

Oil Crops

HANDBOOK OF PLANT BREEDING

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Volume 1

Vegetables I: Asteraceae, Brassicaceae, Chenopodiaceae, and Cucurbitaceae

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Volume 2

Vegetables II: Fabaceae, Liliaceae, Solanaceae and Umbelliferae

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Volume 3

Cereals

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Volume 4

Oil Crops

Edited by Johann Vollmann and Istvan Rajcan

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Editors

Oil Crops

 Springer

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Foreword

When one is privileged to participate long enough in a professional capacity, certain trends may be observed in the dynamics of how challenges are met or how problems are solved. Agricultural research is no exception in view of how the plant sciences have moved forward in the past 30 years. For example, the once grand but now nearly forgotten art of whole plant physiology has given way almost completely to the more sophisticated realm of molecular biology. What once was the *American Society of Plant Physiologists*' is now the *American Society of Plant Molecular Biology*; a democratic decision to indemnify efforts to go beyond the limits of the classical science and actually begin to understand the underlying biological basis for genetic regulation of metabolic mechanisms in plants. Yet, as new technologies open windows of light on the inner workings of biological processes, one might reminisce with faint nostalgia on days long past when the artisans of plant physiology, biochemistry, analytical chemistry and other scientific disciplines ebbed and waned in prominence.

No intentional reference is made here regarding Darwinism; the plant sciences always have been extremely competitive. Technology is pivotal. Those who develop and/or implement innovative concepts typically are regarded as leaders in their respective fields. Each positive incremental step helps bring recognition and the impetus to push a scientific discipline forward with timely approaches to address relevant opportunities.

So, it might be interesting to know how those skilled in the art of statistical analysis and the field of classical plant quantitative genetics are coping with the intensifying research emphasis on biotechnology, genomics, proteomics, and the like. After all, high-throughput whole genome sequence analyses and advanced bioinformatic resources for gene discovery will soon render the characterization of haplotypes, in entire germplasm collections and among progeny of segregating breeding populations, a routine event. Will the day come when breeders are told which parents to mate for a particular objective? No doubt an interesting dialog will ensue, but by-in-large taking the mystery out of plant science should be viewed as a good thing for all the constituent professions.

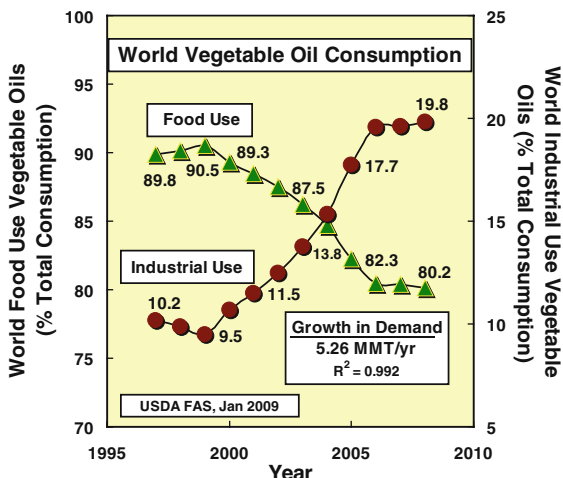
Is a physician's ability impaired by the advent of new diagnostic technologies and a more effective range of pharmaceuticals? Even a NASCAR driver

benefits from all of the computerized signals that monitor every aspect of a race cars performance. So, it is the same for breeding and quantitative genetics. Knowledge and skill are still needed to associate phenotypic traits with a haplotype. Ability is still required to reduce all of these ancillary tools to successful practice. Thus, the renaissance that is underway will position plant quantitative genetics to emerge with increased capacity to provide solutions to major problems and address the needs of world agriculture in a timely manner.

What are those needs with regard to oilseeds? Based on world production, USDA Foreign Agricultural Service reports show that soybean (56.0%), rapeseed (13.4%), cottonseed (10.1%), peanut (8.1%), sunflower (8.0%), and palm plus palm kernel (2.8%) are the major oilseed crops. These commodities represent essentially the entire commercial source of vegetable protein and oil. Annual world consumption of vegetable oil has averaged about 90.0% of total vegetable oil supply since 1997, leaving on average enough end-of-year stocks for about a 30-day buffer; whereas annual world use of oilseed meal has averaged about 95.7% of total supply, leaving on average a carryover equivalent to about an 11-day cushion of meal. These trends suggest that consumer demand for these products is limited only by availability, and that any natural disaster that may limit oilseed production could severely compromise the global food chain.

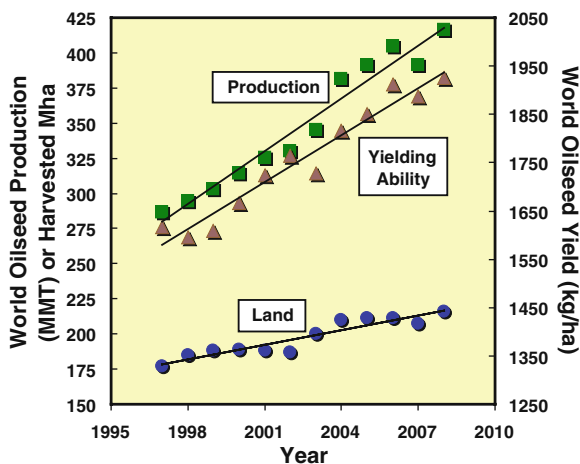
Although crushing capacity has expanded significantly in the US and abroad, the proportion crushed has averaged about 81% of total world oilseed production for decades. Considering the need to service export markets, a significant escalation of oilseed crush levels to increase the supply of meal and oil is unlikely. Hence, the greatest need that oilseed breeders face is simply to ensure a sufficient oilseed supply to meet the elastic demand for protein and oil; which on its own merit is a major contribution to alleviate world hunger.

However in recent years, a number of constraints have emerged that could mitigate efforts to increase global oilseed production for food use. The most prominent factor is renewed interest in vegetable oil as a source of biodiesel fuel. This concern recognizes that annual global vegetable oil resources could barely make a dent in the demand for energy. However, as shown in the adjacent figure, the market forces that direct food and industrial demand for



vegetable oils appear to have established a temporary equilibrium at about 80% (food):20% (industrial). Perhaps this will hold long enough for appropriate adjustments in markets for oilseed products. In addition, breeding efforts to develop varieties for commercial production of industrial oilseeds like lesquerella, cuphea and various non-food biotech innovations should help stabilize this situation.

Achieving greater genetic gain for oilseed productivity may be a lesser priority to some in the oilseed industry who subscribe to the paradigm that farmers will expand harvested area to increase the production of oilseeds. However, in view of escalating costs of oilseed production and competition for land from non-oilseed crops, the flexibility of countries to devote more agricultural resources to oilseeds remains to be seen. At this time, the rate of increase in harvested area since 1997 may be the best estimate of how much more harvested area might be available in future years. Regression analysis of these data in the figure below estimates the rate of increase at +3.45 Mha per year (R^2 , 0.88). Assuming continuation of a linear trend, there might be a total of 258 Mha in global oilseed production in the year 2020, an increase of about 41 Mha over the level in 2008. One must wonder if this would be enough to make a significant difference.



Questions about future levels of harvested area place more pressure on the remaining variable in the yield equation for increased production. Regression analysis of these data in the adjacent figure estimates the rate of increase in world oilseed production at +12.5 MMT per year (R^2 , 0.96). Assuming continuation of a linear trend, there might be a total of 704 MMT in global oilseed production

in the year 2020, an increase of about 196 MMT over the level in 2008. Again, using simple arithmetic and assuming 258 Mha would be available to harvest, the world average oilseed yield in 2020 could be about 2.7 MT per ha (or 3.2 MT per ha if no additional land became available). Reaching that plateau would require a 40% increase in average total oilseed yield (70% without the projected increase in land) given an average global oilseed yield of 1.9 MT per ha in 2008.

In the past decade, average global oilseed yield has increased only 20%. Therefore, it appears that a great deal is riding on the development and application of oilseed biotechnology and genomics in the next decade. These technologies should enable quantum leaps in genetic progress. However, it all

depends upon a renaissance in quantitative genetics and the application of those technologies now and by the next generation of public and private oilseed breeders. Perhaps, it would be wise to redouble the effort to train and deploy that future workforce now.

Raleigh, North Carolina

Richard F. Wilson

Preface

Vegetable oils have gained in importance during the past few decades resulting in the doubling of the world oil crop production in the last 25 years. Oil crops have been increasingly used as raw materials for food, livestock feed and non-food industrial applications. Plant breeding has played an essential role in supporting these developments: Breeding for higher yield and oil content allowed for an increase in oil production per unit area, whereas breeding for better oil quality has improved both the human health value of vegetable oils as well as the suitability of particular oils in specific industrial applications. Moreover, newly developed unique oil qualities are opening new opportunities in agricultural production and processing.

Cereals, legumes or forages each represent relatively homogeneous groups of crops belonging to one or a few plant families with similar botanical characteristics in which comparable breeding procedures could be used. In contrast, oil crop species have been developed in various botanical families from both the monocots and dicots. Thus, oil crops are a highly diverse set of species from short season annuals to perennials with a life span of over 2000 years. Consequently, breeding methods used for oil crop improvement include clonal breeding, pure line breeding, improvement of open-pollinated populations as well as hybrid breeding. In particular, the breeding procedures and techniques include almost every activity from simple mass selection and hybridization to specialized biotechnologies such as *in vitro* propagation or genetic engineering. Despite the differences at the species and breeding levels, some major breeding goals are remarkably similar, which justifies treating them in one volume such as: high oil content, altering fatty acid composition to suit the needs for either human consumption or non-food utilization, and a high quality of by-products. In addition, issues such as the biosynthetic pathways of particular fatty acids and their manipulation, QTL analysis for quality characters, genetic diversity, or oil and fatty acid analytics during selection are of common interest to all oil crop breeders. Therefore, this volume was prepared as a state-of-the-art compilation and a major reference text on oil crop breeding, which has been lacking for several decades. While the information accumulated in this volume is of primary interest to plant breeders, valuable insights are also offered to agronomists, molecular biologists, physiologists,

plant pathologists, food scientists and university scholars from the comparative treatment of various oil crop species.

Apart from an introductory chapter on oil crop breeding and a chapter highlighting genetic modification of vegetable oils, this volume presents 17 chapters devoted to breeding of particular oil crop species. Oil crops with world-wide distribution such as soybean, sunflower, oilseed rape and related brassicas are presented side-by-side with tropical and subtropical species such as cotton seed, peanut or castor, the perennials oil palm, coconut and olive, minor oil crops of regional importance such as safflower, poppy, oil pumpkin or maize, and new oil crops such as lesquerella and cuphea. Origin and domestication, varietal groups, genetic resources, major achievements and current breeding goals, breeding methods, techniques and biotechnologies, and seed production are addressed depending on their relevance in a particular crop.

Each crop chapter has been written by outstanding experts in their respective fields. Whenever possible authors from different institutions or countries worked together on particular chapters, which contributed to broadened and well-balanced views on particular species or topics.

The editors acknowledge the excellent contributions of all chapter authors who devoted much time and effort in delivering their part to this high quality volume. The editors extend heartfelt thanks to the staff at Springer, particularly to Hannah Schorr and Jinnie Kim, for their highly professional support during all stages of the publishing process. Moreover, the editors would like to thank Editors-in-chief of the Springer series *Handbook of Plant Breeding*, Professors Jaime Prohens, Fernando Nuez and Marcelo Carena, both for considering a volume exclusively devoted to oil crops and for their helpful input throughout the preparation of this volume.

Vienna, Austria
Guelph, ON, Canada

Johann Vollmann
Istvan Rajcan

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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

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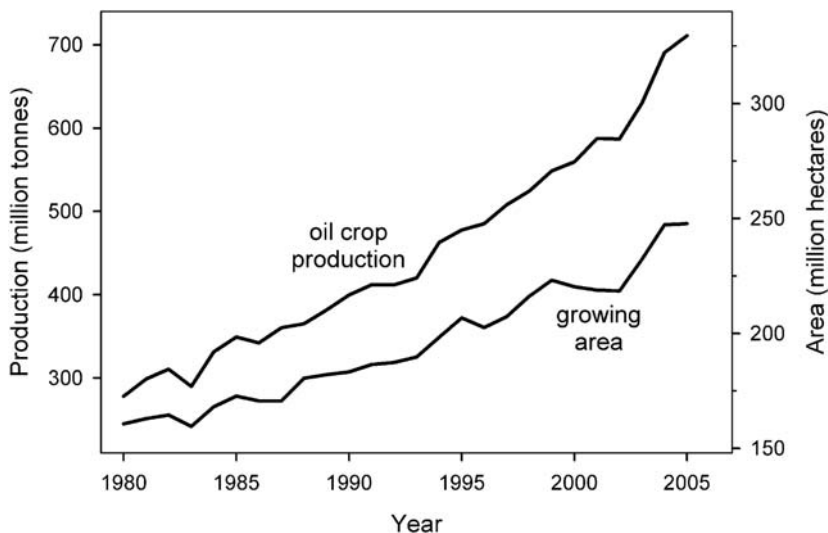


Fig. 1.1 Global oil crop production and acreage from 1980 to 2005 (FAOSTAT 2007)

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

Species	Area in hectares		Change (in %)	Average yield in kg/ha		Change (in %)
	1980	2005		1979–1981	2002–2004	
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 sub-continent 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 independent 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 (SINGER)	<i>Triticum</i> sp.	114, 721	Soybean ¹	15, 904	
	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	<i>Triticum</i> 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	<i>Triticum</i> sp.	55, 942	Soybean	19, 277
Plant Germplasm System	Barley	28, 438	Peanut	6, 831	
	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	
	<i>Phaseolus</i> sp.	14, 928	Sesame	1, 226	
	Chickpea	6, 019	Castor	1, 043	
		USDA total	477, 077		

¹World 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 gene pools. 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 <i>Helianthus petiolaris</i> x <i>H. annuus</i> , introduction of hybrid cultivars in the 1970s	Leclercq (1969)
Cms rapeseed	1968	Cytoplasmic male sterility found in Japanese radish (Ogura-cms), later transferred to <i>Brassica napus</i> 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 alleles 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 (<i>Roundup Ready</i> soybean) containing EPSP synthase from <i>Agrobacterium</i> sp. with tolerance to the herbicide glyphosate, first commercially grown in 1996, reached over 50 million hectares in 2005	Padgett 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

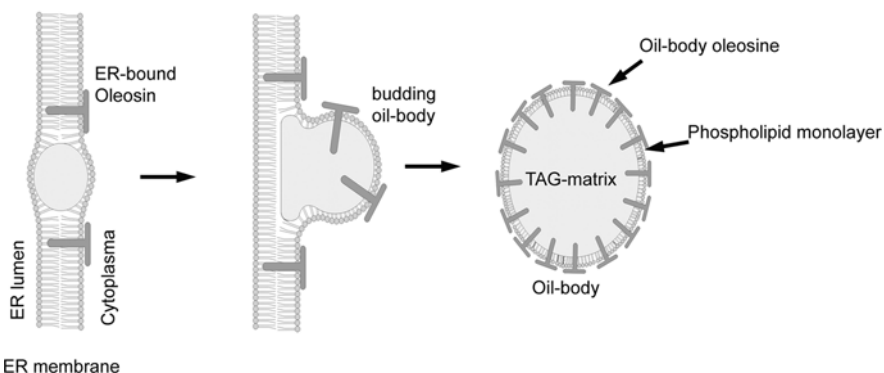


Fig. 1.2 Model of oil body development in oilseeds (from: Wältermann and Steinbüchel 2005; image kindly provided by the authors and used with permission from the American Society for Microbiology)

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 content 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

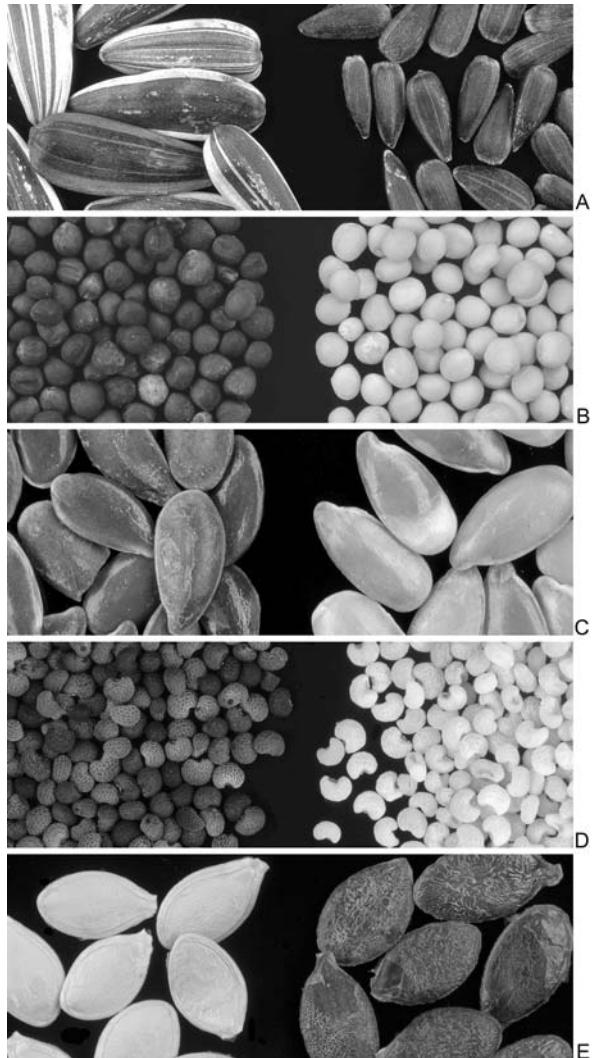


Fig. 1.3 Low (*left*) and high (*right*) oil content accessions of sunflower (A), oilseed rape (B), linseed (C), poppy (D) and oil pumpkin (E), respectively, differing in testa or pericarp thickness