Chapter 15
Unlocking the Potential of Genetic Resources for Improvement of Sesame (*Sesamum indicum* L.): The Current Scenario

Vibhuti Singh, Sachin Kumar, Amrita Singh, Niti Pathak Bhaduri, Kangila Venkataramana Bhat and Suman Lakhanpaul

Abstract Sesame (*Sesamum indicum* L.) economically valued worldwide for its seeds and seed oil has been designated as 'queen of oilseeds'. Antioxidants such as lignans and their derivatives prevent oxidation of the oil and provide longer shelf life making sesame oil one of the most stable oils. Due to the presence of several bioactive compounds it has been often listed among the world's healthiest foods. However, the attempts to improve sesame crop remain scanty resulting in lack of superior genotypes having high yield potential and resistance to biotic and abiotic stresses. Further, traits such as indeterminate growth habit and capsule shattering are also responsible for its reduced yields making it less favorable for large-scale farming. Wild relatives of sesame are important reservoir of useful genes and need to be exploited for sesame improvement. These wild species exhibit crossability with the cultivated gene pool to varying extents and can be utilized for transferring the desirable traits using conventional breeding approaches assisted with modern techniques. Extensive research efforts are therefore desirable in several aspects such as identification of different gene pools of sesame genetic resources, phylogenetic relationships, assessment of genetic diversity in the cultivated gene pool, etc. Molecular approaches to develop genetic map, hybrid testing, identification of core collections, DNA fingerprinting are already underway. Biotechnological interventions required for the successful production of transgenic plants have also been initiated. Recently, most of the genes and biosynthetic pathways involved in oil and other useful components of sesame seeds have been unraveled. An integrated approach based on conventional and modern tools for identification and utilization of useful genes followed by their successful incorporation in the cultivated gene

V. Singh · S. Kumar · A. Singh · N.P. Bhaduri · S. Lakhanpaul (✉)
Department of Botany, University of Delhi, Delhi 110007, India
e-mail: sumanlp2001@yahoo.com

K.V. Bhat
National Bureau of Plant Genetic Resources, Indian Agricultural Research Institute, Pusa Campus, New Delhi 110012, India
e-mail: kvbhat2001@yahoo.com

V.R. Rajpal et al. (eds.), *Gene Pool Diversity and Crop Improvement*,
Sustainable Development and Biodiversity 10,
DOI 10.1007/978-3-319-27096-8_15

pool is desirable for large-scale cultivation of sesame, to meet the increasing demands of healthy food crops due to the ever increasing heath awareness world over.

Keywords Sesame · Germplasm · Wild relatives · Crop improvement · Genomic resources

15.1 Sesame—Introduction

Sesamum indicum L. (Family Pedaliaceae) commonly known as sesame is an important oilseed crop. It is referred as 'queen of oilseeds' due to its regard by the users and owing to its oil quality (Bedigian and Harlan 1986). It is one of the most ancient crops in the world known to mankind, with archeological evidences dating back to 2250 and 1750 BC at Harappa in the Indus valley (Najeeb et al. 2012). Ironically, it is considered as an 'orphan crop' due to meager research efforts attributed to the fact that it is not a mandate crop for any international crop research institute (Bhat et al. 1999).

Sesame is mainly a crop of warmer areas including Asia and Africa (Ashri 1988), but newer cultivars have extended their range to temperate regions. It is an excellent rotation crop of cotton, maize, groundnut, wheat, and sorghum. It reduces nematode populations that attack cotton and groundnut (Elbadri and Yassin 2010). Its deep and extensive root system makes it an excellent soil builder. It also improves soil texture, retains moisture and reduces soil erosion. The left over composted sesame leaves also help in moisture retention of the soil making favorable conditions for planting the next crop. Sesame is resistant to drought, it is a low cost crop and is therefore known as one of the best alternative specialty crops.

15.1.1 Economic Importance

Sesame is cultivated on a worldwide basis for its seeds, oil and protein. Seeds are used either as a whole or decorticated in sweets or confectioneries, in bakery products and milled to get oily paste (tahini) (Abou-Gharbia et al. 1997). Sesame seeds also find place in several rituals in countries such as India, Nepal etc. Interestingly, sesame seed is a reservoir of nutritional components with numerous beneficial effects and promotes human health. The bioactive components present in the seed include vital minerals, vitamins, phytosterols, polyunsaturated fatty acids, tocopherols and a unique class of antioxidant compounds, lignans that impart its antioxidative potential. The seed meal is also high in protein (35–50 %) and contains significant amount of amino acids such as tryptophan and methionine.

Sesame oil is used in cooking, in preparation of salads and finds use in the production of margarine, soaps, pharmaceuticals, paints and lubricants. The seed oil content ranges from 32.5 to 58.8 %, which is generally greater in white than black seeds (Moazzami and Kamal-Eldin 2006). In majority, sesame oil consists of triacylglycerols (95 %), diacylglycerols (2.6 %), and unsaponifiables (2.3 %) (Kamal-Eldin 2010). A high proportion of polyunsaturated fats in sesame oil mainly consist of linoleic (35–50 %), oleic (35–50 %), stearic (3.5–16 %) and palmitic (7–12 %) acids (Kamal-Eldin 2010). Linolenic acid is also present but only up to 1 % of the total fatty acids. Sesame oil used in combination with soybean oil enhances the nutritive value of the lipids and increases vitamin E activity (Namiki 1995) and in combination with canola or mustard oil has been recommended for healthy diets (Ghafoorunissa 1996). Sesame oil has several health benefits like growth arresting and apoptosis prevention properties in cancer cells (Yokota et al. 2007); useful in the treatment of several chronic diseases, including hepatitis, diabetes and migraines (Kita et al. 1995); alleviating depression and fatigue; and has antibacterial and anitviral properties for common skin pathogens. In addition, sesame oil maintains good cholesterol (HDL) and lowers bad cholesterol (LDL) (Sugano et al. 1990) and acts as a UV-protectant (Elleuch et al. 2007).

The beneficial properties of sesame oil are owing to three major constituents namely lignans, tocopherols and phytosterols. Lignans are a group of phenylpropanoid compounds, known for their innate nonenzymatic antioxidant defense mechanism against reactive oxygen species. These important plant phenolics are characterized by the coupling of two phenylpropanoid (C6–C3) units by a bond between β-positions in the propane side chains. Unlike other vegetable oils, where unsaponifiable fraction consists of phytosterols as a major component, sesame oil is an exception which is dominated by the presence of lignans. Two major groups of lignans exist in sesame seeds, namely oil soluble lignans (such as sesamin, sesamolin, pinoresinol) and glycosylated water soluble lignans (such as sesaminol triglucoside, pinoresinol triglucoside) (Katsuzaki et al. 1994; Moazzami and Kamal-Eldin 2006). In addition, sesamol, a free 3, 4-methylenediphenoxy phenol is usually present in traces (Salunkhe et al. 1991).

Sesame seeds have been found to possess high amounts of γ-tocopherol ranging from 468.5 to 517.9 mg/kg lipid along with low quantities of α and δ-tocopherols (Yoshida et al. 2007; Williamson et al. 2008). However, the overall level of tocopherol in sesame is low in comparison to other vegetable oils (Kamal-Eldin 2010). Further, in the unsaponifiable fraction of sesame oil, phytosterols form the second component after lignans in terms of quantity. Phytosterols are triterpenes structurally similar to cholesterol. Predominant phytosterol present in sesame oil is β-sitosterol (231.7–305.2 mg/100 g sesame seed), followed by campesterol and stigmasterol (Shahidi and Tan 2010). In comparison to other seeds and nuts, sesame seeds along with wheat germ have been reported to contain the highest (400–413 mg 100 g^{-1}) phytosterol content (Phillips et al. 2005).

Other nonfood applications of sesame are use of sesame flowers to prepare perfume in Africa (Morris 2002), use of sesamin as a synergist for pyrethrum or rotenone insecticides (Haller et al. 1942) and use of chlorosesamone extracted from

roots of sesame as a fungicide (Hasan et al. 2001). In addition, investigations on use of sesame oil as a source for biodiesel have resulted in a product with fuel properties in parity with mineral diesel but with superior environmental performance (Ahmad et al. 2010).

15.1.2 Sesame Production

The largest producers of sesame in the world are from Asiatic region: India, China, and Myanmar. India ranks first in the world in terms of sesame-growing area (24 %) (Raikwar and Srivastava 2013) however, area harvested and production has shown a significant decrease in past years (Fig. 15.1). The trend is similar in case of sesame production worldwide (Fig. 15.1). Average productivity of sesame has lowered ranging from 144 to 234 kg/ha compared to past 20 years (Raikwar and Srivastava 2013) which has led to a gap in the demand and the supply. In this constrained scenario, increasing the production of sesame by overcoming the hurdles that limit the crop yield are the need of the hour.

15.1.3 Taxonomy and Distribution

Sesame is a member of family Pedaliaceae (Order Lamiales), which is phylogenetically close to families, such as Acanthaceae and Scrophulariacae (Olmstead et al. 1993). Family Pedaliaceae consists of 65 species belonging to 15 genera distributed largely on sea shores and desert areas of three regions viz. tropical

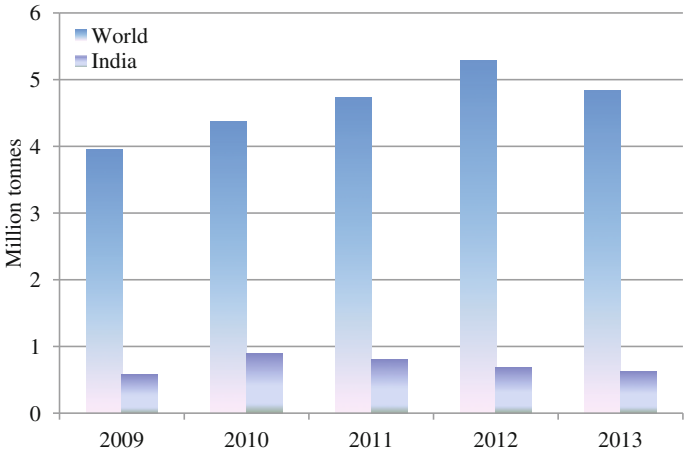

Fig. 15.1 Status of sesame seed production during past five years (FAOSTAT 2015)

Africa, Indian subcontinent (including Sri Lanka) and Far East (Duhoon et al. 2002). The genus *Sesamum* has about 23 species (Bedigian 2004a), of which eight species occur in India. *S. indicum* has its origin in India (Bedigian 2003; Bhat et al. 1999) and is the only species recognized in cultivated form in the family comprising diverse array of cultivars.

With respect to plant habit *S. indicum* is an erect, pubescent, or puberulous herb with usually alternate oblong upper leaves; lower opposite and lobed leaves. Flowers are axillary, pure white or usually with purple, yellow marks; solitary or few, and fascicled on a short-pedicel. Two extrafloral nectaries yellow in color, are usually present at the base of the flower pedicel. Calyx is small, 5-partite. Corolla is tubular with 2-lipped limb and five-rounded lobes. Stamens are four in number, didynamous, included, epipetalous; anthers are sagittate with two subparallel cells. Ovary is 2-celled, early falsely 4-celled bearing many ovules with axile placentation. A nectar disk is present at the base of ovary. Capsule is erect, oblong, loculicidally 2-valved (splitting occurs in the middle of the locule); unarmed and appears to be 4-celled. Seeds are numerous, smooth and obliquely oblong (Hooker 1885). Sesame is normally self-pollinated, although insect cross-pollination has also been reported (Mahfouz et al. 2012).

15.1.4 Wild Relatives of Sesame

Wild species of sesame vary in their habitat, morphological features and ploidy level, latter of which is represented by three chromosome groups 26, 32, 64 (Joshi 1961). Wild relatives have also been delineated into gene pools based on available hybridization studies for limited number of taxa. As per Harlan (1992) the gene pool-1 consists of the crop plant *S. indicum* and its progenitor *S. indicum* subsp. *malabarcium*. Two species namely, *S. alatum* and *S. prostratum* have been placed under gene pool-2 due to barriers in hybridization with *S. indicum* (Raghavan and Krishnamurty 1947; Ramanathan 1950; Tarihal 2003; Rajeswari and Ramaswamy 2004). Although, in few reports no seed set has been observed for *S. alatum* during hybridization studies (Lee et al. 1991). *S. radiatum* is placed in gene pool-3 due to lack of capsule formation (Ram et al. 2006), no seed set (Lopez and Mazzani 1964; Prabhakaran et al. 1992) and use of embryo rescue methods (Dasharath et al. 2007). A recent phylogenetic reconstruction based on two chloroplast loci also supports this categorization as *S. indicum* and *S. indicum* subsp. *malabaricum* were seen to have a closer affinity. *S. prostratum* appeared to be a recent divergence in comparison to *S. alatum* (Gormley et al. 2015).

Interestingly, the wild species of sesame are known to exhibit tolerance and resistance to different pests and diseases and some abiotic stresses (Fig. 15.2). They can thrive on nutritionally poor soils and sites with low moisture availability. They can tolerate heat and drought and have been referred as weedy due to their negligible demanding nature evident by their successful colonization in swarms (Bedigian 2010). Some of the adaptive features in wild species include fleshy roots,

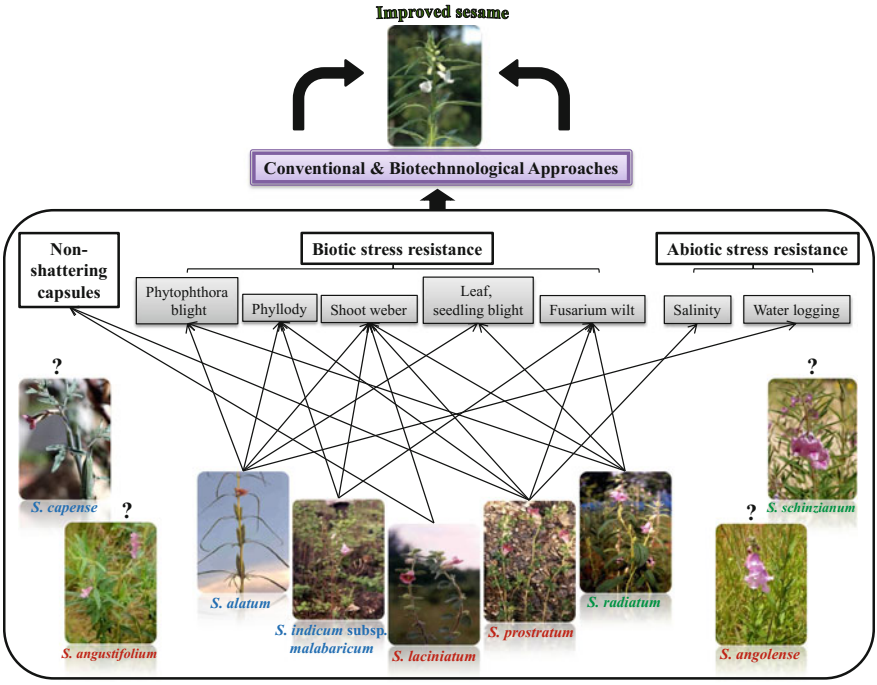

Fig. 15.2 Summary of agronomically useful attributes present in wild relatives of sesame. Question mark (?) indicates major wild species still not screened for useful traits. Font color for species name refers to chromosome number: *Blue* n = 16, *Red* n = 32, *Green* n = 64

small linear leaves, large number of stomata on the adaxial surface, hairiness and increased fruit set in the dry season (Nimmakayala et al. 2011). Seeds of wild relatives show the property of dormancy due to the presence of chemical inhibitors (Bedigian 1984). Germination is brought about by washing away of the inhibitors by natural rainfall in turn protecting the species from unfavorable conditions. A brief description of major wild relatives of sesame is given below. Morphological description is as per 'plants.jstor.org' unless mentioned.

Sesamum indicum subsp. *malabaricum* (Burm.) Bedigian: Recently, a subspecies status for erstwhile taxon *S. malabaricum* has been proposed by Bedigian (2014) which is known as the progenitor of sesame. Plant is an erect annual herb, with unpleasant odor. Stem often divaricately branched, pubescent to glabrescent. Leaves heteromorphic, lower palmately 3-foliolate, tripartite, margin coarsely dentate to serrate, acute apex, obtuse, or ovate base, upper leaves oblong to lanceolate, entire with acute base and apex. Lower surface is densely glandular. Flower pink or white, usually with intense deep purple pigmentation at lower lip. Capsule long, quadrangular, round at base, acuminate into beak at apex. Seeds broadly ovoid, conspicuously reticulate and rugose (Bedigian 2014).

S. alatum Thonn.: An erect annual herb with simple branched, glaberescent stem. Leaves heteromorphic, lower leaves palmately 3–5 foliate or partite, lobes

lanceolate or linearly lanceolate, central lobe longest, cuneate at base, acute or rounded at apex, margins entire or undulate; upper leaves simple, linear-lanceolate. Flowers pink or purple sometimes spotted red within. Capsule narrowly obconical, long beaked, broader in upper part and gradually narrowed at base, slightly compressed. Seeds obliquely overlapping, foveolate with suborbicular long wing at base and apex. It is widely distributed in tropical Africa as a flourishing monoculture plant and is an introduced weed in India. Leaves, flowers, and young shoots of the species are used as a vegetable when cooked (Bedigian 2010). Seed oil is an aphrodisiac, cures diarrhoea and intestinal disorders.

S. capense Burm.f.: An erect, tall conspicuous, sparsely branched herb. Stem is angular and sulcate or subterete. Leaves digitately 3–5 foliolate, leaflets obovate–oblong to linear–lanceolate, subobtuse–obtuse, narrowed at base into petiolule, intermediate the longest, glaucous above. Corolla violet outside, violet–purple inside, obliquely campanulate. Capsule broad, strongly three-nerved, short horns at base, beak long acuminate. Seed faces muriculate–foveolate with wing running all around. It is widely distributed throughout Southern Africa. Seeds of *S. capense* are edible and the plant is used in traditional medicine.

S. latifolium Gillett: An erect herb with densely pubescent quadrangular stem. Leaves generally heteromorphic, lower ones long petioled, large ovate-cordate or 3-lobed, upper leaves smaller ovate-lanceolate, inconspicuous to coarsely serrate, acuminate at apex, densely pubescent below. Flower pale pink or pinkish mauve, bracteoles conspicuous. Capsule shortly pubescent, oblong-quadrangular abruptly narrowed into a short beak. Seed faces foveolate, sides deeply pitted, margins sharply angled. The species has been found growing on granitic outcrops in Eastern Sudan, in Nuba mountains in south of Talodi, west Zalengei, and Agadi in central Sudan (Bedigian 1981).

S. angolense Welw.: An erect annual or perennial herb with simple quadrangular stem. Leaves subsessile or shortly petiolate, narrowly oblong/oblanceolate/elliptic, lower surface white tomentose, cuneate at base, apiculate at apex. Flowers reddish pink or pale mauve with deeper markings. Capsules narrowly oblong, subquadrangular, 4-sulcate, densely pubescent, gradually narrowed into a flattened rather broad and short beak. Seeds with double fringe, faintly rugose on the sides and faces. It shows widespread distribution in the Democratic Republic of Congo, Rwanda, Burundi, Uganda, Tanzania, etc. and grows in dense monoculture. The seeds are flattened, obconical in shape and faintly rugose (Bedigian 2010). Leaves of *S. angolense* are mixed with legumes and made into sauce which is served with cereal such as maize or millet. It is used as a medicinal plant for treatment of skin diseases such as measles and sores (Bedigian 2003) and is also utilized as ornamental and for soap making or as green manure.

S. angustifolium (Oliv.) Engl.: An erect annual or perennial herb. Leaves sessile or subsessile, variable in shape, linear to cultrate, margins entire inrolled or narrowly lanceolate irregularly toothed, cuneate at base, acute at apex, densely glandular below. Flowers purple, pink, or mauve often spotted within. Capsule cultrate in lateral view, appressed to stem, parchment-like when mature, beak straight or bent toward stem. Seeds with transversal ribs on both faces. It shows widespread

distribution in Kenya, Sudan, Tanzania, and Uganda in zones with slightly higher rainfall. The seeds are small, black with rugose surface pattern. The mucilaginous leaves and flowers are cooked with other ingredients as leaf vegetables. The seeds are used in sauce or soup after crushing. The leaf mucilage is used to treat eye troubles, burns, wounds, and diarrhea in children (Bedigian 2003). Leaves are also utilized as ornamental and for soap making or as green manure.

S. prostratum Retz.: Herb with prostrate habit, the leaves are villous, orbicular, or obovate crenate or obtusely lobed with white indumentum beneath. Capsule is ovoid and compressed. Seeds are black in color with reticulate texture and foveolate testa.

S. laciniatum Klein. ex Willd.: Herb with prostrate habit, with hispid, ovate and lobed leaves which are deeply subpedately pinnatified. Flower purple. The capsule is ovoid and compressed. The seeds are black in color with reticulate texture and foveolate testa.

S. radiatum Schumach. & Thonn.: An erect annual woody herb with simple or branched, pubescent stem. Leaves scarcely heteromorphic, petiolate; lower ones ovate, coarsely toothed, acute at both ends; upper leaves lanceolate, entire. Leaves sparingly and persistently hairy and mealy glandular below. Flower purple or purplish. Capsule narrowly oblong in lateral view, with short broad beak. Seeds are rugose or pitted, with sculptural lines radiating perpendicular to the edge all around the margin of the seed faces. Origin of crop is Africa but now found throughout tropics in India, Sri Lanka, etc. The fresh leaves are used in soup and in sauces eaten with porridge (Bedigian 2004b). Mucilage of the plant is used for medical purposes. A cold infusion of macerated fresh young leaves facilitate childbirth (Bedigian 2003).

S. schinzianum Aschers. ex Schinz.: An erect branched annual, softly glandular-hairy, leaves lanceolate to narrowly elliptic, subobtuse, or apiculate, cuneate at base, entire or obscurely repand, pedicels short. Flower pale rose villous. Capsule rounded-quandrangular, deeply 4-sulcate, beak acuminate. Nectary stipitate. Seeds are strongly compressed, faces finely granular. Plants occur in bushes. Its distribution is restricted to Namibia.

15.2 Genetic Improvement of Sesame

Inadequate research efforts due to either lack of funding or their insufficient continuity and limited international cooperation for germplasm exchanges in the past have been responsible for the unsatisfactory improvement work in sesame. Also, genetic and breeding improvement efforts in sesame have been limited and slow as it is a crop of developing countries and within these countries it is a small holder's crop. For improvement of yield potential and traits of economic importance of crop plants it is essential to identify the superior genotypes among cultivars, introgressed linesand within wild relatives. The presence of untapped genetic variation existing

in wild relatives and landraces of crop plants should be exploited gainfully for development of agronomically superior cultivars.

15.2.1 Areas for Improvement

Sesame suffers from both biotic and abiotic stresses leading to drastic reduction in crop yields. This along with the plant architecture which includes indeterminate growth/nonuniform capsule ripening and shattering of seeds at capsule maturity is a cause for its poor adaptability to mechanical harvesting. Thus, major areas for sesame improvement that need urgent attention are as follows.

15.2.1.1 Higher Yielding Genotypes

High and stable yield with applied inputs such as irrigation and farming is an important aspect to consider. Potential area of heterosis during hybrid combination also needs attention. The importance for this area is evident by the fact that India has the largest area under sesame cultivation while China is the largest producer, mainly due to low yielding cultivars in India. Further, there has been a significant and persistent decline in sesame production during the last 2 decades. Average productivity of sesame cultivation in India is approximately 422 kg/ha in comparison to the potential yield of 2000 kg/ha (Mkamilo and Bedigian 2007).

15.2.1.2 Improved Seed and Oil Quality

Expanding use of sesame seeds has resulted in reports on immunoglobulin E (IgE)-mediated food allergies (Agne et al. 2003). Oleosins are major allergens of sesame seeds. Altering of allergenic epitopes in sesame seed storage proteins and oleosins using protein engineering could be beneficial in decreasing sesame seed allergenicity. In addition, high contents of phytic and oxalic acid hinder the use of sesame protein as food (Johnson et al. 1979). Suppression or reduction of such constituents is another challenging area that needs to be taken care of.

15.2.1.3 Modification of Growth Habit and Seed Retention

An important consideration in case of sesame involves the continued and recalcitrant persistence of traits that are generally present in wild plants and have been negatively selected during the process of domestication in most of the other crop plants. Indeterminate growth habit in sesame is one of these highly undesirable traits as it leads to asynchronous capsule ripening, that is mainly responsible for lack of its amenability to modern farming technologies. Determinate sesame

mutants obtained from mutation breeding have low yields compared to indeterminate lines (Ashri 1995), however, high yield in such mutants were reported by altering the production practices (Uzun and Cağirgan 2006). Advancement in such areas is mandatory to increase mechanization of sesame harvesting.

Similarly, dehiscence of the capsule at maturity is yet another trait that results in significant loss of yields and all attempts to develop nonshattering capsules have been unsuccessful so far. Shattering capsules of sesame makes the crop unsuitable for mechanical harvest and thus restricts its commercial potential. Mutants showing closed capsule character have been obtained using γ-ray radiation experiments (Ashri 1987). However, mutant genotypes show deleterious characters, such as semi-sterility, twisted stems, cupped leaves, short capsules and low yield caused either due to pleiotropy or multiple mutations. Therefore, neither the hundreds of years of selection during the process of domestication nor the current traditional as well as recent methods of improvement have resulted in shatter proof and determinate sesame cultivars.

In fact, due to these reasons, sesame is rightly grouped under the category of semi-domesticated crops at times. Therefore, any attempts to incorporate these highly desirable traits require research efforts to delineate these traits in sesame.

15.2.1.4 Resistance to Biotic Stresses

A large group of crop pathogens including fungi, bacteria and viruses are known to affect sesame and are responsible for major biotic stresses such as phyllody disease, *Fusarium* wilt, *Phytophthora* blight, seedling blight etc.

Several fungi reduce sesame seed germination by 30–61 %. *Fusarium oxysporum* is the major one responsible for 34 % of seedling rot (Khati and Pandey 2004) followed by *Alternaria sesami* with losses ranging from 4 to 25 % (Narayanaswamy et al. 2012). Severe leaf infection by *A. sesami* also affects the seed weight component of yield significantly (Narayanaswamy et al. 2012) while *A. alternata* induces blight symptoms of spots in stems and on leaves (Prasad and Reddy 1997). In addition, leaf spot disease caused by *Cercospora sesami* occurs in severe forms in India resulting in an estimated loss of about 30 % (Chowdhury 1945; Prasad and Reddy 1997). In fact, wilt and root rot diseases caused by the soilborne pathogens *F. oxysporum* f. sp. *sesamicola* and *Macrophomina phaseolina*, respectively, are responsible for sesame yield losses in all areas of its cultivation (Elewa et al. 2011). Screening studies have shown that sesame genotypes highly resistant to *Fusarium* wilt result in very low yields, thus demanding attention for improvement (El-Bramawy and Abd Al-Wahid 2009). *Phytophthora parasitica* var. *sesami* causes blight of sesame, observed characteristically as water-soaked spots ensuing in blackening of affected tissues in stems especially near the soil level. Incidence of 78.33 % has been reported during the month of August and losses range from 66 to 100 % especially when infection occurs at seedling stage

(Verma et al. 2005). Powdery mildew in sesame causes yield loss of 42 % and with every 1 % increase in disease intensity yield loss of 5.63 kg/ha has been recorded in India (Adiver and Kumari 2010). The casual fungi include *Luveilluta taurica, Erysiphe cichoracearum* and *Sphaerotheca fulginea* (Anyanga and Obongo 2001). The disease is air-borne and affects all aerial parts, leaves, flowers and pods (Egonyu et al. 2005).

Among bacterial pathogens, phytoplasma (Order Mollicutes) causes one of the most destructive diseases called phyllody in sesame which is responsible for losses of up to 99 % in certain tracts in India. Yields are dramatically decreased especially in warm climates (Salehi and Izadpanah 1992). Major symptom is conversion of flowers into leaf-like structures leading up to 80–100 % loss in capsule formation. Affected plants can easily be identified from the bushy appearance of the apical region at maturity. In addition, *Pseudomonas syringae pv. sesami* cause leaf spot disease and is responsible for substantial yield reduction (Sutica and Dowson 1962) along with *Xanthomonas campestris* pv. *sesami* (Ciferri 1955; Schumutterer and Kranz 1965). Sesame is also susceptible to turnip mosaic virus, watermelon mosaic virus, and tobacco ringspot virus under experimental inoculation conditions.

Nearly, thirty-eight insect pest species have been recorded to infest sesame in Uganda (Egonyu et al. 2005) and twenty nine in India (Baskaran et al. 1997). Of these, sesame webworm (*Antigastra catalaunalis* Dup.) and the gall midge (*Asphondylia sesami* Felt.) are considered most important pests worldwide with elevated occurrences of almost 62 and 98.8 %, respectively (Egonyu et al. 2005). Furthermore, *A. catalaunalis* is found to have the highest relative incidence of 0.63 and mean percentage capsule damage due to *Asphondylia sesami* occurs in a range of 29–34.3 % among the various sesame varieties (Egonyu et al. 2005). Avoidable yield losses of *A. catalaunalis* are known to vary from 6.2 to 43.1 % in different genotypes of *Sesamum* (Gupta et al. 2000) and 18.4–25.7 % in multilocation trials across India (Singh et al. 2014). Such yield losses attain a higher magnitude in rainy season (Baskaran et al. 1997).

15.2.1.5 Tolerance/Resistance to Abiotic Stresses

Abiotic stress is the negative impact of nonliving factors on the living organisms in a specific environment. Sesame suffers from three major abiotic stresses namely water logging, chilling and salinity.

Sesame is very sensitive to waterlogging. Seasonal rainfall often causes water-logging damage to the sesame production in south of China, India and Burma. The stress induces symptoms of wilting and leaf chlorosis, with susceptible accessions showing early onset. Formation of adventitious roots above the flooding level and development of abundant aerenchyma in root and stem have been observed in tolerant accessions (Wei et al. 2013). Moreover, stage dependent yield losses due to water logging have been observed in sesame. Sesame mutant SM7 shows 15 %

yield reduction when water logged for 48 h, at 25 days after sowing at seedling stage, with respect to the control plants. However, similar water logging treatments in vegetative, flowering, and seed filling stage shows yield losses ranging from 12 to 14 % (IAEA 2001). Thus, intermittent heavy rainfall is detrimental to the sesame crop.

Susceptibility to chilling is evident in sesame due to early photoinhibition in comparison to the plants resistant to chilling stress (Hetherington et al. 1989). This is supported by the fact that sesame shows significant reduction in growth below 20 °C, and growth and germination are totally inhibited below 10 °C. Sesame seed shows marked reduction in content of lignans (an antioxidant) viz. sesamin and sesamolin in the oil (Beroza and Kinman 1955) during frost damage. Additionally, sesame lies under the category of salt sensitive plants as indicated by downregulation of *SeMIPS* (Myo-inositol 1-phosphate synthase) gene (Chun et al. 2003) as in case of other susceptible plants like *Arabidopsis*, sunflower (Ishitani et al. 1996; Fernandez et al. 2008).

Further, sesame cultivation is generally confined to semiarid regions where soil salts are a limiting factor. Previous reports indicate that sesame is sensitive to soil salinity (Yousif et al. 1972; Cerda et al. 1977) mostly due to the presence of calcium chloride (Nassery et al. 1979). Salinity stress is shown to affect all traits significantly, causing reduction in germination percentage, germination, normal seedling percentage, seedling length, and dry weight (Tabatabaei and Naghibalghora 2014).

Studies in sesame suffering from different abiotic stresses have shown activation of antioxidative enzymes, proline, plant defense systems, etc. (Gehlot et al. 2005; Koca et al. 2007). Therefore, there is a need to develop or identify stress combating sesame cultivars.

15.2.2 Resources Available

Due to the efforts of scientists involved in germplasm collection, management, and conservation, various resources are now available for sesame improvement which includes wild germplasm, core collections and genomic resources.

15.2.3 Wild Germplasm

A total of 466 accessions belonging to *Sesamum* species that are wild relatives of *S. indicum* are conserved at NBPGR National Gene Bank, India (PGR Portal 2015; Pathak et al. 2014). Other species of genus *Sesamum* that are distantly related to sesame occur in parts of Africa and efforts are required to collect, evaluate, and conserve them.

15.2.3.1 Sesame Germplasm and Core Collections

National Gene Bank at NBPGR, New Delhi, India maintains over 9598 accessions of sesame (Pathak et al. 2014; PGR Portal 2015). Indigenous sesame core comprising of 343 accessions was identified (Bisht et al. 1998), while another set of sesame core comprising of 172 accessions has been developed from recent characterization of world sesame collections (Mahajan et al. 2007).

Further, 7698 sesame accessions, consisting of 3538 exotic collections, 2660 indigenous collections, 1072 improved genetic stocks and 428 others have been conserved by the Gene Bank of Rural Development Administration (RDA) in Suwon, Korea (Kang et al. 2006). Other organization and gene banks in the world undertaking conservation efforts of sesame include the United States Department of Agriculture (USDA), Agricultural Research Service (ARS), Plant Resources Conservation Unit (PGRCU) which have conserved 1226 sesame accessions belonging to Europe, Africa, Asia, North America, and South America (Morris 2009).

15.2.3.2 *Genomic Resources*

Research carried out in past years have led to the availability of a huge repertoire of genomic resources for sesame in the form of Expressed Sequence Tags (ESTs), transcriptomes and the whole genome sequence data.

Suh et al. (2003) obtained 3328 ESTs from a cDNA library of 5–25 days-old immature sesame seeds. Successful identification of genes involved in biosynthesis of sesame lignans, sesamin and sesamolin was carried out. A possible metabolic pathway for the generation of cofactors required for synthesis of storage lipid in non-green oilseeds was elucidated. Therefore, ESTs generated by large-scale single pass cDNA sequencing is a valuable approach for the identification of novel genes involved in specific metabolic pathways.

Wei et al. (2011) reported transcriptome from five different tissues of sesame plants using the approach of next generation sequencing. More than 22,000 unigenes could be successfully mapped onto 119 pathways using KEGG database. Further, in order to exploit the natural variation in the genes involved in lignan and lipid biosynthetic pathways, SSR markers from over 7700 unigenes were developed. The usefulness of these EST-based SSR markers was validated by their ability to detect polymorphism in diverse sesame accessions with varying oil and lignan contents.

Later, Zhang et al. (2013a–c) of Henan Sesame Research Centre, China sequenced the whole genome of *S. indicum* under the aegis of Sesame Genome Working Group (SGWG). A total of 27,148 genes were estimated to be present on the de novo assembled genome having a contig N50 of 52.2 kb and a high scaffold N50 of 2.1 Mb. The comparative genomic and transcriptomic analyses revealed candidate genes and oil biosynthetic pathway contributing to the high oil content in sesame. The expansion of Type 1 lipid transfer genes by tandem duplications and

contraction of lipid degradations genes are some of the most significant findings in this study. Additionally, presence of high genetic diversity in lipid-related genes among twenty nine accessions from 12 different countries is also highly relevant. Such genomic delineation of synthesis and variation in lipid-related genes can be used as an important platform for qualitative and quantitative improvement of oil yield in sesame.

15.3 Mining of Sesame Wild Germplasm

15.3.1 Hybridization

Several studies are available pertaining to interspecific and intergeneric crosses of *Sesamum* sp. This is due to the advantage of epipetalous flowers and thus, emasculation which results in easy pollination in sesame making it amenable to controlled crossing. Moreover, low seed rate (2.0–2.5 kg/ha) and high seed multiplication ratio (1:300) facilitate ease of hybridization and recombination breeding programs (Nimmakayala et al. 2011). The interspecific crosses of sesame with wild relatives have led to the establishment of data depicting either close affinity of compatibility or incompatibility among the species.

Intergeneric crosses of *Sesamum* sp. with other genera of family Pedaliaceae have suggested its relatedness to *Martynia* and *Ceratotheca*. Nonviable seeds were obtained in intergeneric crosses between *S. indicum* and *Martynia* (Srinivasan 1942). However, crosses between *M. annua* and *S. laciniatum*, *S. radiatum* independently showed uninhibited pollen germination and growth of pollen tube in the styles and entrance in the ovule have been observed but the pollinated flowers dropped after 4 or 5 days of hybridization in all the crosses (Subramanian 1995). On the other hand, *Ceratotheca* showed fertile seeds in crosses with *S. indicum* (Falusi et al. 2002).

Cytoplasmic male sterile (CMS) lines in sesame were developed by hybridizing *S. indicum* with its wild relative *S. indicum* subsp. *malabaricum* (Bhuyan et al. 1997). CMS lines provide an opportunity to facilitate cross-pollination process for the production of hybrid seeds. Bhuyan and Sarma (2003) obtained 36 hybrid combinations of diverse origin using CMS system.

Somatic hybridization has also been used to develop sesame hybrid plants. Distantly related species can be fused using somatic hybridization. Dasharath et al. (2007) used ovary and ovule culture to develop interspecific hybrids between cultivated *S. indicum* and its wild relatives, *S. radiatum* and *S. occidentale.*

Parani et al. (1997) carried out hybridization studies between *S. alatum* and *S. indicum* with the objective of transferring phyllody resistance. Identical chromosome number of the parental species used, ambiguous morphological characters, and lack of segregation in F_2 led them to the use of protein and isozyme-based markers for the confirmation of the putative hybrid plants. Sodium dodecyl

sulfate-polyacrylamide gel electrophoresis (SDS-PAGE)-based studies aimed at protein polymorphism revealed a transfer of five male specific protein bands in the hybrid. Out of four loci of esterases namely, *EST* A, B, C, and D, *EST* D was found in the heterozygous condition in the hybrid and homozygous in the parents thus indicating their hybridity. Similarly, out of five loci of peroxidases (*PRX* A, *PRX* B, *PRX* C, *PRX* D, and *PRX* E), two loci, namely, *PRX* A and *PRX* E were found useful.

Further, Parani et al. (1997) also carried out RAPD analysis of the two parental species and the putative hybrid *S. indicum* × *S. alatum* using 20 decamer primers. A total of 56 fragments out of 127 showed polymorphism between the parents. Almost all the fragments observed in the hybrid were shared either by *S. indicum* or by *S. alatum* thereby establishing their hybridity. Twenty-five male specific fragments identified were found to be present in the hybrid progeny and could be used as potential markers to differentiate the hybrids from the selfed progeny. Of the three markers employed, RAPD analysis was advocated as easy, economical, and reliable method for the large-scale screening of the hybrids.

15.3.2 Molecular Analysis of Species Diversity

RAPD analysis was carried out in 42 accessions of cultivated sesame and one accession of wild taxa, namely, *S.indicum* subsp. *malabaricum* using 10 primers (Bhat et al. unpublished). A total of 101 amplicons were scored at an average of 10.1 bands per primer with an overall high polymorphism of 61.4 %. The analysis of genetic diversity among cultivated forms revealed a low level of within accession variation (H_s = 0.011), while coefficient of gene differentiation (G_{st}) was 0.549, indicating high genetic differentiation among accessions which were landraces cultivated by farmers in different agroecological regions. The accessions from Eastern and Northeast regions of India were highly diverse indicating that these regions contain higher diversity requiring more intensive germplasm collections. The results indicated that although wild species, *S. indicum* subsp. *malabaricum* was slightly more genetically diverse (H_t = 0.067) than cultivated *S. indicum* (H_t = 0.024); it did not exhibit any substantial divergence from the cultivated types. Reports on low genetic diversity are also available in *Ceratotheca sesamoides* and *S. radiatum* based on AFLP markers (Adéoti et al. 2011).

15.3.3 Phylogenetic Relationships

Phylogenetic relationship using PCR-RFLP of unilocus markers, such as ribosomal DNA, chloroplast DNA and multilocus multiallellic marker systems such as amplified fragment length polymorphism (AFLP) exhibited high genetic similarity between *S. indicum* and *S. indicum* subsp. *malabaricum* (Fig. 15.3). Similarly,

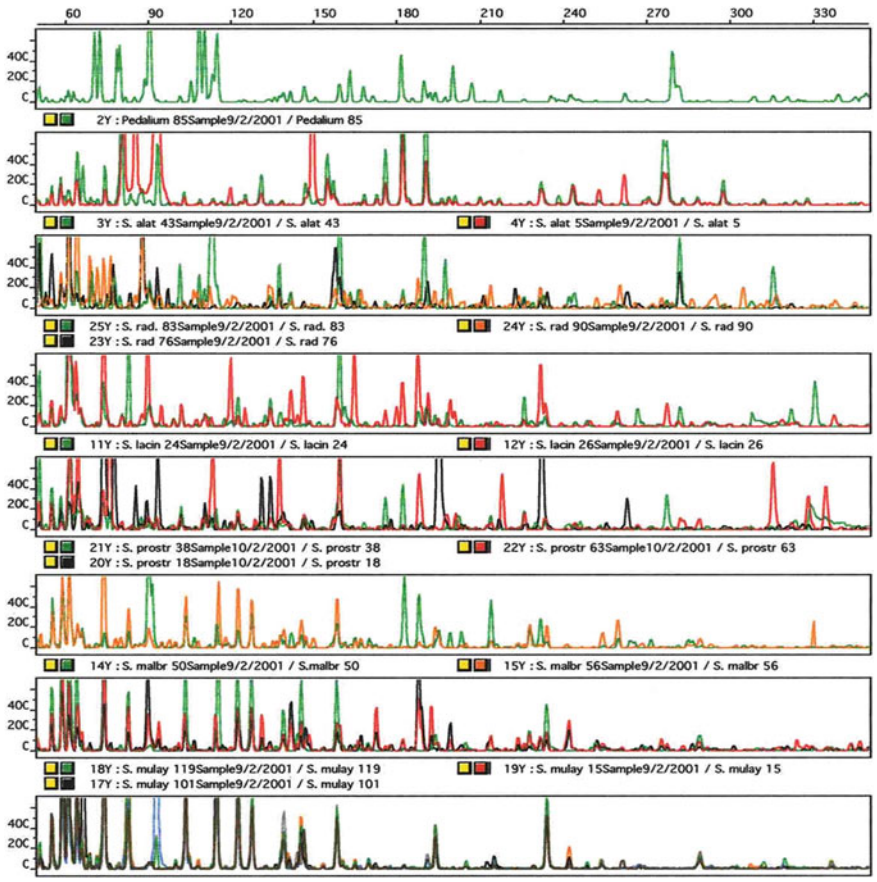

Fig. 15.3 Representative AFLP chromatogram showing profiles for wild relatives of sesame

S. laciniatum and *S. prostratum* appear to be closely related to each other and significantly diverged from other species. *S. radiatum* ($2n = 64$) appear to be distinct from all other species under the genus *Sesamum* occurring in India (Bhat et al. unpublished).

Akhila and Beevy (2011) characterized sesame morphologically and analyzed its seed protein in *S. indicum* L. and *S. occidentale*. Data on 13 quantitative and three qualitative characters of the cultivated species and seven accessions of the wild taxa were analyzed. A dendrogram based on UPGMA analysis of seed protein suggested intraspecific relationships of the wild taxa as evidenced from the morphological characterization.

15.3.4 Seed Oil and Antioxidants

Breeding for enhancing oil quality and content is very important objective in any oilseed crop. Genetic diversity in seed oil content and fatty acid composition in six wild species of genus *Sesamum* viz., *S. mulayanum, S. capense, S. laciniatum, S. latifolium, S. occidentale, and S. schinzianum* was studied and compared with the cultivated species, *S. indicum* (Hiremath et al. 2007). Seed oil content was low in wild species ranging from 20.3 to 33.9 % in comparison to cultivated sesame which was from 46.13 to 53.8 %. In contrast, wild species of sesame are known to contain higher percentages of unsaponifiable fraction (Fig. 15.4; Kamal-Eldin 2010). Analysis of sterols composition in *S. indicum* and three wild species (Fig. 15.5) depicts comparable proportion of sterols in *S. latifolium* while high proportion of campesterol and δ5-avenasterol in *S. alatum* (Kamal-Eldin and Appelqvist 1994). *S. alatum* also stands distinct from all other species with respect to methylated sterol composition under the category of desmethyl sterols (Kamal-Eldin 2010).

With respect to fatty acid composition of oil, wild species exhibit wide range of variation in palmitic and stearic acid contents. Stearic acid and linoleic acid content in all the wild species is significantly higher than the cultivated sesame. On the other hand, wild species have lower oleic acid (Kamal-Eldin 1993). Studies by Mondal et al. (2010) have also revealed high diversity in fatty acid content within Indian sesame germplasm, with oleic and linoleic acid forming the major proportions, i.e., 45.9 and 45 %. Very high linoleic acid content was observed in accessions of three wild species, *S. mulayanum* (49.3 %), *S. malabaricum* (48.2 %), and *S. radiatum* (51.6 %).

As per reports, all wild *Sesamum* spp. have black or brown thick, rough seed coat whereas domesticated sesame, *S. indicum* has thin and smooth seed coat with various shades of white, brown or black color (Kamal-Eldin 1993). Thus, it has

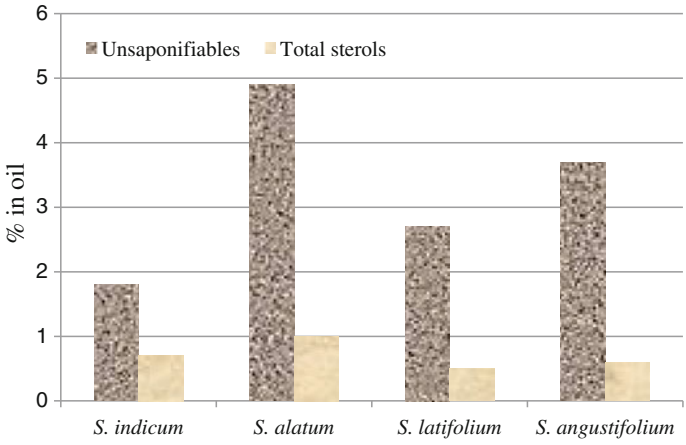

Fig. 15.4 Maximum percentage of unsaponifiables and total sterol fraction in seed oil of sesame and its wild relatives (Adapted from Kamal-Eldin 2010)

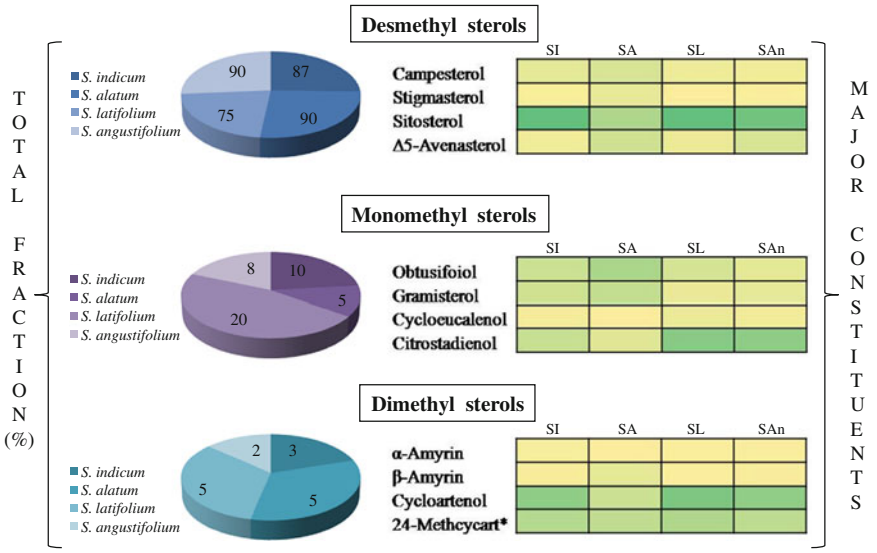

Fig. 15.5 Relative proportions of sterol fractions alongwith their composition in sesame (SI) and three wild species *S. alatum* (SA), *S. latifolium* (SL), *S. angustifolium* (SAn) (Adapted from Kamal-Eldin 2010). Percentage variation: 3 60 %

been proposed that seed oil content can possibly be increased in wild species if selections are made for thinner seed coat (Kamal-Eldin 1993). The content of lignan is variable within sesame ranging from 1550 to 18,600 mg/kg for sesamin and 1230–10,600 mg/kg for sesamolin (Kamal-Eldin 2010). Highest sesamin and sesamolin in capsules is observed at 30 days after flowering (Yasumoto et al. 2005). White seeded sesame is shown to contain high amount of lignans in comparison to the black seeded (Kang et al. 2003). Similarly low lignan content was observed in black seeded sesame by Namiki (1995). Cultivars from north-eastern states in India were found to be rich in lignans (Hemlatha and Ghafoorunissa, 2004). Wild species vary in the amount of lignans present in the seed oil (Fig. 15.6). Few species such as *S. triphyllum* and *S. rigidum* lack the presence of lignans, sesamin and sesamolin while traces are present in *S. alatum*, *S. pedalioides* and *S. capense* (Ashri 2006). Other lignans such as sesangolin is present in *S. angolense* and *S. angustifolium*, while high amount of 2-*epi*-sesalatin is present in *S. alatum* (Kamal-Eldin 2010). Recent studies revealed existence of exploitable levels of lignan (sesamin and sesamolin) and tocopherol contents in sesame germplasm (Pathak et al. 2014). The study carried out on 143 sesame samples showed the average content of sesamin and sesamolin as 0.86 and 0.50 mg g^{-1} seed, respectively. The average tocopherol content (292 μg g^{-1} seed) found in this study indicated presence of very high amount of γ-tocopherol in Indian sesame germplasm. *Sesamum* species namely, *S. indicum* subsp. *malabaricum* and *S. mulayanum* showed high lignan and tocopherol contents (1.31 mg/g seed and 239 μg/g seed; 1.15 mg/g and 281 μg/g seed) and thus could be utilized in sesame breeding programs for nutritional enhancement.

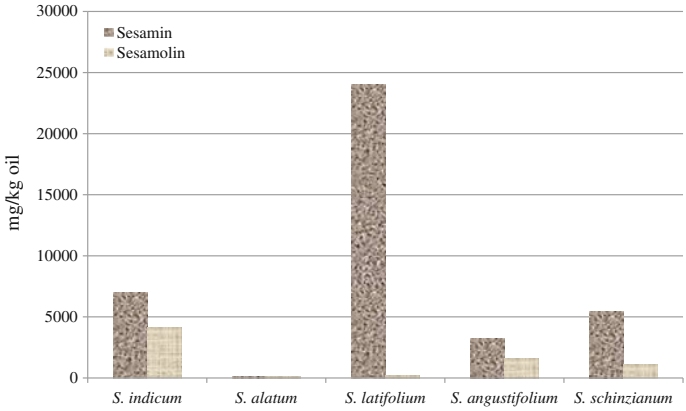

Fig. 15.6 Levels of oil soluble lignans in sesame and its wild relatives. Maximum values of sesamin have been depicted and the respective value for sesamolin has been retained (Adapted from Kamal-Eldin 2010)

Ono et al. (2006) identified a cytochrome P450 gene, CYP8101 responsible for catalysis of sesamin biosynthesis from pinoresinol. The protein is unique due to its dual catalytic ability that results in the formation of two methylenedioxy bridges, which is limited to a single bridge in all P450 proteins known to date. Transient expression system has revealed the localization of sesamin biosynthesis to the cytoplasmic surface of endoplasmic reticulum. Presence of a functional homolog from *S. radiatum* (contains sesamin) and a nonfunctional homolog from *S. alatum* (nearly lacks sesamin) provided functional validation for the role of CYP8101. Recent study by Pathak et al. (2015) examined the functional expression of *sesamin synthase* gene (CYP81Q1) during capsule maturation (0–40 days after flowering) in three wild *Sesamum* species and four sesame cultivars. Among the cultivated accessions of *S. indicum*, only one (CO-1) exhibited transcript abundance of sesamin synthase along with high sesamin content similar to *S. indicum* subsp. *malabaricum* suggesting a close relationship between the two. Additionally, the study demonstrated that the stage at 25 DAF in sesame capsule maturation should be selected for oil collection. Through this work, it has been proposed that interspecific crosses between *S. indicum* subsp. *malabaricum* and elite cultivars of *S. indicum* will prove advantageous in sesame breeding in order to obtain superior genotypes with high-quality oil.

15.3.5 Disease Resistance

Resistance to phyllody disease was reported in the wild species *S. alatum* through artificial screening (Srinivasulu and Narayanaswamy 1992; Singh et al. 2007). Rajeshwari et al. (2010) optimized a protocol for the production of hybrids of a

cross between *S. alatum* and *S. indicum* through ovule culture. The developed hybrids exhibited moderate phyllody resistance. In another study, phyllody resistant sesame lines were developed through intra and interspecific crosses among different cultivated and wild species of sesame. It was reported that disease resistance is governed by one dominant (wild species) and one recessive (cultivated species) gene (Singh et al. 2007).

Further, treatment of *S. prostratum* callus with *F. oxysporum f. sesame* showed accumulation of hydrogen peroxide concentration and lipid peroxidation after 6 h. In addition, total phenolics content, activity of antioxidative enzymes and phenylalanine ammonia-lyase (*PAL*) showed an increase. Results indicate that *S. prostratum* which is resistant against *F. oxysporum* produces reactive oxygen species as defense barriers against the invading pathogen (Rajab et al. 2009).

Possibility of transforming of plant cells with appropriate gene/s involved in signal transduction of phytoalexin induction, that would activate Ca^{2+}-cascade and enhance the biosynthetic activity of secondary metabolites relating plant defense responses was assessed by transforming *S. schinzianum* plants, which is known to show high transformation and re-differentiation efficiency (Mitsuma et al. 2004). Calmodulin gene, *cam-4*, a CAM gene specifically expressed in oligogalacturonide-treated carrot which showed elicitation of a phytoalexin was expressed in the wild *Sesamum* sp. using *Agrobacterium*-mediated transfection method (Mitsuma et al. 2004). Transgenic plants for CAM gene showed enhanced production of phenylpropane derivatives in sesame suggesting that the engineering of signal transduction processes by the transfection of appropriate genes can prove beneficial in molecular breeding of sesame.

15.4 Mining of Sesame Cultivars

Primary gene pool of sesame comprising currently used and obsolete cultivars form an important genetic resource due to their high genetic diversity revealed and absence of crossability barrier among them. Sarwar and Haq (2006) evaluated 106 sesame genotypes from different parts of the world and documented heritability for yield related parameters, such as seed yield, capsule number, and branches per plant. It was concluded that selection of sesame elite genotypes for seed yield is possible on the basis of these characters. Various high yielding sesame varieties have been selected on the basis of these phenotypic and genotypic marker traits.

15.4.1 Molecular Diversity

Isshiki and Umezaki (1997) studied patterns of variations for seven enzyme systems in 68 accessions of sesame from Japan (12), Korea (15), and Thailand (41). Only one out of seven enzyme systems, namely, isocitrate dehydrogenase exhibited

variations and was shown to be controlled by a single locus (*Idh*) with two alleles. The two alleles were found to be very widely distributed in the accessions. The locus *Idh* was proposed as an important genetic marker as few gene markers with simple genetic control are available in this crop. In addition, little variation in the germplasm analyzed suggested a narrow genetic base of the sesame germplasm grown in these countries.

Diaz et al. (1999) studied the isozyme variability in sesame accessions from six centers of diversity namely, India, Korea, Western Asia, Africa, China–Japan, and Central Asia. An analysis of the five putative loci belonging to five isozymes systems (acid phosphatase, isocitrate dehydrogenase, 6-phosphogluconate dehydrogenase, and shikimate dehydrogenase) showed similarity in the extent of polymorphic loci in sesame with the other cultivated plants particularly self-pollinated crop taxa. However, the extent of total diversity was reportedly lower than the other cultivated self-pollinated species. Differences between the values of the total diversity were not found to be statistically significant. Interestingly, 80 % of the species variability and center-wise total variability was found due to differences among populations.

Kim et al. (2002) reported genetic relationships among 75 accessions of Korean and exotic sesame germplasm using ISSR markers. The material analyzed comprised Korean cultivars (26), breeding lines and land races (17), including 32 introductions from 13 countries. UPGMA analysis divided these 75 accessions into seven groups where the largest group consisted of 25 Korean cultivars, 8 Korean breeding lines, and 17 worldwide accessions. No clear division was indicated on the basis of their geographic origin. The grouping of all Korean cultivars in the same cluster indicated their narrow genetic base. Nevertheless, Korean breeding lines differed markedly from the cultivars and thus can prove to be sources of useful traits in the improvement programs. In addition, grouping of exotic accessions with the Korean germplasm indicated that geographical separation did not generally result in the greater genetic distance and was ascribed to the exchange of materials from widely separate locations.

Bhat et al. (1999) analyzed genetic diversity in sesame germplasm of-Indian subcontinent and compared it with germplasm of 21 other sesame growing countries using RAPD analysis. The extent of genetic diversity was greater in the germplasm from Indian subcontinent in comparison to other countries. Among the Indian accessions, the collections from the states of Rajasthan and northeast were highly diverse. Such high diversity in the Indian sesame germplasm indicates nativity of the sesame crop. Relatively lower level of genetic diversity in the exotic germplasm has been ascribed to the comparatively recent introduction of a limited germplasm into these areas.

RAPD analysis of 60 sesame cultivars and improved lines released for general cultivation in India revealed presence of low to moderate genetic diversity. The Jaccard's similarity coefficient values for the 285 amplicons compared ranged from 0.48 to 0.94. This was in contrast to the high genetic diversity reported earlier in sesame germplasm (Bhat et al. 1999). Among the 58 sesame germplasm accessions the similarity coefficients ranged from 0.19 to 0.89. This clearly shows that only a

small fraction of the total genetic diversity present in sesame germplasm has been represented in the improved cultivars of the crop. Results of the RAPD analysis was in agreement with the pedigrees of the cross-bred cultivars. The relative distance of varieties in the dendrogram was comparable to the pedigree data that was available.

An analysis of the Turkish sesame populations (Ercan et al. 2004) has also been carried out using RAPD markers. A total of 38 accessions of sesame germplasm from different regions of Turkey were sampled and were subjected to RAPD analysis using 12 decamer primers. Five out of 12 primers showed monomorphism. Low genetic variation among four main geographic regions was reported. However, analysis of molecular variance (AMOVA) revealed highest genetic variation among the populations within the regions. Of the total genetic diversity, 8.1 % was attributable to differences among regions and 91.8 % was due to population differences. Low level of differentiation among regions was ascribed to high rates of gene flow among populations within the region as a result of both human migration and agricultural trade. Performing AMOVA analysis separately for each region also identified the areas with highest genetic variation.

Nimmakayla et al. (2005) analyzed a set of 124 sesame genotypes collected from different parts of the world and tested for the SSR polymorphism using 14 microsatellites primers. A total of 144 SSR alleles were scored where the largest number of alleles (18) were identified by SSR primer PRU1 that had a repeat motif of $(GA)_7$ $(Y)_{99}GT)_7(GA)$ and the least by PRU 4 with a repeat motif of $(CA)_6CT$ $(CA)_5$ that amplified only 3 alleles. An AFLP analysis using nine primer pairs resulted in high polymorphisms resolving genome wide diversity among 124 genotypes.

Fifty microsatellite sequences have been isolated from an enriched library of sesame (Dixit 2005). Usefulness of 10 polymorphism microsatellites was tested for the diversity analysis using a total of 16 sesame accessions. Three to six alleles per locus at an average of 4.6 alleles having a fragment size of 150 to 307 bp was reported. Microsatellites used were found to be highly informative as the expected heterozygosity (He) and polymorphism information content (PIC) ranged from 0.437 to 0.858 and 0.34 to 0.80, respectively.

15.4.2 Gene Tagging

Identifying a molecular marker closely linked to the closed capsule character can enhance efficiency of the breeding programs aimed at eliminating such negative features. Uzun et al. (2003) identified an AFLP marker linked to closed capsule mutant trait using bulk segregant approach and later confirmed it by analyzing AFLP profile from single plants. The closed capsule mutant *cc3* was cross with a Turkish cultivar and the segregating population for the recessive mutant trait closed capsule was obtained. An F_2 population of 150 individuals was screened for the mutant trait phenotypically. Two bulks contrasting for the trait of interest were prepared and were subjected to bulk segregant analysis using AFLP markers.

A total of 72 primer combinations were screened for linkage to the desirable trait. Only one AFLP marker was found to be polymorphic chiefly due to the almost isogenic nature of the two parents used. Therefore, a 258 nucleotide AFLP marker tightly linked to the closed mutant trait was identified. A large deletion in the closed capsule mutant lines has been suggested resulting in the loss of function mutation though the hypothesis needs further confirmation.

15.4.3 Construction of High-Density Genetic Map and QTL Studies

The first QTL mapping in sesame was done by Zhang et al. (2013a). A high-density linkage map of sesame with 653 marker loci in 14 LGs was assembled. Using this linkage map, it was shown that seed coat color is controlled by two major genes with additive-dominant-epistatic effects plus polygenes with additive-dominant-epistatic effects. Four QTLs, namely, QTL1-1, 11-1, 11-2, and 11-3 were detected and found distributed in three linkage groups. This study provides a platform for further genetics and molecular marker-assisted selection (MAS) breeding research in sesame. Interestingly, seed coat color in sesame is an important agronomic trait. It is associated with biochemical functions involved in protein and oil metabolism, antioxidant activity and disease resistance. It has been suggested that seed coat color trait is a more suitable trait for estimating sesame evolution than geographic origin, since the direction of evolution in sesame has been suggested from wild species to black cultivars and then white cultivars (Zhang et al. 2013a).

A high-density genetic map for sesame has been constructed using Specific Length Amplified Fragment sequencing (SLAF-seq) (Zhang et al. 2013b). It is a recently developed high-resolution strategy for large-scale de novo SNP discovery and genotyping. In total, 28.21 Gb of data containing 201,488,285 pair-end reads were obtained after sequencing. From this data 71,793 high-quality SLAFs were detected of which 3673 SLAFs were polymorphic and 1272 of the polymorphic markers met the requirements for use in the construction of a genetic map. The final map included 1233 markers on the 15 linkage groups (LGs) and was 1,474.87 cm in length with an average distance of 1.20 cm between adjacent markers. A large number of polymorphic markers were developed in a short time using the SLAF-seq approach. The resultant high-density genetic map would be useful in gene/QTL fine mapping, map-based gene isolation, and molecular breeding for sesame. It will also act as a reference for positioning sequence scaffolds on a physical map, thereby assisting in the assembling of sesame genome sequence.

A molecular map of the important agro-botanic traits in sesame has been developed by Rao et al. (2014). Two sesame genotypes differing in important agro-botanic traits were crossed to study the inheritance pattern of nine traits. Seventeen QTLs were identified for these traits by single marker analysis. Out of the total QTLs detected, five explaining high phenotypic variation are promising

which include one QTL for corolla color, two for capsule shape, and one each for capsule hair density and number of nodes.

QTL mapping and generation of high-density genetic maps paves way for better understanding of the genome structure, location of genes of interest on chromosomes, and their linkage with DNA markers. This would also help in further producing a more saturated high-density molecular linkage map, thus assisting in marker-assisted breeding for economically valuable traits such as yield, biotic, and abiotic resistance.

15.4.4 Heterosis to Increase Crop Yield

Commercial exploitation of heterosis is a fast and simple conventional breeding approach to increase crop yield. Though hybrid development is a costly and laborious on-field process, the high outcrossing rate in sesame favors the exploitation of heterosis.

Assessment of the extent of heterosis in sesame for 15 quantitative traits including seed yield per plant was done by crossing twelve lines and three testers in a line x tester fashion to develop forty eight F_1 hybrids (Vavdiya et al. 2013). The analysis of variance indicated highly significant differences among the parents and hybrids for all the characters. This indicates the presence of sufficient amount of genetic diversity for all traits studied. Heterosis was worked-out over better parent and standard variety, G.Til-4. The standard heterosis for seed yield per plant ranged from −12.32 to 137.39 %. The crosses NIC-75 × G.Til-10, IC-81564 × G.Til-10, NIC-75 × G.Til-4, AT-238 × G.Til-10, and Borda-1 × G.Til-10 were good heterotic combinations for seed yield per plant, which recorded 137.39, 128.74, 111.34, 100.42, and 90.84 % standard heterosis, respectively. The heterosis for seed yield per plant was associated with the heterosis expressed by its component characters.

Genetic diversity in parents is considered desirable to exploit heterosis in any breeding program. An investigation was carried out to search whether any relationship existed between heterosis of cross combinations with phenetic divergence, combining ability, and genetic divergence of parents in sesame. For this, seven sesame genotypes and their 21 cross-combinations developed through half-diallel mating were assessed for morphological markers, microsatellite markers, and seed storage protein polymorphism along with estimation of different parameters. The clustering pattern of parents varied for morphological, protein, and simple sequence repeats (SSRs), though some concordance was observed between phenetic and genetic divergence of parents (Das et al. 2013). Mid-parent heterosis % and better parent heterosis % was found to be positively and significantly correlated with specific combining ability and hybrids per se, but no specific trend was seen between morphological, protein and SSR marker data. However, heterotic crosses were more reliably predicted by SSR based genetic diversity value of above 0.5 between parents (Das et al. 2013). Therefore, it was inferred that parental diversity, based on morphological and seed storage protein polymorphism did not corroborate

well with heterotic expression of characters in hybrids. However, the study based on microsatellite markers suggested that heterosis could be explained by parental diversity to some extent (Das et al. 2013).

15.4.5 Biotechnological Interventions in Sesame

Conventional breeding techniques have limited scope in improvement of resistance to biotic stresses and in quality improvement owing to low genetic variability for these traits and crossability barriers. Biotechnology is a viable option for developing sesame genotypes that can perform better under biotic and abiotic stresses. Furthermore, post fertilization barriers restrict the transfer of resistance genes from wild species to cultivated crops. This barrier cannot be overcome through conventional breeding. Therefore, the only option left for improvement of sesame is to transfer genes from other sources through genetic transformation techniques.

Plant tissue culture technology has been extensively used by plant breeders for crop improvement in several oil seed crops. The first report on tissue culture in sesame was that of Lee et al. (1985) on shoot tip culture followed by George et al. (1987) using different explants of sesame. Herbicide tolerant lines of sesame were obtained using in vitro selection by Chae et al. (1987). However, the recalcitrant nature of sesame provides hindrance in genetic transformation. Shoot regeneration with low frequencies from cotyledon and/or hypocotyl explants have been reported (Taskin and Turgut 1997; Were et al. 2006; Seo et al. 2007). Induction of somatic embryos has also been reported from hypocotyl-derived calluses but no plant regeneration was achieved (Mary and Jayabalan 1997). Susceptibility of sesame to *A. tumefaciens* has been shown by Taskin et al. (1999) but no transformed shoot/plant was recovered. However, hairy root cultures using *Agrobacterium rhizogenes* have been established (Ogasawara et al. 1993; Jin et al. 2005).

However, advancement in plant tissue culture approaches has led to increased opportunities for sesame improvement. For instance, regenerated plants can be grown to maturity in less than 4 months from shoot apical meristems and hypocotyls segments (Ram et al. 1990). Somatic embryos have been successfully induced directly from the surface of the zygotic embryos of sesame. As somatic embryogenesis produces stable variants, in vitro mutagenesis has been done on embryogenic sesame cultures to increase variability. Tissue culture methods have also been used to facilitate wide crosses using embryo culture techniques (Ram et al. 1990). Apart from these, nodal explants (Gangopadhyay et al. 1998) and leaf (Sharma and Pareek 1998) have also been used in micropropagating sesame. High frequency plant regeneration through direct adventitious shoot formation from deembryonated cotyledon segments of sesame have now been achieved (Seo et al. 2007). Enhanced shoot regeneration frequency was obtained by pre-culturing cotyledon explants in a high sucrose concentration (6 or 9 %) for 2 weeks.

Protocol optimization for genetic transformation and plant regeneration of sesame is reported (Were et al. 2006). *Agrobacterium*-mediated transformation

protocol for the first time has been established for generation of fertile transgenic sesame plants (Yadav et al. 2010). The method is efficient for plant regeneration with direct multiple shoot organogenesis from cotyledon explants including establishment of an optimal selection medium.

Studies targeting specific areas of improvement in sesame are incredibly meager. Nevertheless, steps are being taken to generate transgenic sesame seeds with lower phytate expression using an antisense expression cassette to enhance the use of sesame protein as food (Suh et al. 2010). An initial step toward developing improved sesame by the production of GFP expressing transgenic sesame plants using an *A. tumefaciens* mediated transformation system has been attempted. The promoter of the seed-specific microsomal δ-12 desaturase gene (*SeFAD2*) has been isolated from sesame. Transient expression of the GUS gene under the seed-specific *SeFAD2* promoter in developing sesame has been successfully achieved after microprojectile bombardment. Further investigations into seed-specific promoter in developing sesame seeds (*SeFAD2*) would help in generating seeds with improved qualities (Kim et al. 2008). Out of eight toco-isomers, sesame seeds are richest in γ-tocopherol. Apart from enhancing the nutritional functionality in humans, the production of other seven toco-isomers in sesame can also help the sesame plant in protection against oxidative stress. Studies pertaining to genetic improvement of nutritional components such as tocochromanols biosynthetic enzymes and the characterization of their recombinant products are underway. These studies can be extended to obtain transgenic sesame producing high tocochromanols thereby enhancing its amelioration ability.

15.5 Future Perspectives

A thorough molecular diversity analysis using robust techniques such as AFLPs, STMS, and SNPs can greatly help in detailed characterization of wild germplasm of sesame. This would also help in designation of diversity rich areas and thereby in the initiation of on-farm conservation activities.

The wild species of *Sesamum* are rich source of genes for resistance to biotic and abiotic stresses. There is a need to undertake detailed molecular phylogeny studies preferably under international network mode so that nomenclature of various species and their relationships with the cultigens are unambiguous.

Molecular tagging and mapping studies have enhanced the use of molecular markers to bring about greater specificity in crop improvement programs for incorporation of desired traits. Such studies are urgently required if sesame as a crop has to survive the future day competition from other more ‘efficient’ and remunerative oil seed crops such as soybean and brassicae. Finally, optimization of efficient protocols for in vitro regeneration and development of transgenic plants are the most important areas for sesame improvement that can bring a paradigm shift in enhancing the production and utilization of this unique oil yielding crop.

References

Abou-Gharbia HA, Shahidi F, Shehata AAY, Youssef MM (1997) Effects of processing on oxidative stability of sesame oil extracted from intact and dehulled seed. J Am Oil Chem Soc 74:215–221

Adéoti K, Rival A, Dansi A, Santoni S, Brown S et al (2011) Genetic characterization of two traditional leafy vegetables (*Sesamum radiatum* Thonn. ex Hornem and *Ceratotheca sesamoides* Endl.) of Benin, using flow cytometry and amplified fragment length polymorphism (AFLP) markers. Afr J Biotechnol 10(65):14264–14275

Adiver SS, Kumari (2010) Fungal diseases of oilseed crops and their management. In: Arya A, Perelló AE (eds) Management of fungal plant pathogens. CABI, pp 263–274

Agne PSE, Rance F, Bidat E (2003) Sesame seed allergy. Rev Franc 43(8):507–516(10)

Ahmad M, Khan MA, Zafar M, Sultana S (2010) Environment friendly renewable energy from sesame biodiesel energy sources. Energy Sources Part A 32:189–196

Akhila H, Beevy SS (2011) Morphological and seed protein characterization of the cultivated and the wild taxa of *Sesamum* L. (Pedaliaceae). Plant Syst Evol 293:65–70

Anyanga WO, Obongo YY (2001) Sesame (*Sesamum indicum* L.). In: Mukiibi JK (ed) Agriculture in Uganda, vol II. Crops, pp 97–102

Ashri A (1987) Report on FAO/IAEA expert consultation on breeding improved sesame cultivars. FAO/AGP, Rome

Ashri A (1988) Sesame breeding-objectives and approaches. In: Oil crops-sunflower, linseed and sesame. In: Proceedings of 4th oil crop network workshop, Njoro

Ashri A (1995) Sesame research overview: current status, perspectives and priorities. In: Bennett MR, Wood IM (eds) Proceedings of the 1st Australian sesame workshop. NT Dept. Primary Industry and Fisheries, Darwin, pp 1–17

Ashri A (2006) Sesame (*Sesamum indicum* L.) In: Singh RJ (ed) Genetic resources, chromosome engineering, and crop improvement oilseed crops, vol 4. CRC Press, pp 231–289

Baskaran RKM, Mahadevan NR, Sathiyananddam VKR, Thangavelu S (1997) Approaches for prevention and control sesame pests. In: Sinha MP (ed) Recent advances in ecobiological research, vol 2. APH Publishing, New Delhi, pp 133–143

Bedigian D (1981) Origin, diversity, exploration and collection of sesame. In: Sesame-status and improvement FAO plant production and protection, Paper 29, pp 164–169

Bedigian D (1984) *Sesamum indicum* L. Crop origin, diversity, chemistry and ethnobotany, PhD, University of Illinois, Champaign-Urbana University Microfilms DA8502071 dissertation. Abs Int 45:3410-B

Bedigian D, Harlan JR (1986) Evidence for cultivation of sesame in the ancient world. Econ Bot 40(2):137–154

Bedigian D (2003) Sesame in Africa: origin and dispersals. In: Neumann K, Butler A, Kahlheber S (eds) Food, fuel and fields—progress in African archaeobotany. Africa, pp 17–36

Bedigian D (2004a) History and lore of sesame in southwest Asia. Econ Bot 58(3):329–353

Bedigian D (2004b) Slimy leaves and oily seeds: distribution and use of wild relatives of sesame in Africa. Econ Bot 58(Suppl):S3–S33

Bedigian D (2010) Cultivated sesame and wild relatives in the genus *Sesamum* L. In: Sesame the genus *Sesamum*, CRC Press, Boca Raton, pp 53–61

Bedigian D (2014) A new combination for the Indian progenitor of sesame, *Sesamum indicum* (Pedaliaceae). Novon 23(1):5–13

Beroza M, Kinman ML (1955) Sesamin, sesamolin, and sesamol content of the oil of sesame seed as affected by strain, location grown, ageing, and frost damage. J Am Oil Chem Soc 32:348–350

Bhat KV, Babrekar PP, Lakhanpaul S (1999) Study of genetic diversity in Indian and exotic sesame (*Sesamum indicum* L.) germplasm using random amplified polymorphic DNA (RAPD) markers. Euphytica 110:21–33

Bhuyan J, Ramalingm RS, Sree-Rangaswamy SR (1997) Development of cytoplasmic-genic male sterile lines in sesame (*Sesamum indicum* L.) through genome substitution. Bull Pure Appl Sci B16:17–20

Bhuyan J, Sarma MK (2003) Identification of heterotic crosses involving cytoplasmic-genic male sterile lines in sesame (*Sesamum indicum* L.). Sesame Safflower Newsl 18:7–11

Bisht IS, Mahajan RK, Loknathan TR, Agrawal RC (1998) Diversity in Indian sesame collection and stratification of germplasm accessions in different diversity groups. Genet Res Crop Evol 45(4):325–335

Chae YA, Park SK, Anand IJ (1987) Selection in vitro for herbicide tolerant cell lines of *Sesamum indicum* 2: Selection of herbicide tolerant calli and plant regeneration. Korean J Plant Breed 19:75–80

Chowdhury S (1945) Control of *Cercospora* blight of til. Indian J Agric Sci 15:110–142

Chun JA, Jin UH, Lee JW, Yi YB, Hyung NI et al (2003) Isolation and characterization of a myo-inositol 1-phosphate synthase cDNA from developing sesame (*Sesamum indicum* L.) seeds: functional and differential expression, and salt-induced transcription during germination. Planta 216(5):874–880

Cerda A, Bingham FT, Hoffman GJ (1977) Interactive effect of salinity and phosphorus on sesame. Soil Sci Soc Am J 41:915–918

Ciferri R (1955) Preliminary list of noteworthy diseases of cultivated plants in continental eastern China. Plant Dis Report 39(10):785–792

Das A, Pandey S, Dasgupta T (2013) Association of heterosis with combining ability and genetic divergence in sesame (*Sesamum Indicum* L.). Intern J Sci Tech Res 2(12):307–314

Dasharath K, Sridevi O, Salimath PM, Ramesh T (2007) Production of interspecific hybrids in sesame through embryo rescue. Ind J Crop Sci 2(1):193–196

Diaz AJP, Layrisse A, Pugh TM (1999) Analisis de la diversidad genetic en el ajan joli mediante electrophoresis de isoenzimes (abstract in english). Trop Agron 49:169–186

Dixit A, Jin MH, Chung JW, Yu JW, Chung HK (2005) Development of polymorphic microsatellite markers in sesame (*Sesamum indicum* L.). Mol Ecol Notes 5(4):736–738

Duhoon SS, Jyotishi A, Deshmukh MR, Singh NB (2002) Optimization of sesame (*Sesamum indicum* L.) production through bio/natural inputs. J Oilseeds Res 19(1):73–78

Egonyu JP, Kyamanywa S, Anyanga W, Ssekabembe CK (2005) Review of pests and diseases of sesame in Uganda. Afr Crop Sci Conf Proc 7:1411–1416

Elbadri GA, Yassin AM (2010) Sesame's protective role in crop nematode control. In: Bedigian D (ed) Sesame: the genus *Sesamum*, CRC Press, Boca Raton, pp 211–217

El-Bramawy MASA, Abd Al-Wahid OA (2009) Evaluation of resistance of selected sesame (*Sesamum indicum*) genotypes to *Fusarium* wilt disease caused by *Fusarium oxysporum* f. sp. sesami. Tunis J Plant Prot 4:29–39

Elewa IS, Mostafa MH, Sahab AF, Ziedan EH (2011) Direct effect of biocontrol agents on wilt and root-rot diseases of sesame. Arch Phytopathol Plant Prot 44(5):493–504

Elleuch M, Besbes S, Roiseux O, Blecker C, Attia H (2007) Quality characteristics of sesame seeds and by-products. Food Chem 103:641–650

Ercan AG, Taskin M, Turgut K (2004) Analysis of genetic diversity in Turkish sesame (*Sesamum indicum* L.) populations using RAPD markers. Genet Res Crop Evol 51(6):599–607

Falusi OA, Salako EA, Funmi FM (2002) Inheritance of hairiness of stem and petiole in a selection from local (Nigeria) germplasm of sesame. Tropicultura 20(3):156–158

FAOSTAT (2015) http://faostat3.fao.org/browse/Q/QC/E (Accessed 20 June 2015)

Fernandez P, Rienzo JD, Fernandez L, Hopp HE, Paniego N et al (2008) Transcriptomic identification of candidate genes involved in sunflower responses to chilling and salt stresses based on cDNA microarray analysis. BMC Plant Biol 8:11

Gangopadhyay G, Poddar R, Gupta S (1998) Micropropagation of sesame (*Sesamum indicum* L.) by in vitro multiple shoot production from nodal explants. Phytomorphology 48(1):83–90

Gehlot HS, Purohit A, Shekhawat NS (2005) Metabolic changes and protein patterns associated with adaptation to salinity in *Sesamum indicum* cultivars. J Cell Mol Biol 4:31–39

George L, Bapat VA, Rao PS (1987) *In vitro* multiplication of sesame (*Sesamum indicum*) through tissue culture. Ann Bot 60:17–21

Ghafoorunissa (1996) Fats in Indian diets and their nutritional and health implications. Lipids 31 (Suppl): S287–S291

Gupta MP, Rai HS, Jakhmola SS (2000) Assessment of avoidable losses in grain yield due to the incidence of leaf roller and capsule borer *Antigastra catalaunalis* Dup. in sesame varieties. Extended summaries. National seminar on oilseed and oils research and development needs in the millennium directorate of oilseeds research, Hyderabad, India, pp 226

Gormley C, Bedigian D, Richard G (2015) Phylogeny of Pedaliaceae and Martyniaceae and the placement of *Trapella* in Plantaginaceae. Syst Bot 40(1):259–268

Haller HL, LaForge FB, Sullivan WN (1942) Some compounds related to sesamin: their structures and their synergistic effect with pyrethrum insecticides. J Org Chem 07(2):185–188

Harlan JR (1992) Crops and Ancient Man, 2nd edn. American Society for Agronomy, Madison

Hasan AF, Furumoto T, Begum S, Fukui H (2001) Hydroxysesamone and 2,3-epoxysesamone from roots of *Sesamum indicum*. Phytochemistry 58:1225–1228

Hetherington SE, He J, Smillie RM (1989) Photoinhibition at low temperature in chilling-sensitive and—resistant plants. Plant Physiol 90:1609–1615

Hiremath SC, Patil CG, Patil KB, Nagasampige MH (2007) Genetic diversity of seed lipid content and fatty acid composition in some species of *Sesamum* L. (Pedaliaceae). Afr J Biotechnol 6 (5):539–543

Hooker JD (1885) Pedaliaceae. In: Flora of British India, London 4:387

IAEA (2001) Sesame improvement by induced mutations. Final reports of an FAO/IAEA co-ordinated research project organized by the Joint FAO/IAEA division of nuclear techniques in food and agriculture 1993–1998:1–180

Ishitani M, Majumder AL, Bornhouser A, Michalowski CB, Jensen RG et al (1996) Co-ordinate transcriptional induction of myo-inositol metabolism during environmental stress. Plant J 9:537–548

Isshiki S, Umezaki T (1997) Genetic variations of isozymes in cultivated sesame (*Sesamum indicum* L.). Euphytica 93(3):375–377

Jin UH, Chun JA, Han MO, Lee JW, Yi YB et al (2005) Sesame hairy root cultures for extra-cellular production of a recombinant fungal phytase. Process Biochem 40(12):3754–3762

Johnson LA, Suleiman TM, Lusas EW (1979) Sesame protein: a review and prospectus. J Am Oil Chem Soc 56:463–468

Joshi AB, Narayanan ES, Vasudeva RS (1961) Sesamum. Indian Oilseeds Central Committee, Hyderabad, p 109

Kamal-Eldin (2010) Chemical studies on the lignans and other minor constituents of sesame seed oil. In: Bedigian D (ed) Sesame: the genus *Sesamum*, CRC Press, Boca Raton, pp 79–91

Kamal-Eldin A (1993) Seed oils of *Sesamum indicum* L. and some wild relatives: a compositional study of the fatty acids, acyl lipids, sterols, tocopherols and lignans, Ph.D. thesis submitted to Swedish University Agricultural Science

Kamal-Eldin A, Appelqvist LA (1994) Variations in the composition of sterols, tocopherols and lignans in seed oils from 4 *sesamum* species. J Am Oil Chem Soc 71:149–156

Kang CW, Kim SY, Lee SW, Mathur PN, Hodgkin T et al (2006) Selection of a core collection of korean sesame germplasm by a stepwise clustering method. Breed Sci 56:85–91

Kang MH, Choi JS, Ha TY (2003) Chemical properties of sesames cultivated in Korea and China. Food Sci Biotechnol 12(6):621–624

Katsuzaki H, Kawakishi S, Osawa T (1994) Sesaminol glucosides in sesame seeds. Phytochemistry 35(3):773–776

Khati P, Pandey KN (2004) Seed mycoflora of sesame and their role in plant health. J Mycol Pathol 34:378–380

Kim DH, Zur G, Danin-Poleg Y, Lee SW, Shim KB et al (2002) Genetic relationships of sesame germplasm collection as revealed by inter-simple sequence repeats. Plant Breed 121(3):259–262

Kim MJ, Go YS, Ahn SJ, Chung CH, Suh MC (2008) Functional complementation of a periila ω3 fatty acid desaturase under the seed-specific *SeFAD2* promoter. J Plant Biol 51(3):174–179

Kita S, Matsumura Y, Morimoto S, Akimoto K, Furuya M et al (1995) Antihypertensive effect of sesamin. II. Protection against two-kidney, one-clip renal hypertension and cardiovascular hypertrophy. Biol Pharm Bull 18:1283–1285

Koca H, Bor M, Ozdemir F, Turkan I (2007) The effect of salt stress on lipid peroxidation, antioxidative enzymes and proline content of sesame cultivars. Environ Exp Bot 60:344–351

Lee JI, Park YH, Park YS, Im BG (1985) Propagation of sesame (*Sesamum indicum* L.) through shoot tip culture. Korean J Breed 17(4):367–372

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

Lopez AM, Mazzani B (1964) Fruit length, number of seeds per fruit and seed size in seven sesame cultivars. Agronomia Trop Venezuela 14:133–135

Mahajan RK, Bisht IS, Dhillon BS (2007) Establishment of a core collection of world sesame (*Sesamum indicum* L.) germplasm accessions. Sabrao J Breed Genet 39:53–64

Mahfouz H, Kamel S, Belal A, Said M (2012) Pollinators visiting sesame (*Sesamum indicum* L.) seed crop with reference to foraging activity of some bee species. Cercetări Agronomice în Moldova 46(2):150

Mary RJ, Jayabalan N (1997) Influence of growth regulators on somatic embryogenesis in sesame. Plant Cell Tiss Org 49(1):67–70

Mkamilo GS, Bedigian D (2007) Sesamum indicum L. In: van der Vossen HAM, Mkamilo GS (eds) Vegetable Oils 14. Wageningen, Plant Resources of Tropical Africa (PROTA), pp 153–158

Mitsuma S, Ishigaki E, Sugiyama R, Asamizu T, Yamada K et al (2004) Activation of 000phenylpropanoid metabolism in sesame by over-expression of carrot calmodulin gene. Biol Pharm Bull 27(10):1621–1625

Moazzami AA, Kamal-Eldin A (2006) Sesame seed is a rich source of dietary lignans. J Am Oil Chem Soc 83:719–723

Mondal N, Bhat KV, Srivastava PS (2010) Variation in fatty acid composition in Indian germplasm of sesame. J Am Oil Chem Soc 87:1263–1269

Morris JB (2002) Food, industrial, nutraceutical and pharmaceutical uses of sesame genetic resources. In: Janick J, Whipkey A (eds) Trends in new crops and new uses. ASHS Press, Alexandria, pp 153–156

Morris JB (2009) Characterization of Sesame (*Sesamum indicum* L.) Germplasm Regenerated in Georgia, USA. Genetic Res Crop Evol 56:925–936

Najeeb U, Mirza MY, Jilani G, Mubashir AK, Zhou WJ (2012) Sesame. In: Gupta SK (ed), Technological innovations in major world oil crops, vol 1. Springer, New York, pp 131–145

Namiki M (1995) The chemistry and physiological functions of sesame. Food Rev Int 11:281–329

Narayanaswamy T, Surendra HS, Rathod S (2012) Fitting of statistical models for growth pattern of root and shoot morphological traits in sesame (*Sesamum indicum* L.). Environ Ecol 30 (4):1362–1365

Nassery H, Ogata G, Maas EV (1979) Sensitivity of sesame to various salts. Agron J 71(4):595–597

Nimmakayala P, Kaur P, Bashet AZ, Bates GT, Langham R, Reddy OUK (2005) Molecular characterization of *Sesamum* using SSRs and AFLPs. In: Plant and animal genomes XIII conference, San Diego, pp 15–19

Nimmakayala P, Perumal R, Mulpuri S, Reddy UK (2011) Sesamum. In: Kole C (ed) Wild corp relatives: genomic and breeding resources oilseeds. Springer, Berlin, pp 261–273

Ogasawara T, Chiba K, Tada M (1993) Production in high-yield of a naphthoquinone by a hairy root culture of *Sesamum indicum*. Phytochemistry 33(5):1095–1098

Olmstead RG, Bremer B, Scott KM, Palmer JD (1993) A parsimony analysis of the Asteridae *sensu lato* based on rbcL sequences. Ann Mo Bot Gard 80:700–722

Ono E, Nakai M, Fukui Y, Tomimori N, Fukuchi-Mizutani M et al (2006) Formation of two methylenedioxy bridges by a *Sesamum* CYP81Q protein yielding a furofuran lignan, (+)-sesamin. Proc Natl Acad Sci USA 103:10116–10121

Parani M, Singh KN, Rangasamy S, Ramalingam RS (1997) Identification of *Sesamum alatum* × *Sesamum indicum* hybrid using protein, isozyme and RAPD markers. Indian J Genet 57:381–388

Pathak N, Rai AK, Saha S, Walia SK, Sen SK, Bhat KV (2014) Quantitative dissection of antioxidative bioactive components in cultivated and wild sesame germplasm reveals potentially exploitable wide genetic variability. J Crop Sci Biotechnol 17(3):127–139

Pathak N, Bhaduri A, Bhat KV, Rai AK (2015) Tracking sesamin synthase gene expression through seed maturity in wild and cultivated sesame species—a domestication footprint. Plant Biol pp 1–8 (in press)

PGR Portal (2015) www.nbpgr.ernet.in/pgrportal (Accessed 09 December 2015)

Phillips KM, Ruggio DM, Ashraf-Khorassani M (2005) Phytosterol composition of nuts and seeds commonly consumed in the United States. J Agric Food Chem 30:53(24):9436–45

Prabakaran AJ (1992) Identification of male sterile sources through wide hybridization and induced mutagenesis in sesame (*Sesamum indicum* L.). Ph. D. Thesis, TNAU, Coimbatore

Prasad PR, Reddy SR (1997) Diseases of sesame in two districts (Warangal and Karimnagar) of Andhra Pradesh. In: Reddy MS, Srivastava H, Purohit DK, Reddy SR (eds) Microbial biotechnology, Scientific Publishers, Jodhpur, pp 169–174

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

Raikwar RS, Srivastva P (2013) Productivity enhancement of sesame (*Sesamum indicum* L.) through improved production technologies. Afr J Agric Res 8(47):6073–6078

Rajab R, Rajan SS, Satheesh LS, Harish SR, Sunukumar SS et al (2009) Hypersensitive response of *Sesamum prostratum* Retz. elicitated by *Fusarium oxysporum* f. *sesami* (Schelt) Jacz Butler. Ind J Exp Biol 47(10):834–838

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

Rajeswari S, Thiruvengadam V, Ramaswamy NM (2010) Production of interspecific hybrids between *Sesamum alatum* Thonn and *Sesamum indicum* L. through ovule culture and screening for phyllody disease resistance. S Afr J Bot 76(2):252–258

Ram R, Catlin D, Romero J, Cowley C (1990) Sesame: new approaches for crop improvement. In: Janick J, Simon JE (eds) Advances in new crops. Timber Press, Portland, pp 225–228

Ram SG, Sundaravelpandian K, Kumar M, Vinod KK, Bapu JK et al (2006) Pollen–pistil interaction in the inter-specific crosses of *Sesamum* sp. Euphytica 152:379–385

Ramanathan K (1950) A note on the interspecific hybridization in *Sesamum*. Madras Agric J 37:397–400

Rao P, Prasuna K, Anuradha G, Srividya A, Vemireddy LR et al (2014) Molecular mapping of important agro-botanic traits in sesame. Electronic J Plant Breeding 5(3):475–488

Salehi M, Izadpanah K (1992) Etiology and transmission of sesame phyllody in Iran. J Phytopathol 135:37–47

Salunkhe DK, Chavan JK, Adsule RN, Kadam SS (1991) Sesame. In: Röbbelen G, Downey RK, Ashri A (eds) World oilseeds-chemistry, technology, and utilization. Van Nostrand Reinhold, New York, pp 371–402

Sarwar G, Haq MA (2006) Evaluation of sesame germplasm for genetic parameters and disease resistance. J Agric Res 44(2):89–96

Schumutterer H, Kranz J (1965) On *Cylindrosporium sesame* (Huss.) causing brown spot disease of sesame. Phytopathologische Zeitshrift 254:193–201

Seo HY, Kim YJ, Park TI, Kim HS, Yun SJ et al (2007) High-frequency plant regeneration via adventitious shoot formation from deembryonated cotyledon explants of *Sesamum indicum* L. Vitro Cell Dev Biol Plant 43(3):209–214

Shahidi F, Tan Z (2010) Physiological effects of sesame bioactive and antioxidant compounds. In: Bedigian D (ed), Sesame-The genus *Sesamum*, CRC Press, Boca Raton, pp 139–153

Singh PK, Akram M, Vajpeyi M, Srivastava RL, Kumar K et al (2007) Screening and development of resistant sesame varieties against phytoplasma. Bull Insectol 60:303–304

Singh TVK, Satyanarayana J, Peshin R (2014) Crop loss assessment in India-past experiences and future strategies. In: Peshin R, Pimental D (eds) Integrated Pest Management. Springer, New York, pp 227–243

Srinivasan AR (1942) Contribution to the morphology *Pedalium murex* Linn. and *Sesamum indicum* D.C. In: Proceedings of Indian acadamic sciences 16(5):155–164

Srinivasulu B, Narayanaswamy P (1992) Four-tier technique for screening *Sesamum* entries against phyllody disease. Oil Crops Newsl 9:38–40

Subramanian M (1995) Pollen germination studies in Sesame. Ann Agric Res 16:225–226

Sugano M, Inoue T, Koba K, Yoshida K, Hirose N et al (1990) Influence of sesame lignans on various lipid parameters in rats. Agric Biol Chem 54:2669–2673

Suh MC, Hyung N, Chung C (2010) Molecular biotechnology of sesame. In: Bedigian D (ed) Sesame-The genus *Sesamum*, CRC press, Boca Raton, pp 219–243

Suh MC, Kim MJ, Hur CG, Bae JM, Park YI et al (2003) Comparative analysis of expressed sequence tags from *Sesamum indicum* and *Arabidopsis thaliana* developing seeds. Plant Mol Biol 52:1107–1123

Sutica D, Dowson WJ (1962) Bacterial Leaf Spot of *Sesamum* in Yugoslavia. J Phytopathol 45:57–65

Tabatabaei SA, Naghibalghora SM (2014) The effect of salinity stress on germination characteristics and changes of biochemically of sesame seeds. Cercetări Agronomice în Moldova 47(158):61–68

Tarihal R (2003) Study of fertilization barriers in crosses between *Sesamum indicum* and its wild relatives. Ind J Genet 63(2):132–136

Taşkin KM, Ercan AG, Turgut K (1999) *Agrobacterium tumefaciens* mediated transformation of sesame (*Sesamum indicum* L.). Turk J Bot 23:291–295

Taskin KM, Turgut K (1997) In vitro regeneration of sesame (*S. indicum* L.). Turk J Bot 21:15–18

Uzun B, Lee D, Donini P, Çagirgan ML (2003) Identification of a molecular marker linked to the closed capsule mutant trait in sesame using AFLP. Plant Breed 122(1):95–97

Vavdiya PA, Dobariya KL, Babariya CA, Sapovadiya MV (2013) Heterosis for seed yield and its components in sesame (*Sesamum indicum* L.). Electron J Plant Breed 4(3):1246–1250

Verma ML, Mehta N, Sangwan MS (2005) Fungal and bacterial diseases of sesame. In: Saharan GS, Mehta N, Sangwan MS (eds) Diseases of oilseed crops, Indus Publishing, New Delhi, pp 269–300

Wei W, Li D, Wang L, Ding X, Zhang Y et al (2013) Morpho-anatomical and physiological responses to waterlogging of sesame (*Sesamum indicum* L.). Plant Sci 208:102–111

Wei W, Qi X, Wang L, Zhang Y, Hua W et al (2011) Characterization of the sesame (*Sesamum indicum* L.) global transcriptome using Illumina paired-end sequencing and development of EST-SSR markers. BMC Genom 12:451

Were BA, Gudu S, Onkware AO, Carlsson AS, Welander M (2006) *In vitro* regeneration of sesame (*Sesamum indicum* L.) from seedling cotyledon and hypocotyl explants. Plant Cell Tiss Org 85(2):235–239

Williamson KS, Morris JB, Pye QN, Kamat CD, Hensley K et al (2008) A survey of sesamin and composition of tocopherol variability from seeds of eleven diverse sesame (*Sesamum indicum* L.) genotypes using HPLC-PAD-ECD. Phytochem Anal 19(4):311–322

Yadav M, Chaudhary D, Sainger M, Jaiwal PK (2010) *Agrobacterium tumefaciens*-mediated genetic transformation of sesame (*Sesamum indicum* L.) Plant Cell Tiss Org 103(3):377–386

Yasumoto S, Sugiura M, Komaki K, Katsuta M (2005) Change in sesamin and sesamolin contents of sesame (*Sesamum indicum* L.) seeds during maturation and their accurate evaluation of the contents. Japanese. J Crop Sci 74(2):165–171

Yokota T (2007) Sesamin, a lignan of sesame, down-regulates cyclin D1 protein expression in human tumor cells. Cancer Sci 98(9):1447–1453

Yoshida H (2007) Antioxidant distributions and triacylglycerol molecular species of sesame seeds (*Sesamum indicum*). J Am Oil Chem Soc 84:165–172

Yousif YH, Bingham FT, Yermanos DM (1972) Growth, mineral composition, and seed oil of sesame (*Sesamum Indicum* L.) as affected by NaCl. Soil Sci Soc Am J 36(3):450–453

Uzun B, Cağirgan M (2006) Comparison of determinate and indeterminate lines of sesame for agronomic traits. Field Crops Res 96:13–18

Zhang H, Miao H, Wei L, Li C, Zhao R et al (2013a) Genetic analysis and QTL mapping of seed coat color in sesame (*Sesamum indicum* L.). PLoS One 8(5):e63898

Zhang Y, Wang L, Xin H, Li D, Ma C et al (2013b) Construction of a high-density genetic map for sesame based on large scale marker development by specific length amplified fragment (SLAF) sequencing. BMC Plant Biol 13:141

Zhang Y, Wang L, Xin H, Li D, Ma C et al (2013c) Construction of a high-density genetic map for sesame based on large scale marker development by specific length amplified fragment (SLAF) sequencing. BMC Plant Biol 13:141