agric Sci 70:334–335

Reddy PS (1988) Genetics, breeding and varieties. In: Reddy PS (ed) Groundnut. Indian Council of Agricultural Research, New Delhi, pp 200–317

Rhodes J (2002) Cotton pollination by honey bees. Aust J Exp Agric 42:513–518

Richharia RH, Kotval JP (1940) Chromosome numbers in safflower. Curr Sci 9:73–74

Rojas Barros P, de HaroJosé María A, Martínez F (2005) Inheritance of high oleic/low ricinoleic acid content in the seed oil of castor mutant OLE1. Crop Sci 45(1):157–162

Rojas-Barros P (2001) Estudios geneticos de androesterilidad contenido en aceite y acido ricino leico en ricino. Ph.D Thesis, University of Cordoba, Spain

Ross A, Fehr WR, Welke GA, Hammond EG, Cianzio SR (2000) Agronomic and seed traits of 1%-linolenate soybean genotypes. Crop Sci 40:383–386

Rowland GG (1991) An EMS-induced low-linolenic-acid mutant in McGregor flax (*Linumusitatissimum* L.). Can J Plant Sci 71:393–396

Ruchi N (2008) Studies ongrowth and development in sesame (*Sesamum indicum*) in relation to seed yield. M.Sc., thesis, Department of Plant Physiology, CSK HP Krishi Vishva Vidyalaya, Palampur-176,062 (H.P.), India, p 69

Schneiter AA (1992) Production of semidwarf and dwarf sunflower in the northern Great Plains of the United States. Field Crop Res 30(3–4):391–401

Seberry D, Parker P, Ayton J (2011) Quality of Australian Canola 2010. Australian Oilseeds Federation, Sydney

Seegeler CJP (1983) Oil plants in Ethiopia. Their taxonomy and agricultural significance, Centre for Agricultural Publication and Documentation, PUDOC, Wageningen

Sharma P, Dupare BU, Patel MR (2016) Soybean improvement through research in India and socio-economic changes. Legum Res 39(6):935–945

Shasidhar Y, Murali TV, Vishwakarma MK, Manohar SS, Gangurde SS, Sriswathi M, Sudini HK, Dobariya KL, Bera SK, Radhakrishnan T, Manish K, Pandey MK, Janila P, Varshney RK (2020) Improvement of three popular Indian groundnut varieties for foliar disease resistance and high oleic acid using SSR markers and SNP array in marker-assisted backcrossing. Crop J 8(1):1–15. https://doi.org/10.1016/j.cj.2019.07.001

Singh RJ (2019) Cytogenetics and genetic introgression from wild relatives in soybean. Nucleus 62:3–14

Singh BB, Hadley HH (1968) Maternal control of oil synthesis in soybeans (*Glycine max* (L.) Merr.). Crop Sci 8:622–625

Singh AK, Nigam SN (2016) *Arachis*gene pools and genetic improvement in groundnut. In: Rajpal VR et al (eds) Gene pool diversity and crop improvement, sustainable development and biodiversity 10. Springer, Cham, pp 17–75

Singh V, Nimbkar N (2007) Safflower (*Carthamus tinctorius* L.). In: Singh RJ (ed) Genetic resources chromosome engineering, and crop improvement: oil crops. CRC Press, New York, pp 168–194

Singh AK, Simpson CE (1994) Biosystematic and genetic resources. In: Smartt J (ed) The groundnut crop. A scientific basis for improvement. Chapman and Hall, London, pp 96–138

Singh V, Kumar S, Amrita Singh A, Bhaduri NP, Bhat KV, Lakhanpaul S (2016) Unlocking the potential of genetic resources for improvement of sesame (*Sesamum indicum* L.): the current scenario. In: Rajpal VR et al (eds) Gene pool diversity and crop improvement, sustainable development and biodiversity 10. Springer, Cham, pp 447–473

Škorić D (1992) Achievements and future directions of sunflower breeding. *Field Crop Res* 30:231–270

Stalker HT (2017) Utilizing wild species for peanut improvement. Crop Sci 57:1102–1120. https://doi.org/10.2135/cropsci2016.09.0824

Sujatha M (2008) Biotechnological interventions for genetic improvement of safflower. Paper presented at the 7th international safflower conference, Waga Wagga, Australia, 3–9 Nov 2008

Swiecicki WK, Surma M, Koziara W, Skrzypczak G, Szukała J, Bartkowiak-Broda I, Zimny J, Banaszak Z, Marciniak K (2011) Modern technologies in crop production—Friendly for man and environment. Pol J Agron 7:102–112. (In Polish)

Syed RA, Law IH, Coroley RHV (1982) Insect Pollination of oilpalm: introduction, establishment, establishment and pollination efficiency of *Elaeidobiuskamerunicus*in Malaysia. Planter 58:547–561

Talukder Z, Guojia M, Hulke Brent S, Chao-Chien J, Lili Q (2019) Linkage mapping and genome-wide association studies of the Rf gene cluster in sunflower (*Helianthus annuus* L.) and their distribution in world sunflower collections. Front Genet 10:216

Tammes T (1925) Mutation and evolution. Z. Induct. Abstamm. u. Vererb Lehre 36:417–426

Tammes T (1928) The genetics of the genus *Linum*. Bibliographia Genetica 25(4):1–36

U., N (1935) Genomic analysis of *Brassica* with special reference to the experimental formation of *B. napus* and peculiar mode of fertilization. Jpn J Bot 7:389–452

Urie AL (1981) Continued studies on inheritance of partial hull in safflower (*Carthamustinctorius* L.). In: Knowles PF (ed) Proceedings first international safflower conference. University of California, Davis, California USA, 12–16 July, pp 264–271

Urie AL (1986) Inheritance of partial hull in safflower. Crop Sci 26:493–498

Vollmann J, Rajcan I (2009) Oil crops breeding and genetics. oil crops, *hand book of plant breeding*, vol 4. Springer, pp 1–30

Wang ML, Barkley NA, Chinnan M, Stalker HT, Pittman RN (2010a) Oil content and fatty acid composition variability in wild peanut species. Plant Genet Resour Char Util 8(3):232–234

Wang X, Liu G, Yang Q, Hua W, Liu J, Wang H (2010b) Genetic analysis on oil content in rapeseed (*Brassica napus* L.). Euphytica 173:17–24

Wang C, Hu S, Gardner C, Lübberstedt T (2017) Emerging avenues for utilization of Exotic Germplasm. Trends Plant Sci 22:624–637

Wang B, Zhikun Wu Z, Li Z, Zhang Q, Jianlin Hu J, Xiao Y, Cai D, Jiangsheng Wu J, King GJ, Li H, Kede Liu K (2018) Dissection of the genetic architecture of three seed-quality traits and consequences for breeding in *Brassica napus*. Plant Biotechnol J 16(7):1336–1348

Wei W, Zhang Y, Lv H, Li D, Wang L, Zhang X (2013) Association analysis for quality traits in a diverse panel of Chinese sesame (*Sesamum indicum* L.) germplasm. J Integr Plant Biol 55:745–758. https://doi.org/10.1111/jipb.1204

Wei X, Liu K, Zhang Y, Qi Feng Q, Wang L, Zhao Y, Li D, Zhao Q, Zhu X, Zhu X, Li W, Danlin Fan D, Gao Y, Lu Y, Zhang X, Tang X, Zhou C, Zhu C, Liu L, Zhong R, Tian Q, Wen Z, Weng Q, Han B, Huang X, Zhang X (2015) Genetic discovery for oil production and quality in sesame. Nat Commun 6:8609. https://doi.org/10.1038/ncomms9609. www.nature.com/naturecommunications

Weiss EA (2000) Oilseed crops (2nd edn, EA Weiss, ed.) Blackwell Science, Oxford, p 364

Williams IH (1991) The pollination of linseed. Acta Hortic:234–238

Xu C, He Y, Sun S, Song W, Wu T, Han T, Wu C (2020) Analysis of soybean yield formation differences across different production regions in China. Agron J 112:4195–4206

Yadava D, Sujata V, Singh NS, Mohapatra T, Prabhu K (2012) Breeding major oil crops: present status and future research needs. In: Gupta SK (ed) Technological innovations in major world oil crops, 17, vol 1: Breeding. Springer. https://doi.org/10.1007/978-1-4614-0356-2_2

Yao Y, You Q, Duan G, Ren J, Chu S, Zhao J, Li X, Zhou X, Jiao Y (2020) Quantitative trait loci analysis of seed oil content and composition of wild and cultivated soybean. BMC Plant Biol 20:51. https://doi.org/10.1186/s12870-019-2199-7

Zhang H, Li Wang M, Dang P, Jiang T, Zhao S, Lamb M, Chen C (2021) Identification of potential QTLs and genes associated with seed composition traits in peanut (*Arachis hypogaea* L.) using GWAS and RNA-Seq analysis. Gene 769:145215. https://doi.org/10.1016/jgene2020145215. Epub 2020 Oct 7

Zheng P, Allen WB, Roesler K, Williams ME, Zhang S, Li J, Glassman K, Ranch J, Nubel D, Solawetz W, Bhattramakki D, Llaca V, Deschamps S, Zhong GY, Tarczynski MC, Shen B (2008) A phenylalanine in dgat is a key determinant of oil content and composition in maize. Nat Genet 40:367–372. https://doi.org/10.1038/ng.85

Zhou R, Dossa K, Li D, Yu J, Jun You J, Wei X, Zhang X (2018) Genome-wide association studies of 39 seed yield-related traits in Sesame (*Sesamum indicum* L.). Int J Mol Sci 19(9):2794. https://doi.org/10.3390/ijms19092794ECPGR

Zhou Y, Zhao W, Lai Y, Zhang B, Zhang D (2020). Edible Plant Oil: Global Status, Health Issues, and Perspectives. *Frontiers in Plant Science*, 11:1315

Zimmerman LH (1958) Castor beans: A new oil crop for mechanized production. Adv Argon 10:257–288