

# Chapter 2

## Brassicaceae in Agriculture

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**Abstract** This chapter reviews the agricultural role of the Brassicaceae (Cruciferae) or mustard family. The family includes many economically important edible and industrial oilseed, vegetable, condiment, and fodder crop, such as. It also includes the molecular plant model, such as *Arabidopsis thaliana*. Current crops are reviewed and new and underutilized crucifer crop species discussed. Proposed new uses for these crops, such as biofuel platforms or green manure covers or biofumigants, are also briefly reviewed. The family also contains a rich source of agronomic and economic traits in its highly diverse wild germplasm. Traits discussed in this chapter include morphological and chemical traits; physiological traits such as C<sub>3</sub>–C<sub>4</sub> photosynthesis, cytoplasmic male sterility, apomixis, and regeneration or transformation ability; and tolerances to various stresses such as salt, heavy metals, cold, drought, herbicides, diseases, insect, and nematode pests. These traits are of potential value in crop improvement programs and many wild crucifers now serve as model species in their study.

**Keywords** Brassicaceae · Cruciferae · Wild germplasm · Agronomic and economic trait sources

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## 2.1 Introduction

The Brassicaceae (Cruciferae) or mustard family includes many economically important edible and industrial oilseed, vegetable, condiment, and fodder crop species. The most important edible oil crop is canola or oilseed rape (*Brassica napus*); while mustard condiment crops include: *Brassica juncea* – Indian mustard and *Sinapis alba* – white mustard. Many Brassica species are also important vegetable crops, e.g., cole crops (*Brassica oleracea*). Several species, e.g., *Brassica carinata*, *Camelina sativa*, *Crambe abyssinica*, *Eruca vesicaria*, have potential as new edible oil/protein crops, biodiesel fuel crops, or platforms for bioproducts or molecular farming (Gugel and Falk 2006, Warwick and Gugel 2003, Warwick et al. 2006b, 2007a). The family is also known for its more than 120 weedy species, several of which are important cosmopolitan agricultural weeds (e.g., wild mustard (*Sinapis arvensis*)), stinkweed (*Thlaspi arvense*) while others form crop-weed complexes (e.g., *Raphanus sativus*–*Raphanus raphanistrum*). Several of these related weeds are able to exchange genes, including transgenes, with crops under natural field conditions (reviewed in Warwick et al. 2003, 2008b), potentially increasing weediness. Several representatives of the family have achieved the well-accepted status of “model organisms” for genomic studies, including *Arabidopsis thaliana* and *Brassica* spp. (Parkin et al. 2005), and other model species have been recently proposed, e.g., *Capsella* and *Arabis* (Koch and Kiefer 2005, Schranz et al. 2006b).

Related wild or lesser known crop species in the family represent virtually untapped and unlimited genetic sources of agronomic and economic traits (Warwick et al. 2009) and several Brassicaceae biodiversity databases are available to guide genomic researchers, genetic resource managers and plant breeders in the selection of appropriate taxa for phylogenetic, genomic and agronomic screening studies. These include the following: a species checklist of 338 genera and 3,709 species currently recognized in the family (Warwick et al. 2006a); a chromosome number index (Warwick and Al-Shehbaz 2006) reporting on over 9,000 chromosome counts from 232 genera and 1,558 species; a summary of all trait genetic studies (Séguin-Swartz et al. 1997); and a guide to the cytodeme status, chromosome number, hybridization potential, life cycle, growth form, ecology, and geographical distribution of all species in the tribe Brassiceae (Warwick et al. 2009).

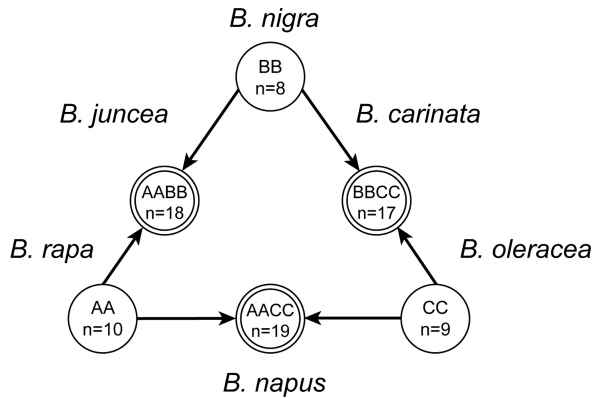
A comprehensive molecular phylogenetic overview of the Brassicaceae is now emerging (Bailey et al. 2006, Warwick et al. 2007b, 2008c). These studies support the division of the family into 34 tribes (Al-Shehbaz et al. 2006, Al-Shehbaz and Warwick 2007, German and Al-Shehbaz 2008). A phylogenetic framework is essential for comparative genomic studies within the Brassicaceae and for the identification of closely related species that could serve as agronomic and economic trait sources. Knowledge of natural phylogenetic relationships allows estimates of derived versus ancestral states for various morphological, cytological, and biochemical characters and estimates of evolutionary distances and divergence times between groups (Lysak and Lexer 2006, Schranz et al. 2006b). For example, after the major split from the basal tribe Aethionemeae, there would appear to be a rapid radiation event in the family at ca. 24 Myr leading to the various tribal lineages including the split between two of the best studied genera *Arabidopsis* (tribe Arabideae) and *Brassica* (tribe Brassiceae).

## 2.2 Taxonomy and Genetic Relationships of *Brassica* Crop Species

The genus *Brassica* belongs to the Brassiceae. A natural tribe of ca. 50 genera, it is distinguished by its two-segmented fruit and unique conduplicate arrangement of the cotyledons or first leaves in the seed (reviewed in Gómez-Campo 1980, 1999, Warwick and Sauder 2005). Molecular and hybridization data now indicate that close relatives of the *Brassica* crop species also include species currently placed in separate genera in three different subtribes – the Brassicinae, Raphaninae, and Moricandiinae. This group of closely related species corresponds closely to the *Brassica* coenospecies, defined by Harberd (1972) as the “group of wild species sufficiently related to the six cultivated species of *Brassica* to be potentially capable of experimental hybridization with them.” The most closely related genera to the *Brassica* crop species include: *Ceratocnemum*, *Coincya*, *Cordyllocarpus*, *Diploaxis*, *Enarthrocarpus*, *Eruca*, *Erucastrum*, *Guiraoa*, *Hemicrambe*, *Hirschfeldia*, *Kremeriella*, *Moricandia*, *Morisia*, *Muricaria*, *Orychophragmus*, *Otocarpus*, *Raffanaldia*, *Raphanus*, *Rapistrum*, *Rytidocarpus*, *Sinapidendron*, *Sinapis*, and *Trachystoma*.

An old world genus, *Brassica* includes about 35 species of mostly annual herbs, with some perennial herbs and small shrubs. Cultivated brassicas are represented by six interrelated species, three of which are diploids – *Brassica nigra* ( $2n = 16$ , genome BB), *B. oleracea* ( $2n = 18$ , genome CC), and *Brassica rapa* ( $2n = 20$ , AA) and three amphidiploid derivatives – *B. carinata* ( $2n = 34$ , BBCC), *B. juncea* ( $2n = 36$ , AABB), and *B. napus* ( $2n = 38$ , AACC). The latter three are derived by hybridization and polyploidization of two of the diploid taxa. The genomic relationships of the six *Brassica* crop species, known as the triangle of U (1935) and shown in Fig. 2.1, has been confirmed by chromosome pairing and artificial synthesis of the amphidiploids, nuclear DNA content and sequence analysis, and the use of genome-specific markers. Both nuclear DNA sequence data and chloroplast restriction site data, suggest separate evolutionary pathways, with *B. rapa* and *B. oleracea* (including wild CC genome species) assigned to one group with *Diplotaxis eruroides* ( $n = 7$ ) or a close relative as the primary progenitor, and *B. nigra* assigned to a second group with *S. arvensis* ( $n = 9$ ) or a close relative as the primary progenitor species (Warwick and Black 1993, Warwick and Sauder 2005).

**Fig. 2.1** Triangle of U showing the genetic relationships among the six cultivated species of *Brassica*. Adapted from U (1935)



*Brassica* species are believed to have originated in the Mediterranean-Middle Eastern area with a secondary center of origin and differentiation of *B. rapa* and *B. juncea* in China. Tremendous morphological variability is observed in the many subspecies, botanical varieties, and cultivar groups of *B. oleracea*, *B. rapa*, and *B. juncea*. Numerous parallel vegetable forms have been selected, and the three species have differentiated historically along similar lines (Prakash and Hinata 1980). The crop brassicas demonstrate great genetic and morphological diversity and plants yield edible roots, stems, leaves, buds, flowers, and seeds. In addition, some of the types are used as forage, sources of oil, or even ornamentals.

### 2.2.1 *B. oleracea*

Designated as cole crops, this species has a great diversity of morphotypes. *B. oleracea* is a member of the CC genome complex, which includes a

number of interfertile Mediterranean species (*Brassica cretica*, *Brassica hilarionis*, *Brassica incana*, *Brassica insularis*, *Brassica macrocarpa*, *Brassica montana*, *Brassica rupestris*, and *Brassica villosa*), wild *B. oleracea* from coastal areas of western Europe, and *Brassica bourgeauii* from the Canary Islands.

The most important *B. oleracea* crops (taxonomic varieties in parentheses) are kales (var. *viridis*, var. *costata*, var. *medullosa*, var. *sabellica*) which develop a strong main stem and are used for their edible foliage; branching bush kales (var. *ramosa*), formerly much cultivated for their edible foliage; cabbages (var. *capitata* and var. *sabauda*) characterized by the formation of heads formed from tightly packed leaves; brussels sprouts (var. *gemmifera*) in which axillary buds form edible heads of tightly packed leaves; kohlrabi (var. *gongyloides*) cultivated for its above ground thickened stem; cauliflower and broccoli (var. *botrytis* and var. *italica*) cultivated for their thickened edible inflorescences; and chinese kale (var. *alboglabra*), a cultivated white-flowering crop grown in China, generally assumed to be an ancient import from the Mediterranean region and often treated as a separate species *Brassica alboglabra*.

Various origins of the different cultivated types have been proposed, including a single origin of all types from wild *B. oleracea* from western Europe, triple and even multiple origins involving related wild species of the CC complex. Molecular studies (Song et al. 1990) supported a monophyletic origin for the cultivated morphotypes of *B. oleracea* from a progenitor that was similar to wild *B. oleracea* consistent with morphological evidence that the earliest cultivated *B. oleracea* was probably a leafy kale from which the other cultivated types originated. Molecular evidence further suggested that selective introgression from other wild CC cytodeme members, *B. insularis* and *B. incana*, may also have contributed to the variability of cultivated *B. oleracea*.

### 2.2.2 *B. rapa*

*B. rapa* is highly polymorphic and contains many crops that have been domesticated over a long period in Europe as well as in Asia. Little is known about its true existence in the wild, plants found under natural conditions seem to be escapes from cultivation (spp. *sylvestris*). *B. rapa* is most closely related to *B. oleracea* and both have arisen from ancestral members of the C genome cytodeme.

The most important crops in *B. rapa* (subspecies in parentheses) are vegetable turnip (spp. *rapa*); fodder turnip (spp. *rapa*) which forms a leaf rosette and/or a turnip; turnip rape (spp. *oleifera*) and toria (spp. *dichotoma*), black seeded with annual spring and biennial winter types, used for oil extraction; yellow sarson (spp. *trilocularis*), annual, yellow seeded, used for oil extraction; Chinese cabbage (spp. *pekinensis*), Asiatic heading vegetable, with petioles winged; Pak choi (subsp. *chinensis*), a Chinese non-heading leaf vegetable, with petioles fleshy but not winged; Mizuma, mibuna, komatsuna, or leaf turnip (spp. *nipposinica*), Asiatic non-heading leafy vegetable, with many tillers and either pinnate (mizuma) or entire leaves (mibuna); broad-beak mustard or Chinese savoy (spp. *narinosa*), an Asiatic

non-heading leafy vegetable, flat rosette of many small leaves; and broccoletto (formerly treated as *Brassica ruvo*, assigned to spp. *oleifera*), European vegetable with an enlarged, compact inflorescence. Most of the above-mentioned crops were described as separate species, but they readily intercross and hence belong to the  $n = 10$  *B. rapa* cytodeme.

Various data (morphology, geographical distribution, isozymes, nuclear RFLPs, and AFLPs) have indicated a division of *B. rapa* into two main groups, perhaps corresponding to two independent centers of origin (Song et al. 1990, Warwick et al. 2008a). The primary center is Europe and includes turnip and turnip rape from which Asian sarson and toria types were derived. The second center is in China and contains the various Asian vegetables indicated above.

### 2.2.3 *B. nigra*

Black mustard, once widely grown as a condiment mustard, has largely been replaced by *B. juncea*. It is still grown as a condiment crop in parts of Asia. Although little information is available, the occurrence of land races in Europe, the Mediterranean, and the Ethiopian plateau indicates that *B. nigra* probably originated in central and southern Europe. It is presumed to have been introduced into India relatively recently. *B. nigra*, has evolved separately from the other two diploid *Brassica* species, and numerous data sets (cytological, isozyme, nuclear and chloroplast DNA restriction site, and sequence data) have suggested a closer genetic relationship to the genus *Sinapis*, particularly the weed species *S. arvensis* ( $n = 9$ ), than to *B. rapa* and *B. oleracea*.

### 2.2.4 *B. napus*

Oilseed rape or canola is of comparatively recent origin and wild populations have not been found (Prakash and Hinata 1980). It is generally accepted that *B. napus* originated in southern Europe or the Mediterranean region, where the ranges of the two parental taxa *B. rapa* and *B. oleracea* overlap. Molecular data have provided evidence for multiple polyploid origins of *B. napus*, including crosses of *B. rapa* with *B. oleracea* and *B. rapa* with one of the wild C genome relatives, *B. montana* (Song and Osborn 1992). Two subspecies are generally recognized: the biennial vegetable rutabaga or swede (spp. *rapifera*) and an annual oilseed or fodder crop (spp. *napus* or spp. *oleifera*).

### 2.2.5 *B. carinata*

Abyssinian mustard is both an oilseed and a vegetable crop in Ethiopia with little differentiation into various crop types. Although wild types have not been located, it is believed to have originated in the Ethiopian plateau of northeast Africa, as a cross between wild-growing *B. nigra* and cultivated kale-like forms of *B. oleracea*.

The agronomic potential and germplasm diversity of *B. carinata* was reviewed in Warwick et al. (2006b).

### 2.2.6 *B. juncea*

Indian or brown mustard is grown in North America and Europe for condiment use, on the Indian subcontinent for seed oil and the Far East as a vegetable. Due to ecogeographical variation and human selection, a number of morphologically distinct forms are available, including oleiferous, semi-oleiferous, rapiferous, and leafy types.

There is some uncertainty as to the probable center of origin of *B. juncea*. It most likely originated in the Middle East or west Asian region, based on geographical sympatry of the parental taxa, *B. nigra* and *B. rapa*, and the presence of wild-growing *B. juncea* in this area. Other hypotheses suggest Asiatic origins with the center of major diversity in China. It seems likely that *B. juncea* may have arisen more than once as a result of hybridization, similar to that revealed for *B. napus*. Indeed, recent molecular studies have suggested more than one origin for each of the three varieties examined (vars. *multisepts*, *rapifera*, and *tsa-tsaï*).

## 2.3 Other Crucifer Crops

### 2.3.1 *Camelina*

*Camelina* is an old world genus (tribe Camelinae) of 11 species. *C. sativa*, a native of southeastern Europe and southwestern Asia, had been gathered or cultivated as an oilseed for many centuries in Europe and the oil apparently used for culinary purposes and in lamps (Facciola 1990). The species has attracted renewed interest as an oil crop (Plessers et al. 1962, Putnam et al. 1993, Hebard 1998, Leonard 1998), with an adaptation to varied climate conditions and nutritionally poor soils and minimal input needs and with relatively high resistance to disease and pests. In Europe, where it is now widely grown, it has shown considerable potential in the food, animal feed, nutraceutical, paint, dye, cosmetic, and biofuel industries. In North America, it is being grown on a trial basis mainly for its potential as a biofuel in Saskatchewan, the Maritime Provinces, and the northern US Great Plains Regions (reviewed in Zubr 1997, Gugel and Falk 2006). Genetic mapping of agronomic traits has already been initiated in this species (Gehring et al. 2006).

### 2.3.2 *Crambe*

*Crambe*, an old world genus of the tribe Brassiceae, is composed of approximately 30 species. *C. abyssinica* ( $n = 45$ ) is an industrial oilseed crop, belonging to *Crambe* Section *Leptocrambe*. The seed oil is of considerable economic importance in industrial applications including use as erucamide (anti-block and slip agent in

plastic films), coatings, lubricants (such as metal cutting oils, automatic transmission fluid supplement, and hydraulic fluid), and nylon. The use of *Crambe* meal as a protein source for feeds has also been investigated (Carlson and Tookey 1983). *C. abyssinica* is endemic to the Abyssinian highlands, and the name has been used not only for the wild Ethiopian population but also for the forms cultivated as an oilseed crop. It is derived from *Crambe hispanica* L. ( $n = 30$ ), a widespread endemic of the Mediterranean region. Cultivation of *C. abyssinica* was apparently initiated in the USSR and has been investigated in many areas of the world, including the midwestern United States, the Netherlands, and Canada (e.g., Erickson and Bassin 1990). The agronomic potential and germplasm diversity of *Crambe* species is reviewed in Warwick and Gugel (2003).

### 2.3.3 *Eruca*

*Eruca*, an old world genus of the tribe Brassiceae, is composed of four species that are native to the Mediterranean region. One taxon is cultivated, *E. vesicaria* spp. *sativa* (frequently referred to as *E. sativa*). Subspecies *sativa* ( $n = 11$ , E genome), is an annual herb that has been cultivated since ancient times as a leafy vegetable (rocket or arugula), either for salad (Mediterranean, North America) or as a cooked green (Italy). It is also grown as a cold weather oilseed crop to produce jamba oil in Asia, mainly in India but also in Pakistan and Afghanistan, and is being considered as a protein meal supplement (Yaniv et al. 1998, Fagbenro 2004). The seed oil is used as an illuminant, lubricant, hair oil, vesicant, and for massage and pickling. Subspecies *vesicaria* occurs in the Mediterranean, whereas spp. *sativa* has been introduced and naturalized in many areas of the world. In some regions, such as in Mexico, naturalized populations are abundant and serious weeds. The agronomic potential and germplasm diversity of *Eruca* species is reviewed in Warwick et al. (2007a).

### 2.3.4 *Raphanus*

The genus *Raphanus*, an old world genus of tribe Brassiceae, is composed of two species: radish, *R. sativus* ( $n = 9$ , R genome), and wild radish, *R. raphanistrum* ( $n = 9$ ). Radish has been cultivated for thousands of years and was grown extensively in ancient Egypt. *R. sativus* is not known in the wild, except for escapes forming weedy naturalized populations. There is some controversy as to the probable center of origin of *R. sativus*. It most likely originated in the Middle East or west Asian region, possibly from *R. raphanistrum*, although other suggestions indicate Asiatic origins with a center of major diversity in China. Important *R. sativus* crop varieties include small radish (var. *sativus* or *radicula*) grown for its edible root; black or large radish (var. *niger* or *longipinnatus*) grown for its roots, leaves, and young seed pods (believed to be the oldest type); mougri, rat-tailed, or aerial radish (var. *mougri*



or *caudatus*) grown primarily for its edible young seed pods; and fodder or oilseed radish (var. *oleifera*) grown for animal fodder or green manure.

### 2.3.5 Sinapis

*S. alba* or white mustard, a Mediterranean species of tribe Brassiceae, is cultivated in many countries in Europe and North America. Seeds of this species are the main ingredient for mustard production (along with *B. juncea*) and for commercial mucilage production. In the last few years it has been increasingly cultivated as a fresh forage and green manuring plant in some countries in Europe and America.

## 2.4 Underutilized Crucifer Crops

Underutilized crucifer crops include *Diplotaxis* spp., rocket; *Lepidium sativum*, cress (e.g. Italy oilseed crop; Angelini et al. 1997); *Nasturtium officinale*, water cress; *Orychophragmus violaceus* (China oil crop; Li et al. 1995, Huang et al. 1999, Luo et al. 1994, 1998a, 1998b) and root crops such as horseradish *Armoracia rusticana*, wasabi *Eutrema wasabi*, and maca *Lepidium meyenii*. Many crucifers are grown as ornamentals, and two such species are being developed as speciality industrial oil crops. *Lunaria annua*, for example, has 30–40% oil and high 44% erucic acid levels, as well as high (23%) concentrations of nervonic acid, which is used medically to treat multiple sclerosis (Marvin et al. 2000, Mastebroek and Marvin 2000, Walker et al. 2003), while *Matthiola incana* is rich in omega-3 linolenic acid (Ecker et al. 1992, Yaniv et al. 1997). *Lesquerella fendleri* is also another potential new speciality oil crop for arid lands in North America (Dierig et al. 2004, Salywon et al. 2005). *L. sativum* on the other hand is being considered for medicinal and functional food health properties (Mathews et al. 1993, Gokavi et al. 2004). Other wild Brassicaceae species, e.g., *Brassica fruticulosa*, are also being considered for vegetable diversification in Mediterranean regions (Branca 1995, Branca and Iapichino 1997).

Past folk medicinal use of other wild crucifer species (Specht and Diederichsen 2001) also suggests new unexplored crop opportunities. These include *Capsella bursa-pastoris* (Europe and Asia), *Cochlearia arctica* and *Cochlearia officinalis* (Europe); *Conringia orientalis* (Europe); *Descurainia sophia* (cultivated in Afghanistan, China; used for digestive troubles); *Erysimum cheiri* and *Erysimum diffusum* (N India, Iraq, Russia); *Hesperis matronalis* (dame's rocket) (Europe); *Lepidium meyenii* (maca or Peruvian ginseng, South America); *Lobularia maritima* (India); and *Rorippa indica* (China, Vietnam – asthma remedy). Indeed two of these species, *D. sophia* and *R. indica*, have been recently used in *B. napus* germplasm enhancement in China (Guan et al. 2007a, 2007b). Diversification of crucifer crop use as fodder, green manure or cover crops are also of increasing agricultural interest (Lange et al. 1989, Mitchell et al. 1999, Bellostas et al. 2007, Larkin and Griffin 2007).

## 2.5 Brassicaceae as Sources of Agronomic and Economic Traits

### 2.5.1 Morphological Traits

Several morphological characters in the family are of agricultural interest or potential utility. Most obvious is resistance to pod shattering, which has been reported for *B. juncea* (Prakash and Chopra 1988a), *B. macrocarpa* and *B. hilarionis* (Mithen and Herron 1991), *Brassica tournefortii*, *C. orientalis* and *Hirschfeldia incana* (Salisbury 1989), and *Raphanus* spp. (Agnihotri et al. 1991). Trichomes (hairs) on the cotyledons and juvenile leaves are also traits of interest, given their role in hampering insect herbivory, and are found for, e.g., on the wild C genome species *Brassica incana* and *B. villosa*. Similarly, increased leaf thickness/waxiness provides drought and insect tolerance in *B. oleracea* and close relatives (Gómez-Campo et al. 1999, Stoner 1990).

Variation in growth form is limited and the family is primarily herbaceous with only 5% of the species typically woody (Al-Shehbaz 1984). These include the vine/woody climbers, e.g., *Heliophila scandens* (South Africa), *Lepidium scandens* (Australia), *Cremolobus peruvianus* (Peru); subshrubs (*Vella* spp.); large shrubs, e.g., *Foleyola* (N. Africa), *Parolinia* (Canary Islands); and small trees, e.g., *Farsetia somalensis* (NE Africa). Fruits are borne above ground, but geocarpy where the fruit is buried underground in a peanut-like manner has evolved independently in a handful of species: e.g., *Morisia monanthos* (Corsica and Sardinia), *Cardamine chenopodiifolia* (South America), and *Geococcus pusillus* (Australia).

The floral structure in the family is also highly conserved, i.e., four yellow petals arranged in a cross-shape, but exceptions in color (white, pink, purple) and shape (e.g., bilaterally symmetrical flowers of *Streptanthus*) are known. Of agronomic interest are species with small petals or with no petals (e.g., *C. orientalis*). Stamen number is usually six, with interesting exceptions of 2–4 stamens in *Lepidium* or 8–24 stamens in *Megacarpaea polyandra*. Nectary types vary with some species having lateral, median, or both, some glucose-, others sucrose dominant (Davis et al. 1998). In contrast, fruit type is highly variable in the family and is typically dehiscent bivalvate capsule (silique or silicule), but can be indehiscent, becoming lomentaceous or achenelike and only rarely nutlet, samara, schizocarp, or even a drupe. In plants with dehiscent siliques, dispersal is generally close to the parental plant, but transport by sea is enhanced by the corky fruit of *Cakile*, *Crambe*, *Raphanus* spp., tumbling action of the weed, *Anastatica hierochuntica* (Rose of Jericho) in the Saharo-Sindian region, explosive dehiscence as in various *Cardamine* spp.; while hooked hairs or spines on the fruits can aid animal dispersal. Seed size varies greatly from the smallest in *Mancoa mexicana* (Mexico) and Saharan species of *Diploaxis* (at 0.02 and 0.05 mg, respectively) to the largest *Megacarpaea gigantea* (central Asia) weighing 90 mg; and measuring  $1.8 \times 1.5$  cm (Al-Shehbaz 1984, 1986). A few crop members of the family have an incredible capacity for vegetative propagation, e.g., American water cress: *Neobeckia lacustris* and horseradish *A. rusticana*. It was this large underground biomass production that led to the suggested use of *A. rusticana* in phytoremediation efforts (Palmer et al. 2001).

### 2.5.2 Chemical Traits

Many genera of the Brassicaceae have been studied for their chemical constitution, especially for variation in oil content and seed fatty acid and glucosinolates composition. Kumar and Tsunoda (1980) reported on oil content and the fatty acid composition of 172 crucifer species representing 70 genera. Other surveys of wild species include wild *Brassica* spp. (Vioque et al. 1990, Yaniv et al. 1991, Ahuja et al. 1998, Velasco et al. 1998). High erucic acids levels (>45–50%) have been reported for *B. cretica*, *B. incana*, *B. rupestris*, and *B. villosa* (Yaniv et al. 1991, Velasco et al. 1998); *C. abyssinica* and *C. hispanica* (Yaniv et al. 1991, Mulder and Mastebroek 1996, Prakash and Bhat 2007); *E. vesicaria* (*E. sativa*) (Yaniv et al. 1991); *Erucastrum cardaminoides* and *Sinapidendron angustifolia* (Prakash and Bhat 2007); *S. alba* (Yaniv et al. 1994) and *S. arvensis* (Daun et al. 2003). High linoleic and/or linolenic acids have been reported in: *Brassica elongata* (Velasco et al. 1998); *C. sativa* (Budin et al. 1995, Shukla et al. 2002, Matthäus and Zubr 2000, Zubr and Matthäus 2002); *D. sophia* (Luo et al. 1999); *M. incana* (Ecker et al. 1992); *O. violaceus* (Wang et al. 1999); *Alyssum*, *Barbarea*, *Cardamine*, *Conringia*, and *L. sativum* (Prakash and Bhat 2007). High hydroxy fatty acids have been found in several *Lesquerella* and *Physaria* spp. (Salywon et al. 2005).

Glucosinolates (mustard oil glucosides) and their glucosinolate hydrolysis products provide the characteristic odors and flavors of crucifers. Their pharmacological role in the prevention of disease and in chemical defense against pathogens, herbivores, and weeds is attracting increasing attention (e.g. Angelini et al. 1998, Clauss et al. 2006). More than 96 glucosinolates have been reported in the Brassicaceae family, and many of these are unique to certain species and genera (Fahey et al. 2001). Many surveys of glucosinolates in wild crucifers have been conducted, including 51 crucifer spp. (Al-Shehbaz and Al-Shammary 1987); 259 crucifer spp. (Daxenbichler et al. 1991); 85 crucifer spp. (Bennett et al. 2004); 25 *Brassica* spp. (Horn and Vaughan 1983, Cole 1997, Velasco and Becker 2000); *B. oleracea* and 9 wild *Brassica* C genome spp. (Mithen et al. 1987a); 13 *Cakile* spp. (Rodman 1974, 1976); *C. sativa* (Schuster and Friedt 1998); 9 crucifer spp.: *C. bursa-pastoris*, *E. vesicaria* spp. *sativa*, *Erysimum allionii*, *E. cheiri*, *H. matronalis*, *L. fendleri*, *L. maritima*, *Matthiola longipetala* (Vaughn and Berhow 2005); *Diplotaxis tenuifolia* and *E. vesicaria* spp. *sativa* (Bennett et al. 2007); *Lepidium peruvianum* (Li et al. 2001); and 3 *Zilla* spp. (El-Menshawi et al. 1980).

Many species have potential for and could be grown for their value-added traits or production of pharmaceuticals. For example, in a survey of 91 crucifer spp. (Goffman et al. 1999), tocopherols, sources of vitamin E levels ranged from 68 mg/kg oil in *Diplotaxis viminea* to 2,479 mg/kg oil in *Schivereckia doerfleri*. The weed species *Lepidium draba*, extensively investigated for potential use in fighting disease (reviewed in Francis and Warwick 2008), ranked third in a survey of 700 plants for presence of compounds that could halt/delay the growth of cancer cells. Glucoraphanin, an alkenyl glucosinolate, which hydrolyzes to form the enzyme inducer sulforaphane, is purified from this species for its use as a dietary additive for cancer and high blood pressure treatments. Sulforaphane is also effective against

pathogens such as bacteria, yeasts, fungi, mycoplasma, protozoans, nematodes, and viruses.

Our knowledge of other secondary metabolites in the family is limited, but deserves further attention. High concentrations of alkaloids (*L. annua*), cardenolides (*E. cheiri*), cucurbitacins (*Iberis amara*) are known (Al-Shehbaz 1984), and high concentration of cinnamoyl esters which is used in sunscreen reported in *L. fendleri* (Compton et al. 2004). Unusual floral pigments, acylated cyanidin glucosides were reported for *E. cheiri*, *L. maritima* and *L. annua* (Tatsuzawa et al. 2006). *A. rusticana*, for example, has served as a commercial source of peroxidases (Kushad et al. 1999). Flavonoid chemistry is less well known in the family, e.g., *Crambe* spp. (Aguinagalde and Gómez-Campo 1984); *Diplotaxis* spp. (Hussiney et al. 1998, Sánchez-Yélamo 1994); *Erucastrum* spp. (Sánchez-Yélamo 2001, 2004); *C. sativa*, *Crambe* spp., and *T. arvensis* (Onyilagha et al. 2003). Sinapine levels have been screened in 23 crucifer species (Bouchereau et al. 1991) and in *D. tenuifolia*, *E. vesicaria* spp. *sativa*, and *L. sativum* (Özeker and Esiyok 1999) and in *Sinapis* and related species (Agerbirk et al. 2008).

Mucilage production in seeds is characteristic of many species in this family, particularly in those occupying droughty areas. A family wide survey would be worthwhile. Mucilage from the seeds of *S. alba* is one of the main commercial mucilage sources (Cui et al. 1993), but other crops have been investigated for this product, e.g., *L. sativum* (Mathews et al. 1993).

Crucifer species with particularly high glucosinolate levels have been investigated for their potential use as a biofumigant or fungicide/nematocide particularly in the invasive *Alliaria petiolata* (McCarthy and Hanson 1998, Roberts and Anderson 2001, Aminidehaghi et al. 2006, Cipollini and Gruner 2007); *A. rusticana* (Kotova et al. 1999); *Barbarea verna* (Curto et al. 2005); *Brassica*. (Turk and Tawaha 2003); *C. abyssinica* (Mohiuddin et al. 1990, Peterson et al. 2000); *D. sophia* (Yang and Mu 2006); *D. eruroides* (anti-microbial compounds) (Peláez et al. 1998); *E. vesicaria* spp. *sativa* (Curto et al. 2005); *Lepidium perfoliatum* (Aminidehaghi et al. 2006); *N. officinale* (anti-nematode) (Kotova et al. 1999); *Rapistrum rugosum* (Curto et al. 2005); *S. arvensis* (anti-mosquito) (Bowers et al. 1997); *Zilla spinosa* (anti-weed and -rhizosphere fungi) (El-Khatib and Abd-Elaah 1998).

### 2.5.3 C<sub>3</sub>–C<sub>4</sub> Photosynthesis

Most members of the Brassicaceae have typical C<sub>3</sub> photosynthesis (Uprety et al. 1995). The C<sub>3</sub>–C<sub>4</sub> intermediate species *Moricandia arvensis*, *Moricandia nitens*, *Moricandia sinaica*, *Moricandia spinosa*, and *Moricandia suffruticosa* (Bauwe 1983, Razmjoo et al. 1996, Apel et al. 1997, Rylott et al. 1998) and *D. tenuifolia* (Apel et al. 1996, 1997, Peisker et al. 1998, Bang et al. 2003, Ueno et al. 2003) have been the subjects of considerable investigation as C<sub>4</sub> photosynthesis is believed to be a more efficient system particularly under drought conditions.

### 2.5.4 Cytoplasmic Male Sterility

Members of the family have provided valuable sources of novel cytoplasmic male sterility genes vital to the production of crop hybrid systems. These include *B. juncea* 126-1 (Sodhi et al. 2006); *B. juncea* hau (Wan et al. 2007); *B. napus* nap and pol (Brown 1999); *Brassica oxyrrhina* oxyrrhina (Prakash and Chopra 1988b, Kanada and Kato 1997); *B. tournefortii* (Pradhan et al. 1991, Pahwa et al. 2004); *Diplotaxis berthautii* (Malik et al. 1999); *Diplotaxis catholica* (Mohapatra et al. 1998, Pathania et al. 2003); *Diplotaxis eruroides* (Malik et al. 1999); *Diplotaxis harra* (Klimaszewska and Keller 1988); *Diplotaxis muralis* (Hinata and Konno 1979, Riungu and McVetty 2000, 2003a, b); *Diplotaxis siifolia* siifolia (Rao et al. 1994, Rao and Shivanna 1996); *Enarthrocarpus lyratus* (Banga et al. 2003b, Deol et al. 1999, 2003, Janeja et al. 2003); *E. vesicaria* subsp. *sativa* (Matsuzawa et al. 1999); *Erucastrum canariense* (Prakash et al. 2001, Banga et al. 2003a); *H. incana* (Horovitz and Galil 1972); *L. fendleri* (Dierig et al. 2001); *M. arvensis* moricandia (Kirti et al. 1998, Prakash et al. 1998, Bhat et al. 2005); *R. sativus* ogura (Ogura 1968, Yamagishi 1998, Murayama et al. 2004); and *Trachystoma ballii* trachystoma (Kirti et al. 1997).

### 2.5.5 Breeding Systems and Apomixis

Most members of the family are outcrossing and insect pollinated (wind pollination rare), and indeed the conserved architecture of the flower in the family is believed to be very closely linked to pollination by insects (Al-Shehbaz 1984). Autogamy or selfing is common in many of the weedy species, e.g., *Erucastrum gallicum*, while cleistogamy, i.e. self-fertilization without flower opening, always occurs in some species such as the submersed aquatic *Subularia aquatica*. The molecular basis of the cleistogamous trait has been recently reported for *Cardamine kokaiensis*, a close relative of *Arabidopsis* (Morinaga et al. 2008). With few exceptions, the flowers of the Brassicaceae are always perfect, but dioecism is reported in some *Lepidium* spp. from New Zealand and monoecism (male and female flowers on same plant) in the central Asian species *Megacarpaea megalocarpa* (Al-Shehbaz 1984). Of primary interest to crucifer breeding is the trait for apomixis which was first described in *Arabis* spp. (Roy and Rieseberg 1989, Roy 1995); additional taxa have been added – *Arabis gunnisoniana* (Taskin et al. 2004); *Arabis holboellii* (Naumova et al. 2001); and *Boechera* spp. (Schranz et al. 2005, 2006a).

### 2.5.6 Plant Regeneration and Transformation

Many crucifers have served as model species for improving plant regeneration and transformation systems, including *Alyssum borzaeanum* (Paunescu 2008), *Alyssum murale* (Vinterhalter et al. 2008), *Arabidopsis halleri* (Dal-Corso et al. 2005), *A. thaliana* (Gaj 2004), *B. carinata* (Verma et al. 2008), *B. juncea* (Dhawan

et al 2000, Eapen 2007, Dutta et al. 2008, Prem et al. 2008, Wang et al. 2008a), *B. oleracea* (Munshi et al. 2007, Zhang et al. 2008), *B. napus* (Ali et al. 2007, Ben-Ghnaya et al. 2008, Haddadi et al. 2008, Munir et al. 2008, Verma et al. 2008), *B. rapa* (Gao et al. 2008), *C. sativa* (Tattersall and Millam 1999, Lu and Kang 2008); *C. abyssinica* and *C. hispanica* (Sonntag and Rudloff 2001, Sonntag and Gramenz 2004); *D. muralis* (Sikdar et al. 1990); *E. vesicaria* spp. *sativa* (Sikdar et al. 1987, Zhang et al. 2005); *Isatis indigotica* (Hu et al. 1999, Zhang et al. 2003, Xu et al. 2004); *L. fendleri* (Skarjinskaia et al. 2003, Wang et al. 2008b); *M. incana* (Mensuali-Sodi et al. 1994, Siemens et al. 1995); *M. arvensis* (Rashid et al. 1996, Craig et al. 1997); *M. nitens* (Tian and Meng 1998); *O. violaceus* (Hu et al. 1999); *R. indica* (Mandal and Sikdar 2003); *R. nasturtium-aquaticum* (Jin et al. 1999); *Thlaspi caerulescens* (Guan et al. 2008); and *Thellungiella halophila* (Li et al. 2007). The transformation of members of the Brassicaceae is described in Chapter 18 by Sparrow et al., this volume.

### 2.5.7 Salt and Heavy Metal Tolerances

Several species in the family exhibit distinct salt tolerance, including those found in coastal strand habitats, e.g. *Cakile* spp. (Boyd and Barbour 1986, Megdiche et al. 2007), *Crambe maritima* and *R. raphanistrum* ssp. *maritimus*. Salt tolerant taxa include desert plants *L. fendleri* (Dierig et al. 2004) and *E. vesicaria* subsp. *sativa* (Ashraf and Noor 1993, Ashraf 1994). *Thellungiella salsuginea* (= *T. halophila*) occupies saline flat habitats and now serves as a model system for studying this trait (Inan et al. 2004).

Many species of the family are tolerant to heavy metals and have the capacity to hyperaccumulate Cd, Ni, Pb, Se, Sr, and/or Zn (Boyd et al. 1994, Kruckeberg and Reeves 1995, Boyd and Martens 1998, Palmer et al. 2001, Prasad and Freitas 2003, Ghaderian et al. 2007, Przedpelska and Wierzbicka 2007). To date, 90 species from 11 genera have been reported, including *Alyssum* (48 spp.), *Thlaspi* (28 spp.), *Bornmuellera* (4 spp.), *Arabidopsis* (3 spp.), *Arabis* (1 sp.), *Cardamine* (1 sp.), *Cochlearia* (1 sp.), *Peltaria* (1 sp.), *Pseudosempervivum* (1 sp.), *Stanleya* (1 sp.), *Streptanthus* (1 sp.). *T. caerulescens* serves as the model plant species for heavy metal tolerance studies (Assunção et al. 2003). *B. juncea* is one of the most tolerant species (Belimov et al. 2007) and a proposed crop species for use in phytoremediation efforts of sites contaminated with heavy metals.

### 2.5.8 Cold Tolerance

Cold tolerance is an important agronomic trait especially for northern temperate climates. Laroche et al. (1992) reported on cold tolerance in the weed species *Barbarea vulgaris*, *D. sophia*, and *T. arvense*, while recent studies have focused on a “Yukon ecotype” of *T. salsuginea* (Wong et al. 2005). Cold tolerance genes have been detected in microarray analyses of *T. salsuginea* (Taji et al. 2004, Gong et al. 2005, Griffith et al. 2007) and *T. arvense* (Sharma et al. 2007). Other arctic or

alpine species in the family are also potential sources of cold tolerance traits. For example, *Arabis*, *Crucihimalaya*, and *Draba* species are adapted to alpine areas up to 6,000 m in the Himalayas, Alps, Rockies, Andes, while *Romanschulzia* (Mexico and Central America) and *Oreophyton* (East Africa) are adapted to high mountains of the tropics (Al-Shehbaz 1984). *Draba*, *Eutrema*, and *Parrya* species occupy arctic habitats, while *Pringlea antiscorbutica*, also the subject of cold tolerance studies (Hennion et al. 2006), occupies sub-antarctic regions. Only a few members of the Brassicaceae occupy alpine habitats (elevations >2,000–2,500 m above snow line), *Brassica nivalis* (Mt. Olympus, Greece); *Brassica jordanoffii* (Mt Pirin Planina, Bulgaria); *Coincya richeri* (Alps in France and Italy) (Leadlay and Heywood 1990), and *Erucastrum abyssinicum* and *Erucastrum pachypodium* (Ethiopian Highlands) (Al-Shehbaz 1985).

### 2.5.9 Drought Tolerance

*T. salsuginea* is also a model species for studying drought tolerance (Wong et al. 2005). Several species in the tribe Brassicaceae show remarkable drought tolerance, including *B. carinata* and *B. juncea* (Mishra et al. 1999); *B. tournefortii* (Salisbury 1989, Prakash and Bhat 2007); *Carrichtera annua* (Boaz et al. 1990); *Diplotaxis acris* and *D. harra* (Boaz et al. 1990, Prakash and Bhat 2007); *Enarthrocarpus strangulatus*, *Erucaria boveana*, *Erucaria microcarpa* and *Erucaria uncata*, *Pseuderucaria clavata*, *Savignya parviflora*, *Schouwia purpurea* (Boaz et al. 1990); *E. vesicaria* spp. *sativa* (Sun et al. 1991, 1999, Prakash and Bhat 2007). Many species occur in the Saharan Desert, e.g., *Foleyola billotii*, *Fortuynia* spp., *Physorhynchus* spp., and *Z. spinosa* (Warwick et al. 2009), while *Lesquerella* spp. occur in the deserts of North America (Ravetta and Soriano 1998, Ploschuk et al. 2001, Prakash and Bhat 2007). *Moricandia* species also show drought tolerance and their higher water use efficiency has been associated with the C3–C4 intermediate photosynthetic pathway (McVetty et al. 1989).

### 2.5.10 Herbicide Resistance

Several weedy crucifer species have developed herbicide resistance (reviewed in Heap 2009, Warwick et al. 2005). A wild biotype of *B. rapa* (Maltais and Bouchard 1978) served as the trait source for development of triazine-resistant lines of *B. napus* in the 1980s. Triazine-resistant biotypes have also been reported in *C. bursa-pastoris*, *R. raphanistrum*, and *S. arvensis*. Acetolactate synthase (ALS) inhibitor-resistant biotypes have been reported in 12 species from seven different countries: *B. tournefortii*, *Camelina microcarpa*, *D. sophia*, *D. tenuifolia*, *Neslia paniculata*, *R. raphanistrum*, *R. sativus*, *R. rugosum*, *S. arvensis*, *Sisymbrium orientale*, *S. thellungii*, and *Thlaspi arvensis*. The latter are generally due to target site mutations of the ALS gene (Hanson et al. 2004, Warwick et al. 2005, Christoffers et al. 2006), but a metabolism-based resistant *S. arvensis* biotype has also been detected (Veldhuis et al. 2000). Paraquat-resistant biotypes have only been reported

in *Lepidium virginicum* (Canada: Smisek et al. 1998) and auxin-resistant biotypes in *S. arvensis* (Canada: Heap and Morrison 1992) and *S. orientale* (Australia). There is much interest in incorporating the *S. arvensis* auxin-resistance trait in *B. napus*. The physiological, biochemical, molecular, and genetic basis of the trait is known (Zheng and Hall 2001, Jugulam et al. 2005); and auxinic-resistant microspore-derived doubled haploid *S. arvensis* plants produced (Mithila and Hall 2007).

### 2.5.11 Disease Resistance

Wild species in the family have provided an invaluable source of disease resistance traits for crop improvement. White rust (*Albugo candida*) resistance has been reported as common in *B. carinata* and more limited in *B. rapa*, *B. juncea*, *B. nigra* (Liu and Rimmer 1991, Gulati et al. 1991, Kolte et al. 1991); *Brassica maurorum* (Chrungu et al. 1999); *E. vesicaria* spp. *sativa* (Bansal et al. 1997); and *R. sativus* (Williams and Pound 1963, Kolte et al. 1991). Resistance to black leaf spot (*Alternaria* spp.) has also been widely reported in the family (Sharma et al. 2002): *A. petiolata*, *B. vulgaris* (Westman and Dickson 1998); *B. elongata* and *B. fruticulosa* (Siemens 2002); *B. maurorum* (Chrungu et al. 1999); *B. nigra* (Westman and Dickson 1998, Westman et al. 1999); *Brassica souliei* (Siemens 2002); *Brassica spinescens* (Agnihotri et al. 1991); *C. sativa* and *C. bursa-pastoris* (Conn et al. 1988, reviewed in Tewari 1991, Westman and Dickson 1998, Westman et al. 1999, Siemens 2002, Pedras et al. 2003b); *Coincya* spp. and *D. catholica* (Prakash and Bhat 2007); *D. eruroides* and *D. tenuifolia* (Siemens 2002, Klewer et al. 2003); *E. vesicaria* subsp. *sativa* (Conn and Tewari 1986, Tewari 1991); *Hemicrambe fruticulosa*, *H. matronalis*, *N. paniculata*, and *R. sativus* (Siemens 2002); *S. alba* (Brun et al. 1987, Sharma and Singh 1992, Siemens 2002, Pedras et al. 2003b); and *S. arvensis* (Siemens 2002). Blackleg (*Leptosphaeria maculans*) resistance has been reported in *A. thaliana* (Brun and Tribodet 1995, Chen and Séguin-Swartz 1997, 1999); *B. carinata*, *B. juncea*, and *B. nigra* (Rimmer and van den Berg 1992); *B. elongata* and *B. fruticulosa* (Siemens 2002); *B. insularis*, *Brassica atlantica*, and *B. macrocarpa* (Mithen et al. 1987b, Mithen and Herron 1991, Mithen and Magrath 1992); *C. sativa* (Siemens 2002, Li et al. 2005); *Coincya monensis* (Winter et al. 1999, 2002, 2003); *E. vesicaria* and *Eruca pinnatifida* (Tewari et al. 1996, Siemens 2002); *Carrichtera*, *Diplotaxis*, *Hirschfeldia*, *Raphanus*, *Rapistrum*, and *Sinapis* weedy species in Australia (Salisbury 1987); *C. monensis* (Siemens 2002); *D. muralis*, and *D. tenuifolia* (Chen and Séguin-Swartz 1997, 1999); *H. incana* (Siemens 2002); *R. raphanistrum* (Chen and Séguin-Swartz 1999); *R. sativus* (Siemens 2002); *S. alba* (Gugel and Séguin-Swartz 1997); *S. avensis* (Siemens 2002, Winter et al. 1999, 2002, 2003); *Sisymbrium loeselii* (Chen and Séguin-Swartz 1997, 1999); and *T. arvense* (Pedras et al. 2003a). Studies in *T. arvense* have indicated for, e.g., that two antifungal phytoalexins wasalexinA and arvelalexin are responsible for the resistance. Downy mildew (*Peronospora parasitica*) tolerance has been reported in *B. oleracea* wild accessions (Greenhalgh and Mitchell



1976) and *E. vesicaria* (Singh and Kolte 1999). Clubroot (*Plasmodiophora brassicae*) tolerance has been reported in *A. thaliana* (Rehn et al. 2004); *A. rusticana* (Prakash and Bhat 2007); *C. bursa-pastoris* (Siemens 2002), and *Raphanus* spp. (Crute et al. 1980, Long et al. 1992). Sclerotinia stem rot (*Sclerotinia sclerotiorum*) tolerance has been reported in *C. bursa-pastoris* (Chen et al. 2007), *E. vesicaria* subsp. *sativa* (Guan et al. 2004) and *E. gallicum* (Lefol et al. 1997, Gugel et al. 1997). Turnip mosaic virus resistance has been reported in *A. petiolata* and *H. matronalis* (Stobbs and Stirling 1990) and *S. alba* and *S. arvensis* (Mamula et al. 1997). Wilt disease (*Verticillium dahliae*) resistance has been reported in *A. rusticana* (Atibalentja and Eastburn 1998). Black rot (*Xanthomonas campestris*) resistance has been reported in *B. nigra* (Marthe et al. 2004); *B. rapa* (Ignatov et al. 1999); *A. petiolata*, *B. vulgaris*, *B. juncea*, *B. nigra*, *Erysimum hieraciifolium*, and *M. incana* (Westman and Dickson 1998). Resistance to peppery leaf spot (bacteria *Pseudomonas syringae*) was recently reported in two *B. juncea* germplasm accessions (Wechter et al. 2007) indicating the often unexplored wealth of diversity in crop germplasm collections.

### 2.5.12 Insect and Nematode Resistance

Resistance to flea beetles (*Phyllotreta cruciferae* and *Phyllotreta striolata*), the most important insect pests of oilseed crucifer crops in North America, has been reported in *A. thaliana* (Prakash and Bhat 2007); *B. incana* and *B. villosa* (Bodnaryk, personal communication, Warwick et al. 2009); *B. juncea* (Bodnaryk 1997); *C. sativa* (Pachagounder et al. 1998, Soroka et al. 2003, Henderson et al. 2004); *C. bursa-pastoris* (Prakash and Bhat 2007); *C. abyssinica* (Anderson et al. 1992, Soroka et al. 2003, Henderson et al. 2004); *C. hispanica* and *C. glabrata* (Soroka et al. 2003); *S. alba* (Lamb 1980, Bodnaryk and Lamb 1991, Bodnaryk 1997, Gavloski et al. 2000, Henderson et al. 2004); and *T. arvense* (Gavloski et al. 2000); whereas *B. vulgaris* was shown to be resistant to the European flea beetle *Phyllotreta nemorum* (Renwick 2002). Resistance to the lepidopteran pests diamond-back moth (*Plutella xylostella*) has been described in *B. vulgaris* (Renwick 2002, Lu et al. 2004, Badenes-Perez et al. 2005); *B. juncea* (Ruwandi and Gillott 1998); *B. oleracea* (Stoner 1990, Ramachandran et al. 1998); *B. napus* (Ramachandran et al. 1998); *C. abyssinica* (Kmec et al. 1998); and *R. raphanistrum* (Lehtila and Strauss 1999); and to the cabbage butterfly (*Pieris* spp.) in *Erysimum cheiranthoides* and *I. amara* (Renwick 2002) and *P. napi oleracea* in *A. petiolata* and *B. vulgaris* (Renwick 2002). Resistance to the cabbage aphid (*Brevicoryne brassicae*) was reported for *B. fruticulosa* and *B. spinescens* (Cole 1994, Singh et al. 1994, Ellis and Farrell 1995); *E. vesicaria* subsp. *sativa* (Singh et al. 1994); and *S. alba* (Thompson 1963) and to the mustard aphid (*Lipaphis erysimi*) in *B. carinata*, *B. nigra*, *B. juncea*, and *Eruca sativa* (Rana et al. 1995, Lal et al. 1997, Chander and Bakhetia 1998). Cabbage white fly (*Aleyrodes proletella*) resistance was described for *B. cretica*, *B. fruticulosa*, *B. incana*, *B. insularis*, *B. spinosa*, *B. villosa* (Ramsey and Ellis 1994). Cabbage root fly (*Delia radicum*) resistance was reported for *B. fruticulosa*

and C genome species *B. incana*, *B. macrocarpa*, *B. spinescens*, *B. villosa* (Ellis et al. 1999); *C. sativa* (Soroka et al. 2003) and *S. alba* (Jyoti et al. 2001). Cabbage seed pod weevil (*Ceutorhynchus obstrictus*) resistance was described for *B. juncea*, *B. nigra*, *B. tournefortii*, *C. sativa*, and *S. alba* (Ulmer and Dossdall 2006, Carcamo et al. 2007). Mustard Sawfly (*Athalia proxima*) resistance was shown for *C. sativa* (Singh and Sachan 1997).

Resistance has been reported in *R. sativus* and *S. alba* to the beet cyst nematode, *Heterodera schachtii* (Thierfelder et al. 1991, Lelivelt and Krens 1992, Lelivelt et al. 1993) and root-knot nematode (*Meloidogyne* spp.) (Buente et al. 1997, Pattison et al. 2006).

## 2.6 Conclusion

Wild Brassicaceae germplasm offers numerous future prospects for agronomic and economic traits and new crops. Characterization of the wild germplasm, however, is still incomplete and available information fragmentary. A systematic investigation of such resources would improve efficacy of their utilization in crucifer crop breeding programs (Prakash and Bhat 2007). Efforts should be made to maintain and expand wild germplasm collections before these species become extinct due to habitat loss or where access is restricted due to global strife. More collections are needed from centers of variability and centers of origin, and an emphasis should also be placed on non-native areas of the species range both for weedy species and neglected landraces (e.g., Farnham et al. 2008). Future introgression of desirable genes/traits will require greater knowledge of the genetic basis or inheritance of these traits, as well as information on precise chromosomal locations. The development of genetic maps for key relatives and or new crucifer crops (see chapters to follow) will be of increasing importance. Some traits can be introduced through artificial hybridization (Warwick et al. 2009), while traits arising from more distant sources will need to be isolated and introduced through transgenic means. Production of addition lines in various crop genome backgrounds will be needed and in situ hybridization techniques will be helpful in identifying such additions with more precision. The ultimate goal will be the pyramiding of traits in crop cultivars. New crop opportunities exist among the many species currently cultivated for ornamental or vegetable/salad use and diversification of crucifer crop use whether as fodder, green manure or cover crops, biofumigants, etc., also offer exciting future agricultural possibilities.

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