Chapter 1
Oil Crop Breeding and Genetics

Johann Vollmann and Istvan Rajcan

1.1 Introduction

Oil crops have considerably gained in importance to world agriculture and associated industries over the past 25 years. The total area of land devoted to oil crop cultivation has seen an increase from 160 million hectares in 1980 to 247 million hectares in 2005 (Fig. 1.1), whereas the world-wide acreage of cereals has dropped from 717 to about 670 million hectares over the same period of time. Annual world oil crop production has risen from 278 million metric tonnes in 1980 to about 711 million metric tonnes in year 2005 (Fig. 1.1). This remarkable expansion of production is due to the process of concentration on major oil crop species and at the same time to yield increases per unit area through refined agronomic practice and plant breeding. As illustrated in Table 1.1, soybean, rapeseed, sunflower and oil palm are the major crops contributing to the increase of the overall oil crop cultivation area, whereas the acreages of cotton seed, linseed, safflower and castor had significant decreases. Increases in yield per unit area from the 1979–1981 period to the 2002–2004 period (Table 1.1) were 82.2 and 69.0% for oil palm and rapeseed, respectively, and were also high for linseed and castor. A more moderate yield increase from 1701 to 2284 kg/ha (i.e. 34.3%) was noticeable for soybean, whereas progress was very slow in sunflower and safflower, and even negative in poppy. Taking the 2005/2006 marketing year and the medium-term prospects assessment for agricultural commodities of FAO and OECD as a basis, world oil crop production and vegetable oil output were estimated to rise by another 25–30% by the year 2015 (Thoenes 2006). Projections for the period 2006–2015 show that production increases will slow down in Europe and North America, while they will notably grow in Brazil, Argentina, Malaysia and Indonesia. Both the oil crop production increases since 1980 and the projected growth until 2015 correspond with a steadily growing demand for

J. Vollmann (✉)
University of Natural Resources and Applied Life Sciences Vienna (BOKU),
Institute of Agronomy and Plant Breeding, Vienna, Austria
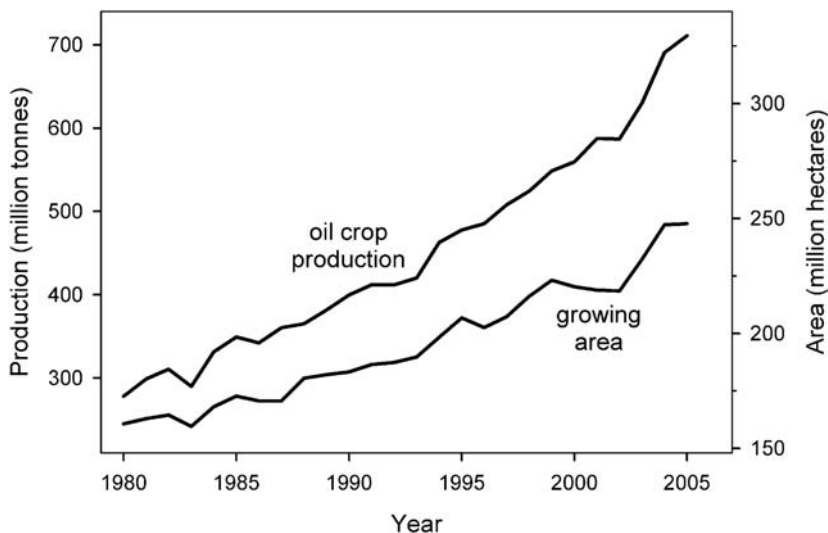e-mail: johann.vollmann@boku.ac.at

Fig. 1.1 Global oil crop production and acreage from 1980 to 2005 (FAOSTAT 2007)

Table 1.1 Changes in world acreage and average annual seed or fruit yield of major oil crops over a 25 years period of time

	Area in hectares		Change	Average yield in kg/ha		Change
Species	1980	2005	(in %)	1979–1981	2002–2004	(in %)
Castor	1, 540, 418	1, 408, 773	−8.5	572	934	63.1
Coconut	8, 768, 644	10, 685, 108	21.9	3, 717	4, 994	34.4
Cotton seed	34, 523, 000	30, 000, 000	−13.1	1, 246	1, 821	46.1
Groundnut	18, 364, 563	23, 427, 479	27.6	988	1, 452	47.0
Linseed	5, 371, 117	3, 182, 058	−40.8	456	767	68.2
Oil palm	4, 277, 328	12, 395, 528	189.8	7, 052	12, 847	82.2
Olive	5, 130, 401	7, 550, 561	47.2	1, 853	2, 042	10.2
Poppy	58, 573	109, 164	86.4	579	504	−12.9
Rapeseed	10, 992, 015	27, 448, 263	149.7	970	1, 639	69.0
Safflower	1, 322, 348	916, 443	−30.7	694	741	6.7
Sesame	6, 265, 283	7, 279, 469	16.2	303	435	43.7
Soybean	50, 649, 297	92, 369, 299	82.4	1, 701	2, 284	34.3
Sunflower	12, 425, 559	22, 823, 330	83.7	1, 170	1, 225	4.7
Total	160, 618, 770	241, 961, 583	50.6			

Source: FAOSTAT 2007.

and consumption of vegetable oils and fats. From 1980 to 2003, the availability of vegetable oils for food was rising from 19.9 to 26.4 kg per caput per year for North America and from 11.6 to 19.6 kg for Western Europe, whereas it developed from 4.8 to 10.3 kg for Asia and from 7.1 to 8.3 kg for Africa

(FAOSTAT 2007). Subsequently, the projected rise in vegetable oil consumption by 30% during the decade from 2005 to 2015 will be caused by increases of per caput food oil consumption in China, India and Latin American countries, whereas in the European Union and North America it will be driven by the strongly growing demand for bio-fuels (Thoenes 2006).

The largest increases in world average yield were found in oil palm and rapeseed (Table 1.1), which can only partly be attributed to plant breeding, as for both crops the expansion in planting area occurred predominantly in highly productive environments, i.e. Indonesia and Malaysia for oil palm, and Europe for rapeseed. Nevertheless, plant breeding has undoubtedly played a key role in production increases over the past 25 years: In oil palm, the introduction of hybrid cultivars derived from crosses between Deli (thick-shelled dura population) and shell-less pisifera or thin-shelled tenera populations, reciprocal recurrent selection, and the achievement of homogeneous planting populations of a favourable genotype through clonal micro-propagation of hybrids instead of seed propagation are considered driving forces of the huge yield increase (Soh et al. 2003). In oilseed rape, genetic progress is attributable to pure line improvement through enhancement of agronomic features, disease resistance and incorporation of the doubled-haploid technique, whereas high-yielding hybrid cultivars are gaining momentum only recently (Snowdon et al. 2007).

Generally, oil crop breeding is a more complex undertaking than breeding of cereals or legumes, as most oil crops are dual- or multi-purpose crops, which requires the simultaneous manipulation of different quality characters. In soybean, oilseed rape, sunflower and a number of other oil crops, the protein-rich meal is of economic significance beside the oil. However, a highly negative correlation between oil and protein content is a major impediment to breeding progress in these crops. In soybean, average seed oil content is 20% and protein content is 40% with a long-term tendency of slight increases in oil and decreases in protein content; as both constituents are important in international trade, economic models based on oil and protein prices have been proposed as a selection index in breeding of high value soybeans (Leffel 1990). In oilseed rape, selection of strains exhibiting the yellow seed color character, which is associated with a thinner seed coat and lower fibre content than in black-seeded genotypes could be a strategy of simultaneous improvement of both oil and protein content (Badani et al. 2006b). In cotton, fibre yield and fibre quality are the main crop features, whereas cotton seed oil is a by-product and therefore oil content is not the major breeding objective. In linseed or flax, there are two main morphotypes of cultivars for either oil production from seed (linseed) or bast fibre production from stems (fibre flax), whereas dual-purpose cultivars are rare, and production of both high quality seed and fibre from the same crop is difficult agronomically. Only recently, the utilisation of short-fibre linseed straw is discussed for applications in the emerging field of non-woven materials, and selection criteria for breeding of

dual-purpose linseed cultivars have occasionally been suggested (Rennebaum et al. 2002; Foster et al. 2000). Moreover, issues such as the specific requirements of oilseed quality analytics, crop product diversification, the handling of cytoplasmic male sterility in hybrid crops with hermaphroditic flowering, and the introduction of genetically engineered cultivars or traits add to the complexity of oil crop breeding.

Earlier reviews of oil crop breeding have focused on major breeding objectives (Knowles 1983), on breeding methods (Knowles 1989) or on the reproductive systems of oil crop species which determine both the breeding strategy applicable and the resulting type of cultivar (Arthur 1994). More recently, excellent reviews have been published on breeding for specific fatty acid composition (Burton et al. 2004), on the different aspects of improving oil quality (Velasco and Fernández-Martínez 2002), and on genetic engineering the pathways of oil biosynthesis (Dyer and Mullen 2005). This review addresses two key features of present day oil crop breeding, genetic diversity and oil content; the emphasis will be put on annual oilseeds rather than on perennial crops.

1.2 Domestication and Genetic Diversity

Domestication is an evolutionary process of genetic development, in which natural selection is replaced by human selection shaping crop plants for specific needs. Typical changes occurring during the development from a wild plant to a domesticated crop are referred to as the domestication syndrome; they include the loss of seed dormancy, increased rates of self-pollination, adoption of vegetative propagation, increase in yield of seed or other plant organs utilized, compact growth habit, loss of seed dispersal, increase in number and size of seeds and inflorescences, changes in color, taste and texture, and decrease in the content of toxic substances (Gepts 2002). Other important changes include the alteration of photoperiod sensitivity, adaptation to agricultural soils and agronomic treatments, and the adaptation to new environments often far away from the center of origin.

Cereals, legumes and fruits were among the first crop plants utilized by mankind; domestication of cereals dates back some 12 000 years and is considered as the decisive impetus of Neolithic revolution, the transition from a hunting and gathering lifestyle to a sedentary agriculture-based society (Salamini et al. 2002). Oil plants were not among those first crops domesticated, most of them appeared much later in history, as their utilization and handling requires specific knowledge and techniques not available to early agriculturalists. The comparatively late appearance of major oil crops does have consequences on their status of domestication, on the development of genetic diversity, and subsequently on availability of germplasm resources.

1.2.1 Domestication of Oil Crops

The domestication status of oil crops is fairly divergent depending on their agricultural history. While few oil crops are fully domesticated, many others express various wild type characteristics, as illustrated in some prominent examples: Seed dormancy is still a problematic feature of sunflower which disallows rapid germination of lost seed, but instead causes volunteer sunflowers in the following season; pod dehiscence and subsequent seed shattering may cause considerable yield losses in soybean, oilseed rape, sesame and other oilseeds; self-pollination is prohibited in several oilseed brassicas due to self incompatibility; anti-nutritional factors such as protease inhibitors are present in soybean, oleuropein, a bitter phenolic compound is found in olive; and toxic components such as glucosinolates in oilseed brassicas or gossypol in cotton have only been reduced recently. In addition, new oil crops only grown for their unique fatty acid patterns, such as lesquerella, crambe, cuphea, meadowfoam or jojoba exhibit numerous wild type characteristics apart from poor productivity.

Flax or linseed (*Linum usitatissimum* L.) is today considered to be the oldest oilseed in the world having been domesticated in the Near East region 10 000 years ago and serving as a source of both oil and fibre from prehistoric time until present (Allaby et al. 2005). It has been under discussion whether oil or fibre was the primary reason of domestication, and whether domestication took place once or happened several times in independent domestication events in different diversity regions of flax (Diederichsen and Hammer 1995). New evidence from network analysis of genetic diversity in the stearic acid desaturase locus *sad2* suggests a single domestication event of cultivated flax from its wild progenitor *Linum angustifolium* Huds.; moreover, an oilseed type of flax is proposed as the first domesticate, while fibre flax appears as a later descendant from oilseed flax (Allaby et al. 2005).

Sesame (*Sesamum indicum* L.) has often erroneously been described as the oldest oilseed in human use with a probable origin in Africa, as sesame is a historically and culturally important crop plant, and there is a high diversity of *Sesamum* species on the African continent (Bedigian 2003). However, clear evidence from archeology, history as well as from botanical, chemical and genetic data suggests that sesame has been domesticated on the Indian subcontinent during the period from 3050 to 3500 BC, and that *S. malabaricum* Burm., a wild sesame species occurring in India exclusively is the progenitor of cultivated sesame (Bedigian 1998, 2003).

Sunflower (*Helianthus annuus* L.) was domesticated by Native North Americans about 4, 300 years ago from wild *H. annuus* in the now east-central United States (Wills and Burke 2006); in addition, multiple evidence for an indepentent domestication event in Mexico has also been presented (Lentz et al. 2008). Sunflower was then utilized as a multi-purpose crop, but became an oilseed only in the late 18th and early 19th century in Russia, from where it spread over

Europe and was later re-introduced from Russia to North America as an oilseed crop (Putt 1997). From the cross between a cultivated and a wild sunflower genotype with subsequent QTL analysis, Burke et al. (2002) gained insight into the genetics of sunflower domestication: Only a few major QTL were found, the two strongest QTL affected the number of selfed seeds (self-compatibility); moreover, selection for increased achene size was an important feature of sunflower domestication, a high frequency of favourable alleles was present in wild sunflower, and a majority of sunflower domestication traits was non-recessive.

Soybean (*Glycine max* (L.) Merr.) was domesticated from the wild *Glycine soja* Sieb. & Zucc. in the northeast of China (Manchuria) in the period 1500–1100 BC (Hymowitz 2004) probably in multiple domestication events, as suggested by chloroplast DNA diversity between wild and cultivated soybeans (Xu et al. 2002). So, despite the popular myth claiming soybean to be one of the oldest crops utilised by mankind (Hymowitz and Shurtleff 2005), it is a comparatively young crop plant. And much later, during the North Song Dynasty (960–1127) soybean was recognized as a source of vegetable oil (Huan and Bao 1993).

Oilseed rape (*Brassica napus* L.) is known only since the 13th century as an oil crop (Snowdon et al. 2007; Downey and Röbbelen 1989). As an amphidiploid interspecific hybrid and probably with a polyphyletic base (Song et al. 1988) it originated in the Mediterranean region of southwest Europe, where the two diploid parental species *B. oleracea* L. (cabbage) and *B. rapa* L. (turnip) overlap in their natural habitats. Apart from oilseed rape, the species *Brassica napus* is comprised of related forage and vegetable forms (e.g. Soengas et al. 2006), but no true wild forms are known, which also underlines the recent origin of this species.

1.2.2 Oil Crop Germplasm

The availability of germplasm with sufficient genetic diversity is essential for a continuous breeding progress. Jones (1983) emphasized the particular need of preserving oil crop germplasm, as almost all of the major oil crops are now cultivated far away from their primary centers of origin. Therefore, they do have a comparatively narrow genetic base classically made up by relatively few plant introductions who represent the ancestors, from which elite germplasm and further breeding material is developed.

As shown above, most oil crops gained economic importance during the last couple of decades only, and many of them are very young crops in terms of their cultivation and utilisation history as oil plants. These appear to be the main reasons why oil crops are poorly represented in ex situ germplasm collections at present. In Table 1.2, a summary is presented on numbers of accessions for oil crops versus other crops held by the three major genebank associations, which represent the most significant institutions conserving genetic resources. For all three associations, cereals such as *Triticum* sp. (mainly bread and durum

Table 1.2 Accession numbers of crops in general and oil crops in three major genebank associations (ex situ collections)

Genebank association	Crops in general	Accessions	Oil crops	Accessions
CGIAR centers	*Triticum* sp.	114, 721	Soybean[1]	15, 904
(SINGER)	Rice	111, 303	Peanut	14, 694
	Sorghum	36, 805		
	Barley	38, 067		
	Maize	25, 827		
	Chickpea	30, 063		
	Lentil	10, 733		
	CGIAR total	689, 578		
EURISCO	*Triticum* sp.	156, 045	Linseed/flax	17, 226
European Plant	Barley	75, 033	Soybean	11, 408
Genetic	Maize	42, 267	Oilseed rape	4, 879
Resources	Oat	23, 149	Sunflower	4, 444
Search	Rye	10, 254	Poppy	4, 114
Catalogue	Sorghum	6, 234	Peanut	2, 575
	Common bean	30, 845	Cotton	1, 957
	Pea	24, 767	Sesame	1, 661
	Lentil	5, 635	Safflower	728
	Faba bean	5, 600	Olive	421
	EURISCO total	1, 000, 175		
USDA National	*Triticum* sp.	55, 942	Soybean	19, 277
Plant Germplasm	Barley	28, 438	Peanut	6, 831
System	Sorghum	42, 666	Cotton	5, 794
	Corn	25, 468	Linseed/flax	2, 863
	Oat	21, 837	Sunflower	2, 759
	Rice	19, 470	Safflower	2, 373
	Phaseolus sp.	14, 928	Sesame	1, 226
	Chickpea	6, 019	Castor	1, 043
	USDA total	477, 077		

[1]World Vegetable Center (AVRDC, Taiwan, as part of SINGER network).
Sources: CGIAR: http://www.singer.cgiar.org/, 30 April 2007
EURISCO: http://eurisco.ecpgr.org/, 30 April 2007
USDA: http://www.ars-grin.gov/npgs/stats/, 30 April 2007

wheat), rice, barley or sorghum and legumes such as chickpea, pea, lentil or phaseolus beans have been conserved in clearly higher numbers than oil crop species: The genebanks of the international agricultural research centers (CGIAR group, SINGER network) hold a significant peanut collection and a partly vegetable type soybean collection, but generally oil crops are not on their list of mandate crops. The European national germplasm collections, linked together in EURISCO, an internet germplasm search catalogue, hold significant numbers of linseed/flax and soybean accessions; for oilseed rape and sunflower, the two most important European oil crops, accession numbers are much lower and in the same magnitude as for poppy, which is of very regional importance only. The United States National Plant Germplasm

System holds significant collections of soybean, peanut and cotton accessions in their genebanks, which represent the major US oil crop species. In addition to the accessions listed in Table 1.2, important oil crop germplasm is also maintained by institutions in Canada, Argentine, Brazil, China, India, Australia and few other countries.

Generally, the number of accessions per species held in ex situ collections is an indicator of past collection activities and the availability of germplasm, but not a sound measure of genetic diversity. For the accessions of linseed/flax, Diederichsen (2007) reviewed the ex situ collections world-wide: More than 46, 500 accessions of linseed are present in at least 33 public genebanks; however, based on analyses of duplications, the author estimates that only 10–15,000 accessions are unique. In soybean, more than 170,000 accessions are maintained in genebanks, out of which more than two thirds are duplications and about 45,000 are considered unique genotypes (Carter et al. 2004).

Although present in lower number than cereals and legumes, oilseeds such as linseed, soybean and peanut appear to be well represented in ex situ collections, while germplasm availability of minor and new oil crops is very limited (Thompson et al. 1992), and therefore enhancing germplasm collections of these species will be an important activity ensuring future breeding progress.

1.2.3 Genetic Diversity in Oil Crops – Selected Examples

An overview of the genetic diversity present in the primary and further gene-pools of a given species is of great interest both to plant breeding and conservation management. Technically, estimates of genetic relationship may be obtained from pedigree information, phenotypic data, or molecular polymorphisms on the protein or DNA level, and by applying an appropriate measure of genetic distance (Mohammadi and Prasanna 2003). In oil crops, various conclusions for plant breeding have been drawn from analyses of genetic diversity for particular species and populations, as outlined in selected examples from soybean and oilseed rape.

Soybean genetic diversity has meticulously been investigated from various points of view and was reviewed by Carter et al. (2004). Pedigree analysis and calculation of coefficients of parentage revealed that the genetic base of North American soybean cultivars is narrow as compared to Asian soybeans: While only 26 ancestors contributed 90% of genes to 258 public cultivars in North America (Gizlice et al. 1994), it is more than 339 ancestors which contributed 90% of genes to 651 Chinese soybean cultivars (Cui et al. 2000) and more than 74 ancestors which contributed 90% to 86 modern public Japanese cultivars (Zhou et al. 2000).

Using RAPD markers, Li and Nelson (2001) found a larger genetic diversity in Chinese accessions than in Japanese or South Korean accessions and were able to clearly separate Chinese soybeans and those from Japan or South

Korea, respectively. In a diversity study based on AFLP markers, Ude et al. (2003) suggested to utilize Japanese elite cultivars in order to widen the narrow genetic base of North American soybeans, as they are more distinct from North American cultivars than Chinese ones. In numerous other studies, molecular markers were used to investigate special issues such as variation in vegetable soybeans (Mimura et al. 2007) or diversity between cultivated and wild soybean accessions and their geographical genetic differentiation (Chen and Nelson 2004; Xu and Gai 2003).

The phenotypic diversity determined for 15 traits of over 20,000 soybean accessions from the Chinese national soybean collection is representing a highly valuable information pool for breeding and has further been used to propose a single geographical center of soybean diversity downstream the Yellow River Valley (Dong et al. 2004). Phenotypic data from 25 leaf, stem and seed composition traits of North American and Chinese soybean cultivars have also been utilized to verify the narrow genetic base of North American soybeans, which probably represents a subset of the wider genetic base of Chinese cultivars (Cui et al. 2001); phenotypic distinctness of these two genetic pools is considered to be the result of continuous selection for adaptation to contrasting environmental conditions, which now offers new opportunities for reciprocal broadening the genetic bases by introducing exotic parents.

Marker-assisted introgression of genes from exotic or wild sources through backcrossing is occasionally considered as enhancing the genetic base of soybean (Lee et al. 2007). However, while backcrossing may bring in the beneficial effect of a particular allele into adapted breeding material, it does not enlarge the overall genetic base (Carter et al. 2004); otherwise, backcrossing the genetically engineered tolerance to the herbicide glyphosate into many commercial soybean cultivars also did not reduce the genetic base of North American soybean cultivars (Sneller 2003).

In oilseed rape, genetic diversity is considered to be low because of the short cropping history and the strong breeding focus on seed quality characters, i.e. low erucic acid and low glucosinolate contents which narrowed down the genetic base. Therefore, artificial resynthesis of oilseed rape from its diploid progenitors cabbage and turnip is practised in order to broaden the genetic base of oilseed rape (Becker et al. 1995; Seyis et al. 2003; Basunanda et al. 2007), although resynthesized rapeseed lines exhibit a low yield potential and inferior seed quality. Resynthesis has repeatedly been used for gene introgression into cultivars, e.g. for various disease resistances or yellow seed color (Snowdon et al. 2007). Apart from resynthesis, enriching the genetic base of oilseed rape has been suggested by hybridizing European and Chinese elite oilseed rape lines (Hu et al. 2007), or by utilizing diversity existing in vegetable or fodder crop types of *Brassica napus*, despite their inferior oil and meal quality (Hasan et al. 2006).

Due to the present transition from pure line breeding to hybrid breeding, genetic diversity in oilseed rape is receiving new attention, as heterotic

pools of accessions with sufficiently large genetic distance need to be formed for maximum hybrid performance (Snowdon et al. 2007). Significant relationships between parental genetic distance and hybrid oilseed rape performance have been described (Diers et al. 1996; Riaz et al. 2001; Shen et al. 2006), but were considered not sufficient for prediction of heterosis. For improvement of hybrid performance, Quijada et al. (2004) suggested the introgression of European winter oilseed rape genomic segments into Canadian spring canola, as superior hybrid performance was found in testcrosses between these two genepools. A different strategy for increasing hybrid performance of oilseed rape has been proposed by Li et al. (2006a), who found considerable heterosis in crosses between natural *Brassica napus* parents and a new type of *Brassica napus* containing the A subgenome of *B. rapa* and the C subgenome of *B. carinata* thus realizing intersubgenomic heterosis.

1.3 Recent Milestones in Oil Crop Breeding

Over the past few decades, breeding research in oil crops has seen a number of crucial results which had significant impacts on the subsequent development of world-wide oil crop production (Table 1.3). Improvement of both oil and meal in oilseed rape by reducing erucic acid content of oil (canola quality) and glucosinolate content of meal are two most prominent milestones contributing to the expansion of world oilseed rape acreage from less than 10 million hectares in the early 1970s to more than 27 million hectares in 2005 (FAO-STAT 2007). Moreover, high oleic (Schierholt et al. 2001) and low linolenic (Rücker and Röbbelen 1996) oilseed rape represent further improvements of nutritional value and oxidative stability. Relevant changes in fatty acid composition have also been achieved in sunflower, soybean and linseed (Table 1.3). Additional examples of alterations in fatty acid composition for particular crops have been summarized by Velasco and Fernández-Martínez (2002). In sunflower and oilseed rape, cytoplasmic male sterility (cms) allowed for the development of hybrid cultivars (Table 1.3), whereas in oil palm hybrid breeding and micropropagation of planting material have contributed to the success of that crop (Basri et al. 2005). Other biotechnologies such as the production of doubled haploids in rapeseed (Chen et al. 1994) helped to accelerate the breeding progress. The perhaps most prominent examples of genetic engineering and molecular genetics in oilseeds are glyphosate tolerant soybean and the integrated soybean linkage map (Table 1.3), but genetic engineering also has a significant impact in oilseed rape (herbicide tolerance, engineering fatty acid biosynthesis pathways; Snowdon et al. 2007) and in cotton (*Bacillus thuringiensis* toxin mediated insect resistance; Christou et al. 2006) at present.

Table 1.3 Recent milestones in oil crop breeding with relevance to world oil crop production

Milestone	Year	Comment	References
Low erucic acid rapeseed	1959	Character found in German spring-type rapeseed cv. Liho, allowed for the development of high oil quality rapeseed cultivars and subsequent conversion to 'canola' quality cultivars in Canada and Europe in the 1970s	Stefansson et al. (1961)
Low glucosinolate rapeseed	1968	Found in the Polish spring-type rapeseed Bronowski, lead to release of low glucosinolate meal cultivars from the 1970s on (00-quality cultivars)	Josefsson and Appelqvist (1968) and Lein (1970)
Cms sunflower	1968	Source of cms from interspecific cross *Helianthus petiolaris* x *H. annuus*, introduction of hybrid cultivars in the 1970s	Leclercq (1969)
Cms rapeseed	1968	Cytoplasmic male sterility found in Japanese radish (Ogura-cms), later transferred to *Brassica napus* in France; cms in Chinese rapeseed cv. Polima; at present the two major cms sources for hybrid seed production in oilseed rape	Ogura (1968) and Fu (1981)
High oleic sunflower	1976	Induced mutant in sunflower variety VNIIMK 8 931, base of cultivar Pervenets, from which high oleic sunflower lines with over 90% oleic acid and high oleic hybrids were developed	Soldatov (1976) and Burton et al. (2004)
Low linolenic acid linseed	1986	Two induced mutants from cv. Glenelg with a combined linolenic acid content below 2% for linseed oil with improved oxidative stability	Green (1986)
Low linolenic soybean	1986	Three induced mutant allels with reduced linolenic acid content combined together for a 1% linolenic acid soybean oil with better stability and less trans fatty acid formation	Fehr et al. (1992) and Ross et al. (2000)
Glyphosate tolerant soybean	1996	Genetically engineered soybean (*Roundup Ready* soybean) containing EPSP synthase from *Agrobacterium* sp. with tolerance to the herbicide glyphosate, first commercially grown in 1996, reached over 50 million hectares in 2005	Padgette et al. (1995)
Integrated soybean linkage map	1999–2004	Integrated high-density soybean linkage map with more than 1800 genetic markers (mainly SSRs), useful in fine-mapping genes, map-based cloning or QTL analysis	Song et al. (2004)

1.4 Specific Breeding Objectives

Apart from agronomic performance and resistances, oil content of seed or fruit is the breeding objective economically most important to growers and primary processors. While breeding for oil quality, i.e. fatty acid composition, has been the subject of earlier reviews (e.g. Velasco and Fernández-Martínez 2002) and is being dealt with in dedicated crop chapters, various aspects of oil content will be presented here. Additionally, newly arising breeding objectives of altering seed composition for health and industrial applications will as well be covered within the present section.

1.4.1 Oil Content

1.4.1.1 Oil Bodies and the Cytology of Oil Content

Most storage lipids of oilseeds are composed of triacylglycerols which are synthesized during seed filling. De-novo biosynthesis of fatty acids has been well presented in earlier reviews (e.g. Stumpf 1989; Harwood and Page 1994), whereas newer reviews also cover the potentials of genetic engineering fatty acid synthesis in oil plants (Dyer and Mullen 2005; Napier 2007; Singh et al. 2005).

Fatty acid synthesis is located in plastids of cells in developing embryos, from where fatty acids activated with coenzyme A are released and accumulate in a compartment formed by layers of the endoplasmatic reticulum. Inside the endoplasmatic reticulum, fatty acids may undergo different modifications and finally are esterified to form triacylglycerols. Due to their hydrophobic nature, the accumulation of triacylglycerols results in bulges of the endoplasmatic reticulum from where oil bodies (oleosomes) are developing (Dyer and Mullen 2005) which are the microscopically visible oil bearing structures in mature seeds. Wältermann and Steinbüchel (2005) have illustrated the most widely accepted model of oil body formation in oilseeds (Fig. 1.2). From a bulge formed by triacylglycerols, an oil body is developing and surrounded by a monolayer of phospholipids, which is derived from the outer leaflet of the endoplasmatic reticulum. Subsequently, oleosine protein units are embedded in the phospholipid layer, and the oil body is separating from the endoplasmatic reticulum. The central domain of the oleosine protein is hydrophobic and therefore contacting the lipid matrix, whereas both termini are directed towards the cytoplasm. Oleosine proteins are present in all oilcrops with seeds undergoing dehydration during seed maturation but are not found in oil bodies of non-desiccating species such as olive, avocado or other tropical oil plants (Murphy and Vance 1999; Wältermann and Steinbüchel 2005). The size of oil bodies is dependent on the plant family; the diameter of oil bodies is between 0.3 and 0.8 μm in Brassicaceae oilseeds, between 0.5 and 2.0 μm in cotton, linseed and maize, and often above 2 μm in poppy, sunflower and sesame (Menge and Seehuber 1988; Tzen et al. 1993; Mantese et al. 2006);

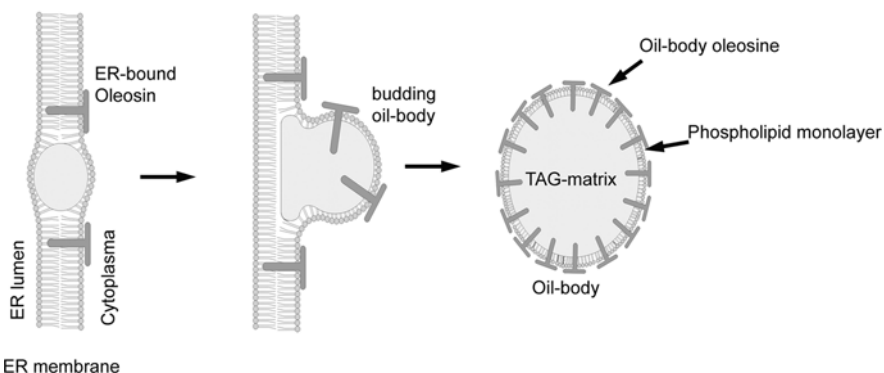## Oil-body formation in plant seeds

Fig. 1.2 Model of oil body development in oilseeds (from: Wältermann and Steinbüchel 2005; image kindly provided by the authors and used with permission from the American Society for Microbiology)

very large oil bodies (5–50 μm in diameter) are found in non-desiccating species (Murphy and Vance 1999). Oleosines regulate the size of oil bodies, they provide stability during desiccation and rehydration (Peng et al. 2003; Murphy and Vance 1999) and might be a target to genetic modification of lipid accumulation (Siloto et al. 2006) and subsequently oil content.

1.4.1.2 Botanical Features of Oil Content

Storage lipids are synthesized, stored and later re-metabolized in the same tissues within seeds or fruits, as they cannot be translocated within a plant because of their hydrophobic nature. As storage lipids are a seedlings major source of energy during germination and emergence, oil bodies are concentrated in embryonic tissues, i.e. parenchymatic cells of cotyledons and the embryo axis in oilseeds, or in the embryo (mainly the scutellum) of cereals, whereas endosperm tissue is devoid of storage lipids except for castor and few other species. The basis of genetic variation in oil content may therefore be variation in size or density of oil bodies, or variation in the proportion of embryonic tissue containing storage lipids relative to total seed or fruit mass which is most relevant in practical breeding for high oil content.

In sunflower, Mantese et al. (2006) investigated the temporal and histological patterns of lipid accumulation in genotypes with achene oil content ranging from 300–330 g/kg (low oil content) up to 450–550 g/kg (high oil content). They reported a tendency of a slightly larger oil body diameter in high oil content genotypes as compared to a low oil content genotype. While absolute oil mass of embryo was similar in high and low oil content genotypes, embryos of low oil genotypes were larger and thus had a lower density of oil bodies; moreover, in

cotyledon transsections of low oil genotypes a significantly larger cell area was occupied by protein bodies than in high oil genotypes.

While variation in size and density of oil bodies would contribute to the increase of oil content in small increments, major steps towards improvement of oil content have been achieved in many oilseeds through selection for reduced pericarp or thin testa mutants, as shown in Fig. 1.3 for sunflower, rapeseed, linseed, poppy and oil pumpkin, respectively.

In sunflower (Fig. 1.3A), confectionary genotypes have large achenes with a thick pericarp (hull) and an oil content of 200–300 g/kg, whereas oilseed
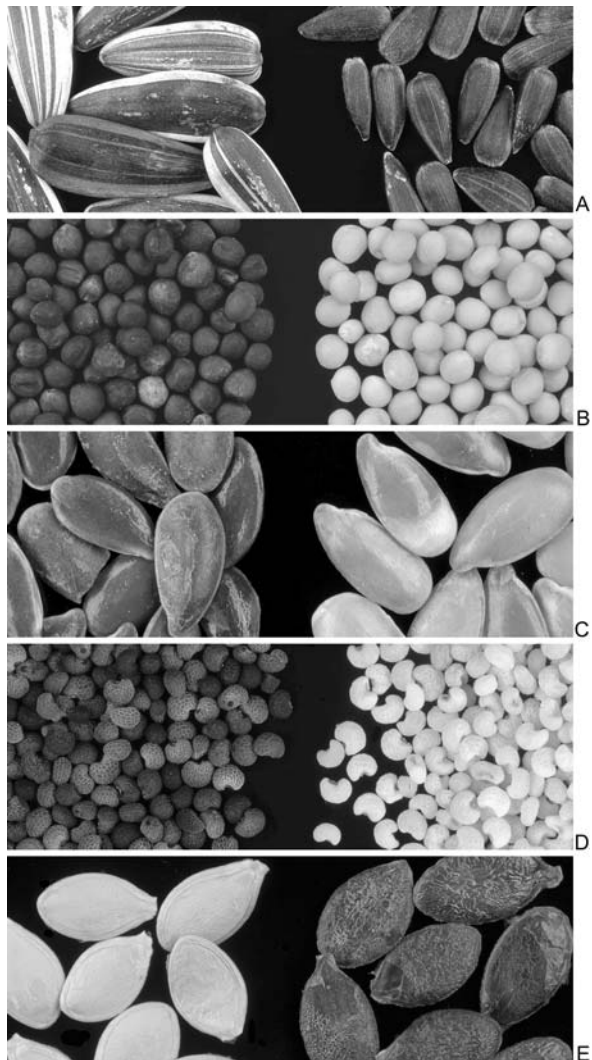
Fig. 1.3 Low (*left*) and high (*right*) oil content accessions of sunflower (**A**), oilseed rape (**B**), linseed (**C**), poppy (**D**) and oil pumpkin (**E**), respectively, differing in testa or pericarp thickness

cultivars have small achenes with thinner pericarp and an oil content of 400–550 g/kg (Mantese et al. 2006; Tang et al. 2006). It has been estimated that prior to 1970 two-thirds of increase in sunflower oil content resulted from a reduction of hull percentage and one-third from increases in kernel (seed) oil content, while over the last decades almost all of the increase in achene oil content has been achieved through an increase in kernel oil content (Miller and Fick 1997). In sunflower cultivars released in Argentine from 1930 to 1995, achene oil content was increased from 350 to 550 g/kg, while the ratio of kernel to achene weight was increased from 0.6 to 0.8 by selection for high oil content (López Pereira et al. 2000). In safflower, another Asteraceae oil crop, increases in oil content from 390 to 470 g/kg were similarly achieved through selection of achenes with thinner hulls (Knowles 1983).

In oilseed rape (Fig. 1.3B), the yellow seed character was introduced through resynthesis from a *Brassica rapa* source (Liu et al. 2005). The oil content of yellow-seeded lines with thin testa is 445 g/kg, whereas in comparable lines with black seeds an oil content of 399 g/kg has been reported (Badani et al. 2006b). Moreover, a major QTL for yellow seed colour was located in the same position as a QTL for reduced fibre content in different populations, and candidate genes for the yellow seed coat character have been proposed from the flavonoid biosynthesis pathway (Badani et al. 2006a), as the black seed colour of oilseed rape is made up by proanthocyanidins (condensed tannins).

In linseed, the yellow seed character (Fig. 1.3C) is known to be associated with higher oil content and larger seed weight, but has shown agronomic disadvantages such as a lower seed germination rate due to seed injury and a higher incidence of root rot (Culbertson et al. 1960; Bradley et al. 2007). In a large linseed germplasm collection, yellow seed is also associated with a significantly higher oil content and a larger seed weight than brown seed (Diederichsen and Raney 2006). The yellow seed character is controlled by several independent loci (Mittapalli and Rowland 2003), but causal relations for the association between yellow seed and high oil content are missing. Similar to other oilseeds, yellow seed colour in linseed may be due to a thinner seed coat of yellow seeds as compared to brown seeds. This view is also supported by the finding that linseed mucilage, which consists of polysaccharides located in the epidermis of the seed coat, is present in lower concentrations in yellow-seeded accessions than in brown-seeded ones (Diederichsen et al. 2006). Similarly, yellow or white seeds of poppy (Fig. 1.3D) are superior in oil content to blue seeds (Azcan et al. 2004; Bernáth 1998), which may as well be due to a thinner seed coat. In oil pumpkin (Fig. 1.3E), a mutation prohibiting the lignification of testa (hull) gave rise to utilising pumpkin as an oilseed crop instead as a vegetable in some Central European countries. Oil content of seeds with thick, lignified testa is below 300 g/kg, whereas oil content of cultivars utilizing the thin testa mutation (Styrian oil pumpkin cultivars) is between 350 and 500 g/kg (Idouraine et al. 1996; Murkovic et al. 1996). Lignification is controlled by one major gene with the thin testa character being recessive, and

several minor genes may cause partial lignification of thin testa genotypes (Teppner 2004; Zraidi et al. 2003).

In maize, 100 generations of selection for either high or low oil content yielded strains with an oil content of above 20% or below 1%, respectively, in the Illinois long-term selection experiment for oil and protein (Dudley and Lambert 2004). As the oil-bearing tissue of a maize seed is the embryo, high oil content was associated with an enlargement of the scutellum (Moose et al. 2004). In another maize synthetic (Lambert et al. 2004), high oil content was associated with a reduced starch content, whereas protein content remained unaffected; moreover, seed weight was reduced, and the proportion of the embryo was increased, while endosperm was decreased through selection for high oil content.

As cotyledons hold the oil-bearing tissues in most of the annual oilseeds, selection for cotyledon size, as demonstrated for *Brassica rapa* (Tel-Zur and Goldman 2007), might be an alternative route to improve seed oil content.

1.4.1.3 Genetics of Oil Content

Oil content is a quantitative character controlled by both the genetics of a cultivar and the environment. While the genetics of particular fatty acids had been well characterised in many oil crops, information about the inheritance of oil content was meagre for a long time. As an example, oil content of rapeseed was assumed to be controlled by mainly additive gene action with dominance being not significant and epistasis absent, and the number of genes involved in oil content was estimated to be lower than that for seed yield (Röbbelen and Thies 1980). During the last decade, however, mapping of quantitative trait loci (QTL) has brought more insight into the genetics of oil content and the functional principles behind particular QTL.

In soybean, 69 QTL for oil content were listed in the USDA SoyBase database (http://soybeanbreederstoolbox.org, October 2007) with most listings occurring for linkage groups A1, E, I and L. While most putative QTL do have small effects on oil content, one to four major QTL explain more than 10% of the phenotypic variation in different segregating populations (Lee et al. 2007). Three to eight QTL affecting oil content have also been reported for oilseed rape (Ecke et al. 1995; Burns et al. 2003) and other cruciferous oil crops such as *Brassica juncea* (Mahmood et al. 2006) or *Camelina sativa* (Gehringer et al. 2006), while one or two of up to 14 QTL explained more than 10% of oil content variation in oilseed rape (Delourme et al. 2006). Additive gene action has been proposed as the way of action for most QTL influencing oil content. In addition, Leon et al. (2003) reported dominant QTL effects for oil content in a bi-parental sunflower population. Digenic epistasis in oil content QTL has been described for oilseed rape (Zhao et al. 2005; Delourme et al. 2006), *Brassica juncea* (Mahmood et al. 2006), soybean (Lark et al. 1994), or oat (Zhu et al. 2004). In the maize long-term selection for oil and protein, large numbers of epistatically acting QTL for oil,

protein and starch content suggest the importance of epistasis for continuing selection response, particularly at lower levels of genetic variability (Dudley 2008).

The negative correlation between seed oil and protein content known from various oilseeds is also evident on the QTL level. QTL regions associated with oil content are frequently found to control protein as well and vice versa. This association may be due to tight linkage between oil and protein alleles in repulsion phase or to pleiotropic effects. In soybean, Lee et al. (2007) estimated that about 58% of oil content QTL are also associated with protein across a number of studies. Chung et al. (2003) described a QTL affecting oil content, protein content and grain yield of soybean and proposed the presence of a single QTL pleiotropically affecting both oil and protein. Nichols et al. (2006) narrowed down an oil and protein QTL region on soybean linkage group I to a 3-cM marker interval by fine-mapping, but still could not discriminate between either pleiotropy or close linkage of two loci affecting both traits. In oilseed rape, conditional mapping of QTL for oil content (Zhao et al. 2006) allowed for discriminating between true oil or protein QTL as well as the identification of additional oil QTL as compared to unconditional mapping.

Knowledge on the functional genetic mechanisms and regulatory metabolic factors controlling oil content is rather limited. In Brassicaceae, genes coding for erucic acid content may be considered 'candidate genes' for oil content, because the increased chain length and molecular weight of the erucic acid molecule (C22-body) as compared to C18-fatty acids causes an increase of total oil content. In oilseed rape, two QTL affecting oil content were at the same time associated with the two genes for erucic acid content (Ecke et al. 1995) in a cross between a high and a low erucic acid line. Subsequently, these genes were characterised as fatty acid elongase genes homologous to the *Arabidopsis FAE1* gene coding for the elongation of C18:1 (oleic acid) to C22:1 (erucic acid) in oilseed rape (Fourmann et al. 1998) and in *Brassica juncea* (Gupta et al. 2004). Contrary to erucic acid, palmitic acid (C16:0) has a lower molecular weight than C18-fatty acids, which may partly explain its negative correlation with oil content in oilseed rape, sunflower or soybean (Möllers and Schierholt 2002; Velasco et al. 2007; Hartmann et al. 1996). Differential gene expression studies using oilseed rape lines either high or low in oil revealed a major involvement of genes related to chloroplast function (photosynthesis) and sucrose metabolism in the expression of oil content (Li et al. 2006b). In oat, a plastidic acetyl-CoA carboxylase gene which catalyzes the initial step of de novo fatty acid synthesis was identified as a candidate gene strongly affecting oil content (Kianian et al. 1999). In an *Arabidopsis* transformation experiment, Jako et al. (2001) showed an increase in oil content through over-expression of a diacylglycerol acyltransferase. The metabolic complexity of oil content as a trait is also depicted on the proteomics level, where proteins related to energy, carbohydrate and amino acid metabolism are prominently expressed during

seed filling in oilseed rape and sunflower (Hajduch et al. 2006, 2007), which may contribute to identifying high level genes regulating oil content.

1.4.1.4 Breeding for Oil Content

Due to the diversity in reproductive systems of different oil crop species, cultivars can be ascribed to each of the four classical plant breeding categories, i.e. clones (olive, clonally propagated oil palm), allogamous populations (coconut, oil palm, castor, outcrossing brassicas), autogamous pure lines (soybean, linseed, peanut, poppy, sesame), and hybrids (sunflower, oilseed rape, oil palm, castor). As oil content is mainly controlled by additive gene action, the transition from open-pollinated or pure line types of cultivars to hybrids such as in sunflower or oilseed rape did not affect oil content to a great extent. In oilseed rape, considerable heterosis is present in grain yield, whereas heterosis is not relevant for oil content (Qian et al. 2007). In soybean, a strictly autogamous species, heterosis in testcrosses was high for maturity date, plant height and grain yield, but low for oil and protein content (Lewers et al. 1998). Thus, the additional gain from hybrid oil crop cultivars is primarily due to higher grain yield and a subsequent oil yield increase rather than a higher oil content. In oil palm, contrary to annual oilseeds, not fully inbred parents are used to produce heterogeneous hybrids; a transition from seed to clonal propagation through in vitro culture techniques would allow for the multiplication of high-yielding individual palm trees thus enhancing oil yield per unit area (Soh et al. 2003).

Oil crop breeding is a complex undertaking, and selection for oil content needs to be considered in the context of various other traits and their biological and economic values. In most breeding populations, the correlation between grain yield and oil content is positive or not significant, whereas the correlation between grain yield and protein content is negative. Additionally, correlations between oil content and time to flowering, seed weight or fatty acid concentrations may also be of relevance, particularly in recurrent selection for oil content or in trait introgression programs. Oil content usually appears as quantitative character with medium to high heritability in most populations, which ensures a significant selection response.

On the technical level of selection, efficient analytical tools such as nuclear magnetic resonance (NMR) or near-infrared reflectance spectroscopy (NIRS) have been established for non-destructive measurement of oil content. In addition to the widely used NIRS-based prediction of oil, protein and moisture content, NIRS calibrations have been developed for measuring amino and fatty acids (Pazdernik et al. 1997; Velasco et al. 1999; Kovalenko et al. 2006) and antinutritional components such as glucosinolates (Font et al. 2006) or phenolics (Velasco et al. 1998). Moreover, NIRS procedures for analyzing single seeds for oil content or fatty acid concentration (Jiang et al. 2007; Tillman et al. 2006; Velasco et al. 1999, 2004) have

been presented. Thus, high-throughput technologies for screening large numbers of samples for oil content and related quality features on the basis of individual seeds, individual plants (e.g. Fasoula and Boerma 2005) or small plots such as hill or single-row plots (Pazdernik et al. 1996) are available for selection and quality monitoring at various stages of breeding programs.

1.4.2 Altered Seed Composition for Health and Industrial Applications

Besides altering the relative amounts of oil and protein in the seed of oil crops, considerable efforts have been made by oil crop breeders to alter the fatty acid profile of the oil. There are five major fatty acids found in most of the annual oilseeds, palmitic, C16:0; stearic, C18:0; oleic, 18:1; linoleic, C18:2; and linolenic acid, C18:3. Additional fatty acids are found in specific oil crops such as erucic acid C22:1 in oilseed rape or ricinoleic in castor bean. The manipulation of relative proportion of the fatty acids has often been practised to address issues of the healthfulness of oil by reducing the saturated fats (e.g. C16:0) or increasing the levels of monounsaturated fats such as C18:1. Mutagenesis, natural variation, recurrent selection and genetic engineering have been the approaches that have been used by oil crop researchers over the past several decades. It is noted that, although some of these EMS-derived mutations such as the low linolenic have been developed more than 30 years ago (Rajcan et al. 2005; Röbbelen and Nitsch 1975; Fehr 2007), many of them have gained in market importance only recently. The main interest in the low linolenic acid oils (with less than 3% of C18:3) is due to the lack of need for partial hydrogenation, which in high C18:3 oils results in the production of the by-product trans-fatty acids that have been shown as more detrimental to heart health than saturated fat. The low C18:3 oil only became economically attractive when the Food and Drug Administration regulated the compulsory food labelling of trans fat content in the USA, which in turn prompted considerable interest and market demand by food manufacturers. Similarly, while high oleic sunflower mutants have been available for a long time, the mid-oleic NuSun sunflower only gained market popularity when such hybrids developed by the USDA (Miller and Vick 2002) became readily available and a solid customer base had been generated. It would appear that healthier oils that have been developed as result of mutagenesis and selection work by oil crop breeders often have to wait until the market is ready for them, which sometimes political decisions rather than biological or health considerations. It is reasonable to expect that other fatty acid profiles that could address health issues, stability of oil or provide feedstock for specific food or industrial products will gain market acceptance after years of selection work by oil crop breeders. Some of the novel profiles that may be of interest in the future could be a high stearic oil for margarine production, low palmitic

combined with low linolenic for a healthier and more stable oil, high palmitic oil for biodiesel engines, high polyunsaturates for polyol and other biomaterials industries, etc.

Numerous clinical studies have been conducted that confirm the health benefits of non-oil nutritional components of oil crop seeds such as soybean protein (or peptides as part of it), or nutraceutical components such as glucosinolates of oilseed rape, lignan of linseed, isoflavones and saponins of soybean. The effects of these compounds include a reduction of heart and coronary disease, osteoporosis, certain types of cancer, e.g. prostate and breast cancer, and menopausal symptoms in women. These findings have opened a new avenue of research for plant breeders and geneticists in their efforts to widen the array of uses for oil crops and/or their products in support of the nutritional and nutraceutical industries. Recent efforts by plant breeders have concentrated around improving their understanding of the genetic control of the already recognized functional food components such as isoflavones (Primomo et al. 2005), tocopherols (Wohleser 2007) or saponins (Rupasinghe et al. 2003). The options for breeders and industry are plentiful and seemingly limited only by the type and variation of compounds in the seeds as well as market considerations. Faced with stagnating commodity prices, oil crop breeders are looking toward nutraceuticals, biobased industrial feedstocks and biofuels as means to alleviate low and fluctuating profitability in agriculture. The development of value-added oil crops and products for the current and emerging niche markets appears an attractive alternative for breeders and producers.

1.5 Perspectives in Oil Crop Breeding

1.5.1 Technology

On the level of technology, new tools are on the horizon which may affect strategies and efficiency of oil crop breeding in the near future.

Mutation induction is a well-established technique with special relevance to oilseed crops: At present, numerous mutants induced and isolated decades ago are being incorporated in widely grown cultivars to improve their fatty acid composition and nutritional value (Bhatia et al. 1999); while phenotyping large populations for a desired mutation is a major bottleneck in mutation breeding programs, new approaches such as TILLING combine conventional mutation induction and PCR-based high throughput reverse genetics mutant identification (Henikoff et al. 2004; Cooper et al. 2008); thus, numerous new alleles could be isolated at a given gene locus and phenotyped for their usefulness to breeding thereafter.

Although genetic markers are widely applied in oil crop breeding at present, their utilization could be further stimulated by the wider availability of high-throughput methods, SNP-markers and other techniques. Monitoring of

genetic diversity, prediction of hybrid performance, QTL analysis, marker assisted introgression and transfer of specific alleles, or marker assisted selection for traits difficult to phenotype such as disease/pest resistance, seed quality or health components would undoubtedly increase the efficiency of oil crop breeding programs.

Other biotechnologies such as doubled-haploids for rapid recovery of homozygous recombinants or micropropagation of superior planting materials in perennial crops such as the oil palm are well established techniques in particular applications. However, while doubled-haploids are widely used in cereals, oilseed rape and numerous other crops (Forster et al. 2007), species such as the soybean are considered recalcitrant to haploid production, and almost no research is devoted to that area despite its huge potential.

Oil crops are the earliest and major group of genetically modified (GM) crops grown world-wide: The total acreage of GM crops reached over 114 million hectares in 2007 (James 2007) with soybean, maize, cotton and canola being the lead crops, and herbicide tolerance and insect resistance being the major traits targeted. Despite of the benefits attributed to biotech crops, consumer acceptance of GM crops and products is low; wider evidence on crop biosafety and the development of 'second generation biotech crops' (Napier 2007) with new traits beneficial both to the environment and to consumers as well as farmers are considered crucial with respect to public opinion on GM crops. Meanwhile, separate breeding programs are maintained in parallel for GM and GM-free cultivar development in some crops to serve the different market requirements.

1.5.2 Biology

On the level of biology, issues such as maintenance of genetic diversity, the development of new oil crops, stability of quality features in crop harvests, or adaptation of oil crops to particular growing conditions such as organic farming may gain importance for future oil crop breeding.

Genetic diversity is comparatively low in most oil crops due to their specific crop and breeding histories. While this may not be a problem for immediate breeding work, it could negatively affect the long-term breeding progress, impede the adaptation to new environments or enhance crop vulnerability with respect to epidemic pests or diseases. Introgression of wild type alleles by backcrossing is efficient with respect to a specific target character such as the protein content of soybean (Sebolt et al. 2000), but will not increase overall genetic diversity. Wide crosses, recurrent programs, pre-breeding on a wild species level or hybridizations between wild and domesticated species for transferring complex characteristics such as the outstandingly high oil content found in some wild sunflower species (Seiler 2007) are long-term concepts for

increasing diversity while being challenged by the need to maintain an acceptable level of agronomic performance.

Instead of transferring various traits into few established oil crop species, development of new crops with specific qualities or the revival of forgotten and underutilized species represent alternative strategies with the long-term goal of enhancing agro-biodiversity at large. While various different species of that kind have been discussed during the past decades, few have appeared on the crop production and marketing level so far, and considerable research input may be needed for others.

1.5.3 Utilization

Oil crop utilization perspectives are most difficult to predict due to increasing market volatility of agricultural commodities in general and a high level of substitution among oils of different species.

Nevertheless, oil crop breeding for product quality features has been successful in generating diversified markets for vegetable oils. In food utilization of oils, diversification of products through breeding is constantly producing new features such as improved shelf life, suitability for frying, reduction of trans-fatty acid generation during hydrogenation, human blood cholesterol reducing properties, anti-oxidant and various other health promoting properties. In non-food utilization, demands from oleochemistry have prompted for the development of crops producing long- or mid-chain fatty acids as well as hydroxy and epoxy fatty acids, while many other properties may be realized by genetic engineering approaches (e.g. Dyer and Mullen 2005). Demands for energetic utilization of vegetable oils, e.g. for bio-diesel production, have been less specific in terms of oil quality so far, and the future position of bio-diesel production is unpredictable because of the rise of ethanol producing crops as well as high competition for land due to increasing world market prices for food and agricultural commodities. Apart from improving oil qualities itself, significant plant breeding efforts will also have to be devoted to the wide range of possible by-products of oil crop production such as protein meals for feeding or other industrial applications, as successful marketing of by-products has become a key factor for economic success of oil crop processing.

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