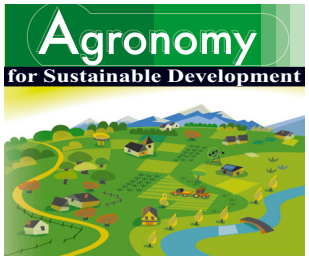
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Review article

Defence mechanisms of Brassicaceae: implications for plant-insect interactions and potential for integrated pest management. A review

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Abstract – *Brassica* crops are grown worldwide for oil, food and feed purposes, and constitute a significant economic value due to their nutritional, medicinal, bioindustrial, biocontrol and crop rotation properties. Insect pests cause enormous yield and economic losses in *Brassica* crop production every year, and are a threat to global agriculture. In order to overcome these insect pests, *Brassica* species themselves use multiple defence mechanisms, which can be constitutive, inducible, induced, direct or indirect depending upon the insect or the degree of insect attack. Firstly, we give an overview of different *Brassica* species with the main focus on cultivated brassicas. Secondly, we describe insect pests that attack brassicas. Thirdly, we address multiple defence mechanisms, with the main focus on phytoalexins, sulphur, glucosinolates, the glucosinolate-myrosinase system and their breakdown products. In order to develop pest control strategies, it is important to study the chemical ecology, and insect behaviour. We review studies on oviposition regulation, multitrophic interactions involving feeding and host selection behaviour of parasitoids and predators of herbivores on brassicas. Regarding oviposition and trophic interactions, we outline insect oviposition behaviour, the importance of chemical stimulation, oviposition-deterring pheromones, glucosinolates, isothiocyanates, nitriles, and phytoalexins and their importance towards pest management. Finally, we review brassicas as cover and trap crops, and as biocontrol, biofumigant and biocidal agents against insects and pathogens. Again, we emphasise glucosinolates, their breakdown products, and plant volatile compounds as key components in these processes, which have been considered beneficial in the past and hold great prospects for the future with respect to an integrated pest management.

Brassicas / insect pests / chemical ecology / trophic levels / glucosinolates / isothiocyanates / defence mechanisms / biocontrol / trap crops / integrated pest management

1. INTRODUCTION

1.1. The origin and excellence of "brassicas"

"Brassicas: Oil-, food- and fodder-bearing crops with small seeds; that can grow as fast as Wisconsin rapid cycling brassicas; can grow as big as ornamental plants; can be seen as vast green fields of vegetable crops or as oilseed crops with fields of bright yellow flowers; lead to the production of economically important agricultural products; used as food for humans and animals; are important as valuable renewable bioenergy resources; are huge reservoirs of plant innate defences; show multiple defence responses in response to stresses; possess anticancer properties; hold ample potential for pest management" (*Ishita Ahuja*).

The Brassicaceae or Cruciferae, also known as crucifers, is a broad family of around 375 genera and 3200 species (LeCoz and Ducombs, 2006), which includes crops, ornamentals and many weeds. The genus *Brassica* belongs to the subtribe Brassicinae of the Brassicaceae family and comprises about 159 species, which, along with cultivated species, also includes wild brassicas (Zhou and Zhang, 2001; Zhang and Zhou, 2006).

The cultivated species of Brassicaceae include oilseed rape, cabbage, cauliflower, broccoli, Brussels sprouts, turnip, kale, swede, various mustards and other leafy vegetables. They are grown worldwide with a wide spectrum of adaptation for cultivation under varied agro-climatic conditions (Suwabe et al., 2006; Hong et al., 2008). The archaeological evidence of importance of brassicas dates back to 5000 BC, and *Brassica* plants are considered among the oldest cultivated plants known to humans, with written records dating back to ca. 1500 BC (Raymer, 2002). The genetic relationship among different *Brassica* species was established in the classical work by U (U.N., 1935), which is now ascribed as U's triangle (Fig. 2).

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Figure 1. The classical view of yellow *Brassica napus* fields and a closer view of oilseed rape plants.

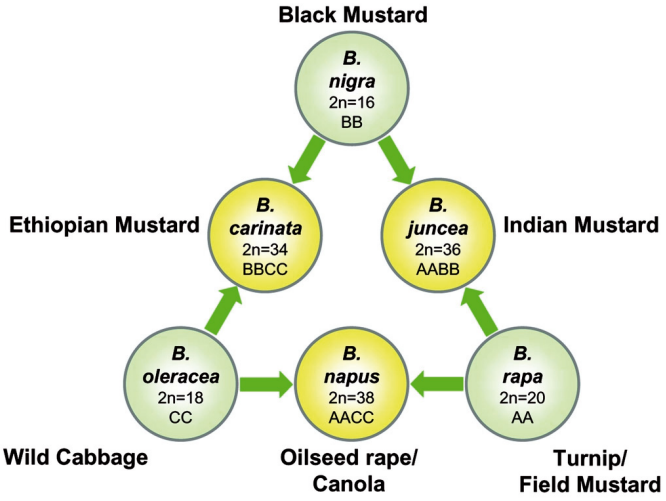


Figure 2. U-triangle showing the affiliations among different *Brassica* species (U.N., 1935).

The corners of the U-triangle include three diploid species: *B. rapa* L. (2n = 20; AA), *B. nigra* L. Koch (2n = 16; BB) and *B. oleracea* L. (2n = 18; CC), and the other three in the middle of the triangle are amphidiploid species: *B. napus* L. (2n = 38; AACC), *B. juncea* (L.) Czern. (2n = 36; AABB) and *B. carinata* Braun (2n = 34; BBCC) (Gomez-Campo, 1999). These six species of the U-triangle are also referred to as: *B. rapa* (*syn. B. campestris*) (Chinese cabbage and Turnip), *B. nigra* (Black mustard), *B. oleracea* (Cabbage, Brussels sprouts, Cauliflower and Broccoli), [*B. napus* var. *oleifera* (Oilseed rape, Rapeseed and Canola) var. *rapifera* (Swede, Rutabaga)], *B. juncea* (Indian mustard/Brown mustard) and *B. carinata* (Ethopian mustard) (Labana and Gupta, 1993). *B. rapa*, *B. nigra*, *B. oleracea*, *B. juncea*, *B. napus* and *B. carinata* are all designated as crop brassicas. Cauliflower, cabbage, Brussels sprouts, broccoli and turnip fall into the category of important vegetable crops. Among these vegetable crops, broccoli (var. *botrytis*) has been a valuable asset in the USA, both from a nutritional and economic point of view. Apart from being an excellent source of vitamin C, it provides dietary fibre, protein, iron, calcium and vitamin A and also contains anticancer components (Verhoeven et al., 1997; Cintas et al., 2002). *Brassica* crops carry properties of nutritional value, health benefits and biocontrol agents, and their use in crop rotations has been valued both by traditional and organic farmers (Guerena, 2006). The worldwide production of cabbages and kale-like brassicas in 2007 was 69 Mio t/3.1 Mio ha area, rapeseed 50 Mio t/30.2 Mio ha, cauliflowers and broccolis 19 Mio/1.0 Mio ha, and mustard seed 0.4 Mio t/0.7 Mio ha (FAOSTAT, 2009). Due to the increased oilseed production of *B. rapa*, *B. juncea*, *B. napus* and *B. carinata* in the past three decades, the oilseed brassicas have become an important source of oil and protein among cultivated brassicas (Font et al., 2003). Oilseed *Brassica* species are the major oilseed crops cultivated in India and around the world, and India produces about 11.3% of the world's rapeseed mustard (Damodaram and Hegde, 2002 as cited by Chattopadhyay et al., 2005). Oilseed *Brassica* species are also an important commodity in the world economy, as they are an important source of nutrition in developing countries (Rana, 2005). Amidst oilseed brassicas, oilseed rape has become a major crop in Europe, and one of the significant oil crops worldwide (Graner et al., 2003; Dubuis et al., 2005). The rapeseed and rapeseed oil production in 2007 from different countries that ranked in the first twelve worldwide are listed in Table I.

Table I. Rapeseed and rapeseed oil production in the first 12 highest producing countries worldwide in 2007 (FAOSTAT, 2009).

Country	Rapeseed (Mio t)	Rapeseed oil (Mio t)
China	10.38	4.35
Canada	8.86	1.30
India	7.10	2.34
Germany	5.32	2.20
France	4.55	1.05
Poland	2.11	0.68
United Kingdom	2.11	0.72
Australia	1.07	0.17
Ukraine	1.06	0.06
Czech Republic	1.04	0.31
USA	0.66	0.50
Russian Federation	0.60	0.07

B. napus stands as the third most important oilseed crop at the international level for both oil meal (after soybean and cotton) and vegetable oil (after soybean and oil palm) (Snowdon et al., 2007). The worldwide rapeseed oil production was 16.8 Mio t after palm and soybean (FAOSTAT, 2009). The significance of oilseed rape has increased during the present decade, not only because of its consumption as a nutritional food, but also due to its role as a renewable energy source as biodiesel in transport. Biodiesel is the methyl ester of oilseed rape oil (RME) (Souckova, 2006). *B. juncea*, an important source of edible oil, is cultivated in many countries across the globe. During the year 1999–2000, oilseed rape and mustard occupied, e.g., 6 Mio ha with an annual production of 5.8 Mio t in India (Dutta et al., 2005).

1.2. Important insect pests of brassicas

"*An insect is considered a pest if it threatens a resource valued by human beings, including human health*" (Foster and Harris, 1997). Insect pests pose a great challenge to *Brassica* crop production worldwide. A huge number of insect pests attack brassicas, and several insect specialists have *Brassica* species as preferred host plants (Lamb, 1989; Sekhon and Åhman, 1993; Sibanda et al., 2000). These insect pests are the major un-equalisers of growth and crop yield of brassicas and their importance varies by geographical location (Hokkanen and Wearing, 1996; Kanrar et al., 2002). Some of the major insect pests that attack Brassicacea crops worldwide are listed in Table II and presented in Figure 3.

Sources: AgroAtlas, 2009; Bromand, 1990; Bartlet et al., 1996; Hokkanen and Wearing, 1996; Ruther and Thiemann, 1997; Girard et al., 1998; Kift et al., 2000; Ulmer, 2002; Ester et al., 2003; Du Toit, 2007; Kazana et al., 2007; Khattab, 2007; Lehrman, 2007; Valantin-Morison et al., 2007; Smallegange et al., 2007; Knodel and Ganehiarachchi, 2008; Cartea et al., 2009.

1.2.1. The diamondback moth (Plutella xylostella)

The diamondback moth (*P. xylostella*) (Fig. 3) is a highly mobile insect, and is considered as the most damaging insect pest of *Brassica* crops worldwide. With an estimated control cost of nearly US$ 1 billion annually (Talekar and Shelton, 1993; Pivnick et al., 1994; Sarfraz et al., 2006; Golizadeh et al., 2007; Shelton et al., 2008), it has been the greatest threat to *Brassica* production in many regions of the world, with crop loss of 90% in some cases (Verkerk and Wright, 1996; Charleston and Kfir, 2000). The diamondback moth was first noticed as a pest in South Africa in the early 1900s (Charleston and Kfir, 2000). In Canada, the short generation time and high fecundity of the diamondback moth allows it to become a significant pest of oilseed crops in this region (Ulmer et al., 2002). Diamondback moth can attack plants at all stages of growth and female moths attach their eggs singly or in groups of two or three to the underside of leaves. Larval chewing make small holes in leaves, with larger larvae making larger holes. Their chewing may make leaves appear "windowpaned", with a clear cuticle left after feeding. Diamondback moth larvae feed on most of the *Brassica* plants such as *B. campestris*, *B. napus*, *B. juncea* and *B. oleracea*.

1.2.2. The cabbage looper (Trichoplusia ni)

The cabbage looper feeds on a diverse range of plants and is an important pest on Brassicaceae plants (Chow et al., 2005). The cabbage loopers (Fig. 3), which often attack broccoli, cauliflower, cabbage, kale, collards and mustard, are pale green larvae of a grey-brown moth, feed on foliage and tender above-ground parts and generally lead to plant decline (Du Toit, 2007; Capinera, 2008). Young larvae initially are dusky white, but become pale green as they begin to feed on foliage. The cabbage looper is found throughout Canada, Mexico and the United States, wherever crucifers are cultivated, and on other continents (Capinera, 2008). The cabbage looper females can produce 300 to 600 eggs in their 2 week life span, laying eggs singly and mostly on the lower surface of leaves. Larvae emerge from eggs in 3 to 4 days and feed on leaves (Chow et al., 2005; Mossler, 2005).

1.2.3. The cabbage moth (Mamestra brassicae) and Bertha armyworm (Mamestra configrata)

The cabbage moth, *M. brassicae* (Fig. 3), is a polyphagous insect, and the observed food plants of the cabbage moth include more than 70 species of 22 families, of which Brassicaceae and Chenopodiaceae are among the most preferred (Popova, 1993 as cited by Rojas et al., 2001; Ulland et al., 2008). The cabbage moth is widely distributed throughout most of Europe and Asia, from 30°N to about 70°N (Klingen et al., 2002b and references therein). The cabbage moth is native to Norway and is an important pest on various cabbage crops in Southern Norway up to about 62°N (Johansen, 1997). The Bertha armyworm, also referred to as the 'Miller Moth' or 'climbing cutworm', is native to North America and is a pest of oilseed and canola production in the northern Great Plains (Ulmer, 2002; Knodel and Ganehiarachchi, 2008). Young larvae feed on the underside of leaves and chewing makes irregular-shaped holes. The economic damage occurs due to significant larval feeding on foliage as well as on developing seedpods of canola. In years with outbreaks, larval feeding has resulted in economic crop losses and increased production costs from spraying insecticides (Knodel and Ganehiarachchi, 2008).

1.2.4. The cabbage white butterflies (Pieris brassicae, Pieris rapae and Pieris napi)

The cabbage white butterflies *P. brassicae, P. rapae* and *P. napi* (Fig. 3), are specialised on the Brassicaceae family and they have been used as a model species in the field of insect pest biology (Smallegange et al., 2007 and references therein). *P. brassicae* and *P. rapae* are cabbage herbivores that are closely related, yet show drastic contrasts in the amount of eggs they lay on plants (Bruinsma et al., 2007). *P. rapae* occurs in temperate regions around the world, and is generally confused with other common cabbage white butterflies (Capinera, 2004). In North America, it is known as "imported cabbageworm" and in Europe it is known as the small white cabbage butterfly. *P. rapae* is a cosmopolitan species, which is widespread throughout Europe, Asia and North America. The damage to foliage caused by *P. rapae* is slight, although it can be severe in seasons with a high infestation of caterpillars (Hern et al., 1996). *P. napi* is spread throughout the northern hemisphere ranging from North America, Europe and Asia to North Africa. Although larvae mainly feed on wild Brassicaceae species, infestation of *Brassica* vegetable crops such as cabbage, turnip and swede occurs and potentially leads to significant crop losses.

Table II. List of some important insect pests that attack Brassicaceae plants worldwide.

	Common names	Scientific names	Host plants
	Lepidoptera		
1	Diamondback moth/Cabbage moth (Specialist)	*Plutella xylostella* L.	Broccoli, Brussels sprouts, cabbage, cauliflower, kale, mustard, turnip
2	Cabbage looper (Generalist)	*Trichoplusia ni* Hübner	Broccoli, cabbage, cauliflower, kale, collards, mustard, rutabaga, turnip
3	Cabbage moth (Generalist)	*Mamestra brassicae* L.	Cabbage, mustard, turnip,
4	Bertha armyworm (Generalist)	*Mamestra configrata* Walker	Canola, rapeseed, mustard
5	Small white butterfly/Imported cabbage worm/ Cabbage butterfly (Specialist)	*Pieris rapae* L.	Broccoli, Brussels sprouts, cabbage, cauliflower, kale, kohlrabi
6	Large white butterfly (Specialist)	*Pieris brassicae* L.	Kale, cabbage, turnip, black mustard, Ethiopian mustard, swede
7	Green-veined white (Specialist)	*Pieris napi* L.	Cabbage, Brussels sprouts, turnip, swede, mustard, oilseed rape
	Hymenoptera		
8	Cabbage sawfly/Turnip sawfly (Specialist)	*Athalia rosae* L.	Mustard, turnip, oilseed rape, cabbage
	Diptera		
9	Cabbage maggot/Cabbage root fly/ Cabbage fly (Specialist)	*Delia radicum* syn. *brassicae* L.	Broccoli, Brussels sprouts, cabbage, kale, swede
10	Turnip root fly (Specialist)	*Delia floralis* Fallen	Turnip
11	Brassica/Pod midge (Specialist)	*Dasineura brassicae* Winnertz.	Oilseed rape
	Coleoptera		
12	Flea beetles/pollen beetles	*Phyllotreta*, *Psylliodes* and *Meligethes* spp.	
	Crucifer flea beetle (Specialist)	*Phyllotreta cruciferae* Goeze	Broccoli, Brussels sprouts, cabbage, cauliflower, kale, collards, turnip, mustard, oilseed rape
	Striped flea beetle (Specialist)	*Phyllotreta striolata* F.	Broccoli, Brussels sprouts, cabbage, cauliflower, kale, collards, canola, turnip, mustard, oilseed rape
	Cabbage stem flea beetle (Specialist)	*Psylliodes chrysophela* L.	Cabbage, mustard, turnip, oilseed rape
	Pollen beetles	*Meligethes* spp.	Turnip, swede, mustard, oilseed rape
13	Weevils	*Ceutorhynchus* spp.	
	Rape stem weevil (Specialist)	*C. napi* Gyll.	Oilseed rape, cabbage
	Cabbage seed weevil (Specialist)	*C. assimilis* Paykull	Cabbage, turnip, oilseed rape
	Cabbage seedpod weevil (Specialist)	*C. obstrictus* Marsham	Turnip, mustard, cabbage, brown mustard, canola, cabbage, broccoli
	Cabbage stem weevil (Specialist)	*C. pallidactylus* Marsham	Oilseed rape, cabbage, cauliflower, turnip
	Homoptera		
14	Aphids		
	Cabbage aphid/Mealy cabbage aphid (Specialist)	*Brevicoryne brassicae* L.	Cabbage, mustard, turnip, oilseed rape, broccoli, Brussels sprouts
	Mustard aphid (Specialist)	*Lipaphis erysimi* Kaltenbach	Mustard
	Turnip aphid (Specialist)	*Hyadaphis erysimi* Kaltenbach	Turnip
	Green peach aphid (Generalist)	*Myzus persicae* Sulzer	Broccoli, Brussels sprouts, cabbage, cauliflower, turnip

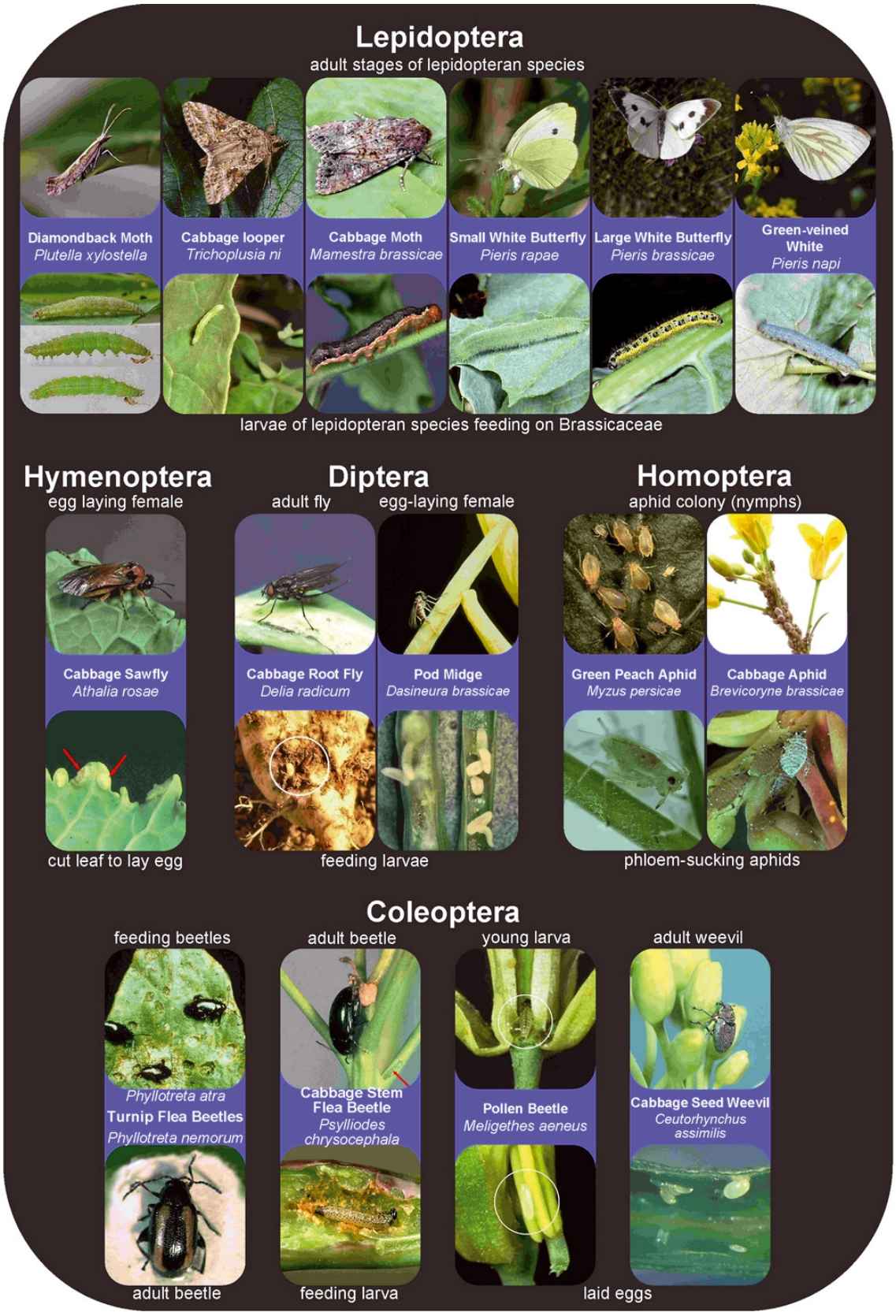


Figure 3. Important insect pests that attack Brassicaceae plants worldwide.

1.2.5. The cabbage sawfly/Turnip sawfly (Athalia rosae)

The turnip sawfly, *A. rosae* (Fig. 3), is oligophagous, i.e. it feeds on a few types of plants in nature. The pest eats leaf mass, buds, flowers and young pods (AgroAtlas, 2009). Among cruciferous plants its preferred hosts are white mustard (*S. alba*) and turnip (*B. rapa*), but the pest can also rear on young oilseed rape (*B. napus*) crops (Barker et al., 2006).

1.2.6. The cabbage root fly (Delia radicum syn., brassicae) and the turnip root fly (Delia florales)

The cabbage root fly (*D. radicum* syn. *brassicae*) (Fig. 3) and the turnip root fly (*D. florales*) are considered to be economically important pests on *Brassica* crops such as broccoli, Brussels sprouts, cabbages and kales, and are members of a large family of root flies (Klingen et al., 2002b and references therein; Ester et al., 2003). The larvae of *Delia* flies cause damage to plants by feeding on plant roots and through eggs and neonates (Klingen et al., 2002b). The plant mortality rate is unusually high, and the recovered plants are of reduced marketable quality (De Jong and Städler, 1999). Cabbage root fly and turnip root fly damaging *Brassica* spp. roots lead to significant reductions in yield, flowering and seed production as well as leaf, stem and root biomass (Blossey and Hunt-Joshi, 2003). Both cabbage root fly and turnip root fly are oligophagous in nature. Gravid females of the cabbage root fly arrive at a host-plant odour source by a series of short upwind flights, landing and reorientating into the wind between flights (Hopkins et al., 1999). The adult female oviposits in the soil close to the stem of *Brassica* plants (Nottingham and Coaker, 1985; De Jong and Städler, 1999), while damage to the plants is caused by hatched larvae feeding on the roots.

1.2.7. The Brassica pod midge (Dasineura brassicae)

The brassica pod midge is a common pest on Brassicaceae plants, particularly on oilseed rape, throughout north-western Europe and is attacked by over 20 species of hymenopteran parasitoids, among them *Omphale clypealis* and members of the genus *Platygaster subuliformis* (Murchie et al., 1997 and references therein; Murchie and Hume, 2003). Females deposit their eggs inside *Brassica* pods, where larvae feed and develop. Larvae spend their feeding period within the same pod (Åhman, 1985).

1.2.8. The flea and pollen beetles (Phyllotreta, Psylliodes and Meligethes spp.)

Phyllotreta nemorum and *Phyllotreta undulata* are the main flea beetle species infesting *Brassica* crops, such as Brussels sprouts, broccoli and cauliflower (Ester et al., 2003). The crucifer flea beetle, *Phyllotreta cruciferae*, and the striped flea beetle, *Phyllotreta striolata*, are the most serious insect pests of canola in North America and both were introduced from Eurasia. *P. cruciferae* has become the dominant flea beetle pest of canola. Adult flea beetles emerge in the spring and feed on the cotyledons and true leaves. When emerging in huge numbers, they can quickly devastate a seedling canola field. Therefore, a timely detection and management of this pest is important. The damage to oilseed *Brassica* crops through flea beetles exceeds US$ 300 million annually in North America (Knodel and Olsen, 2002). *Psylliodes chrysocephala* (cabbage stem flea beetle) is the major stem-mining pest of oilseed rape (Barari et al., 2005) and an important pest of other *Brassica* spp. in Europe (Bromand, 1990; Bartlet and Williams, 1991; Bartlet et al., 1996; Vig, 2002; Valantin-Morison et al., 2007). The genus *Meligethes*, generally known as pollen beetles (Fig. 3), occurs worldwide and includes more than 400 species (Kirk-Spriggs, 1996 as cited by Blight and Smart, 1999). Of the 10 *Meligethes* species reported from brassicaceous plants in Europe, *M. aeneus* is by far the most common on cultivated brassicas (Blight and Smart, 1999). Pollen beetles are considered important pests on oilseed brassicas and cause serious yield losses to oilseed rape crops, with yield reductions of more than 80% reported (Lamb, 1989; Ekbom, 1995; Ekbom and Borg, 1996; Ruther and Thiemann, 1997; Ekbom and Ferdinand, 2003; Bartlet et al., 2004; Hansen, 2004; Williams, 2006; Kazachkova, 2007; Lehrman, 2007). Although pollen beetles are important pests, particularly for oilseed rape in Northern Europe (Jönsson and Anderson, 2007), and turnip rape, they do not oviposit on all Brassicacea plants (Bartlet et al., 2004).

1.2.9. The weevils (Ceutorhynchus spp.)

The cabbage seed weevil (*C. assimilis*) (Fig. 3) is an important pest of oilseed rape in Europe and North America (Lamb, 1989; Bartlet et al., 1997; Smart and Blight, 1997; Girard et al., 1998; Ferguson et al., 1999b), causing reduction in crop yield in heavily infested fields (Smart et al., 1997; Girard et al., 1998). The cabbage seed weevil is an oligophagous insect that feeds and develops on *Brassica* species. The cabbage seed weevil invades oilseed rape crops, the adults colonise flowering host plants and feed on pollen, and the larvae feed on the developing seeds before leaving the pods and pupating in the soil. The cabbage seedpod weevil (*C. obstrictus*) is native to Europe, and is a serious pest of brassicaceous oilseed crops in Europe and North America (Bartlet et al., 1993; Ferguson et al., 1999b; Ulmer and Dosdall, 2006; Valantin-Morison et al., 2007). The cabbage seedpod weevil is a small, dark grey "snout beetle" normally occurring after peak flowering and lays eggs in the pods of cruciferous plants. The larvae feed on seeds in the pods, which results in seed loss (Bartlet et al., 1993; Du Toit, 2007). When mature, the larvae leave the pods, and fall on the ground to pupate. Adults emerge in late July and feed before diapausing until the following spring. The cabbage seedpod weevil therefore needs to find a host plant at two stages of its life cycle: upon emergence from pupation in the summer (pre-diapause weevils), and upon emergence from hibernation the following spring (post-diapause weevils) (Bartlet

et al., 1993). The cabbage stem weevil (*C. pallidactylus*) is the major stem-mining pest of oilseed rape (Barari et al., 2005).

1.2.10. The aphids (Brevicoryne brassicae, Myzus persicae and Lipaphis erysimi)

Aphids have been considered as the main insect pests in India and northern European agriculture, and are also important pests in horticulture both in field and greenhouse production, causing damage to crops either directly by feeding or by transmitting plant viral diseases (Dawson et al., 1990; Sekhon, 1999). Aphids feed by piercing plant tissue with their needle-like mouthparts (stylets), sucking water and nutrients from the phloem vascular system of the plant. Feeding damage and toxins in the saliva cause thickening, crumpling and downward curling of leaves (Mossler, 2005). The nymphs and adults suck sap from leaves, stem, flowers and pods, hence resulting in poor pod formation and reduced oil content in grains. A severe aphid attack can result in up to 75% loss to *Brassica* crops (Sekhon, 1999). *B. brassicae* (Fig. 3) is a global problem with a strong negative impact on agriculture and horticulture. *B. brassicae* is controlled by multiple insecticide treatments (Kift et al., 2000; Pontoppidan et al., 2003) and is a severe pest on brassicas (Cole, 1994; Kift et al., 2000). *B. brassicae* is highly host-specific, feeding almost exclusively on the phloem sap of *Brassica* or other closely related plant species (Cole, 1997). *B. brassicae* produces parthenogenic, viviparous females throughout the year, which overwinter on horticultural brassicas and forage crops of rape and swede (Schroeder and Dumbleton, 2001). During spring, these females change into winged forms, fly to seedlings of brassicas and produce offspring (nymphs). The peach aphid (*M. persicae*) is a generalist (Fig. 3) reported to have more than 400 species as host plants (Quagila et al., 1993 as cited by Francis et al., 2001). The mustard aphid (*L. erysimi*) is the most important pest of cruciferous crops worldwide, causing damage of 10–90% depending upon the severity of the infestation and crop stage. Apart from causing damage as a sapsucker, it is also a vector of several viral diseases (Rana, 2005). A 2-year study on the preference and performance of *L. erysimi* on different *Brassica* species in the field and under greenhouse conditions revealed that rapeseed (*B. campestris* varieties BSH-1 and YSPB-9) and mustard (*B. juncea* RH-30) were better hosts for this aphid than other *Brassica* species (*B. napus*, *B. nigra*, *B. carinata*) (Rana, 2005). Moreover, *L. erysimi* is a harmful insect on *Brassica* oilseeds, especially on *B. juncea* in India and in other tropical regions of the world, causing up to 83% yield loss (Sekhon and Åhman, 1993; Mandal et al., 1994 as cited by Chattopadhyay et al., 2005; Agarwala and Datta, 1999; Aslam and Ahmad, 2001; Dutta et al., 2005; Hossain et al., 2006 and references therein). Aphids reproduce at a higher rate during the early vegetative stage of mustard plants when the developmental period is shortest and the production of winged morphs is lowest (Agarwala and Datta, 1999). The nymphs and adults cause damage by sucking away the plant sap, often covering the entire surface of the shoots, floral buds and pods. The pest breeds parthenogenetically, and an individual female gives birth to nymphs, which grow very fast and are completely bred in 7–10 days. About 45 generations are completed in a year. The high propagation rate of the pest affects the crop vitality, because the flowers fail to bear healthy pods, subsequently producing seeds of poor quality (Hossain et al., 2006 and references therein).

1.3. Plant defence mechanisms – General information

Typical defence mechanisms that exist or are expressed in plants include constitutive, inducible, induced, direct and indirect defences. The existence, expression and functioning mechanism of these defences show both parallelism and contrasts to each other. These defence mechanisms are defined and addressed in this section, and are referred to and documented in other sections of the article with regard to the chemistry of Brassicaceae plants towards insect interactions.

Plants and animals both possess the potential to differentiate between self and non-self (hostile organisms), which may vary according to the heredity and environment. A major difference between plants and animals is that plants are sessile and animals mobile and the latter therefore can spread infections more easily (Jones and Takemoto, 2004). In order to overcome infections, plants are not only equipped with diverse constitutive/innate/preformed but also adapted defence mechanisms, to defend themselves. Likewise, striking similarities and obvious differences have evolved in animals which also form the basis of inducible or induced defence mechanisms (Nürnberger and Brunner, 2002; Montesano et al., 2003). Constitutive defence mechanisms, which are also regarded as ancient defence systems, are weapons that involve various receptors that recognise classes of microbial cell-surface molecules, the related signal transduction pathways that activate transcription of genes related to host defence, and the ubiquitous cationic peptides and proteins that act as antimicrobial effectors (Boman, 1995; Borregaard et al., 2000; Thomma et al., 2002).

An ecosystem comprises plants circumvented by herbivorous insects that continuously affect plant fitness. In order to overcome these herbivorous insects or to protect themselves from damage by herbivoral arthropods, plants have developed physical and chemical defences, which can either be innate or inducible in response to a certain attack (Takabayashi and Dicke, 1996; Karban and Baldwin, 1997; Paré and Tumlinson, 1999; Dicke and Hilker, 2003). The occurrence of both defence responses establishes an intricate network of defences for plants against insect herbivores. Inducible defences may provide an adaptive defensive strategy in which non-lethal cues from predators, herbivores or parasites provide a reliable indicator about the future risk of attack (Agrawal et al., 1999). In order to reduce the impact of insect attacks, plants have developed different defence strategies that include chemical and physical barriers such as induction of defensive proteins, volatiles that attract predators of the insect herbivores, toxic secondary metabolites, and trichome morphology and density (Mello and Silva-Filho, 2002). These defence components produced by plants act both as constitutive substances

to repel herbivores through direct toxication, or by lowering the digestibility of plant tissues, and as inducible substances produced in response to tissue damage by herbivores.

Induced defences are activated in the presence of an enemy, and then emerge or develop to their full strength. This particular kind of defence is important with regard to innate resistance, in case the defence is metabolically expensive, and when the attack is unpredictable but frequent (Haukioja, 1999). Plant responses that affect herbivore arthropods directly through systemic production of toxic metabolites are named direct defences, whereas responses that result in the attraction of natural enemies of the herbivores are designated as indirect defences (Dicke, 1999; Mattiacci et al., 2001). The term indirect defence, that is generally used when plants attract, nourish or house other organisms to reduce pressure from their enemies, has been referred to in the literature only in the last 20 years (Dicke and Sabelis, 1989; see review by Heil, 2008). Indirect defence mechanisms contribute towards the efficiency of the natural enemies of herbivores, e.g. through the emission of blends of volatile compounds and other secondary metabolites (Vet and Dicke, 1992; Hilker and Meiners, 2002; Kessler and Baldwin, 2002; Dicke et al., 2003; Rohloff and Bones, 2005). Such release of volatile compounds from plants has been considered as the cry or call for help by the plant from the carnivorous enemies (which are predators of herbivores) that might assist in reducing damage to plants. The release of volatile compounds from damaged plants derives from at least three biosynthetic pathways: first, the fatty acid (or octadecanoid) pathway that produces green leaf volatiles and (*Z*)-jasmone; second, the shikimic acid pathway that produces indole and methyl salicylate; and third, the isoprenoid pathway which produces terpenes (Hilker and Meiners, 2002). Indirect defences are mostly referred to as an environmentally-friendly crop protection strategy, but their plant fitness effects require more information in order to understand their ecological and evolutionary relevance before trophic interactions can be used as a reliable tool in agriculture (Heil, 2008).

2. DEFENCE COMPONENTS OF BRASSICACEAE: GLUCOSINOLATES, THE GLUCOSINOLATE-MYROSINASE SYSTEM, PLANT VOLATILES, PHYTOALEXINS, PHYTOANTICIPINS AND SULPHUR

2.1. Glucosinolates

The characteristic feature of the Brassicaceae family is their production of specific secondary metabolites, the so-called glucosinolates (anionic thioglucosides) (Fahey et al., 2001; Bones and Rossiter, 2006). The glucosinolates constitute a large group of non-volatile and sulphur-containing secondary plant metabolites, which occur in all economically important *Brassica* crops (Tripathi and Mishra, 2007). Their known number totals almost 140 structures to date, 30 of which are present in *Brassica* species (Bellostas et al. 2007). Glucosinolates are β-thioglucoside *N*-hydroxysulphates with at least two sulphur atoms, one originating from cysteine, the other from phosphoadenosine phosphosulphate, possessing a β-D-glucopyranose moiety and a side chain derived from the amino acids methionine, tryptophan or phenylalanine (Fahey et al., 2001; Wittstock and Halkier, 2002; Rausch and Wachter, 2005). The content and composition of glucosinolates varies depending on *Brassica* species, the cultivar plant parts within the same plant, agronomic practices and climatic conditions (Sang et al., 1984; Clossais-Bernard and Larher, 1991; Rangkadilok et al., 2002; Font et al., 2005; Tripathi and Mishra, 2007). Glucosinolates are known to mediate interactions between Brassicaceae and their associated insect herbivores. They have been recognised as a class of natural pesticides since they exhibit toxic or repellent effects, by which they establish a significant defence mechanism to protect *Brassica* plants against pests and diseases (Mithen, 1992; Zukalová and Vašák, 2002). Glucosinolate levels and proportions of individual glucosinolate compounds have been demonstrated to be altered due to the damage caused by several insect pests (Koritsas et al., 1991; Bodnaryk, 1992; Hopkins et al., 1998). The glucosinolate concentration can increase in response to herbivore feeding, and this high level of glucosinolates can affect both generalist and specialist herbivores, and glucosinolates can be equally effective as stimulants as well as deterrents (Bodnaryk, 1992; Bartlet et al., 1999; Li et al., 2000; Rask et al., 2000; Agrawal and Kurashige, 2003; Kuśnierczyk et al., 2007, 2008; Gols et al., 2008a).

2.2. The glucosinolate-myrosinase defence system

The term *myrosin cell*, initially used by (Guignard, 1890), was discovered by (Heinricher, 1884). The myrosin cells can be easily distinguished from their neighbouring cells by light, electron and confocal microscopic observations (Bones and Iversen, 1985; Thangstad et al., 1990, 1991; Bones et al., 1991; Thangstad et al., 2004; Kissen et al., 2009). The myrosin cells contain less lipids, a high content of endoplasmic reticulum and harbour smooth-looking protein bodies referred to as myrosin grains (Bones and Iversen, 1985; Thangstad et al., 1991). Myrosin cells exist as scattered cells in stems, leaves, seeds, seedlings, petioles and roots. *Brassica* plants contain the enzyme myrosinase (β-thioglucoside glucohydrolase, thioglucosidase, EC 3.2.3.147 (formerly EC 3.2.3.1) (Bones and Slupphaug, 1989; Bones, 1990; Bones and Rossiter, 1996, 2006), which is thought to be exclusively present in myrosin cells (Thangstad et al., 1990, 1991; Bones et al., 1991; Höglund et al., 1991; Husebye et al., 2002; Thangstad et al., 2004; Kissen et al., 2009). In brassicas, myrosinases can be divided into three different gene families; the MA, MB and MC families (Xue et al., 1992; Chadchawan et al., 1993; Lenman et al., 1993; Thangstad et al., 1993; Falk et al., 1995). Furthermore, myrosinases are glycosylated dimeric proteins with subunit molecular weights from 62 to 75 kDa (Bones and Slupphaug, 1989; Bones and Rossiter, 1996). Myrosinases that belong to the MA family occur as free dimers (140 kDa), while members of the MB and MC families are found in high molecular complexes (200–1000 kDa), with myrosinase

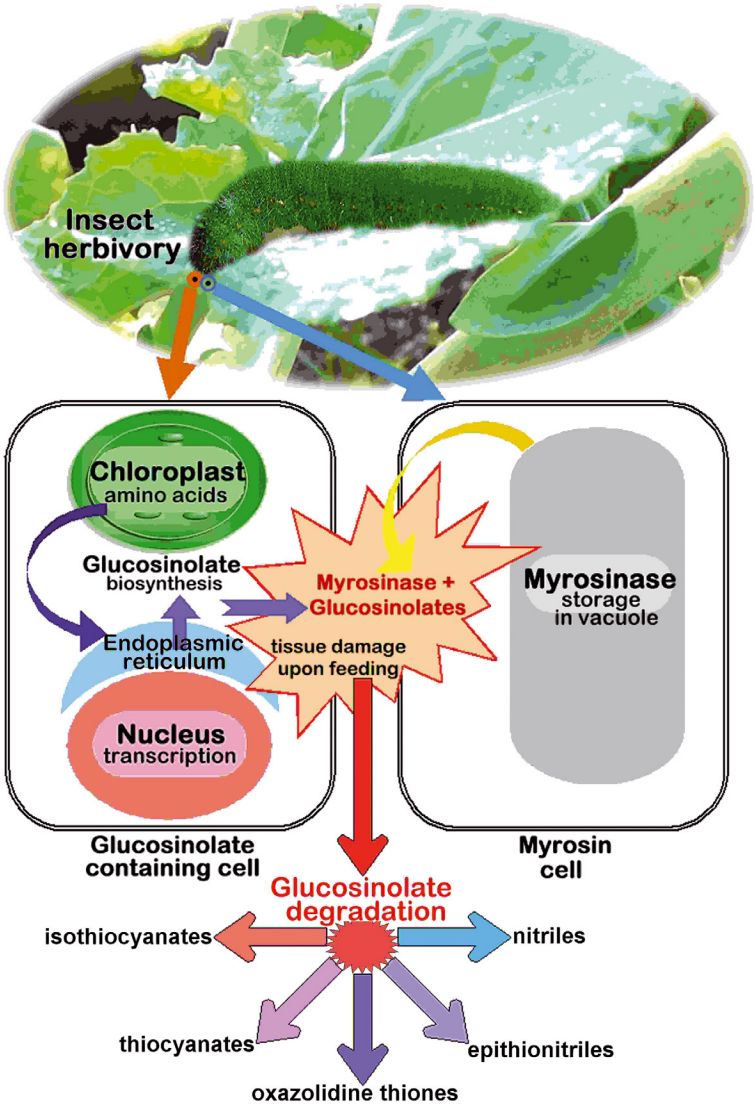


Figure 4. Insect herbivory brings glucosinolates and myrosinase together and facilitates the hydrolysis of glucosinolates.

binding proteins (MBP) and the myrosinase associated proteins (MyAP) (Rask et al., 2000).

Glucosinolates and myrosinases are spatially segregated (Kelly et al., 1998; Koroleva et al., 2000; Husebye et al., 2002), but insect herbivory or tissue damage bring them together, which facilitates glucosinolate hydrolysis into thiocyanates, isothiocyanates, nitriles, oxazolidine-2-thiones and epithionitriles, depending upon pH and other conditions (Fig. 4) (Pivnick et al., 1992; Bones and Rossiter, 1996, 2006; Wittstock and Halkier, 2002).

The biosynthesis of glucosinolates still poses questions with, e.g., respect to transport and tissue, cell and subcellular spatial separation and organisation (Svanem et al., 1997; Thangstad et al., 2001; Halkier and Gershenzon, 2006). Glucosinolates such as progoitrin, sinigrin, gluconapin and glucobrassicanapin can give rise to cyanoepithioalkanes (epithionitriles). The exact mechanism behind the formation of epithionitriles from these glucosinolates is not known, but depends on the presence of a protein known as epithiospecifier-protein (ESP) (MacLeod and Rossiter, 1985; Foo et al., 2000; Zabala et al., 2005; Bones and Rossiter, 2006). The breakdown products resulting from glucosinolate hydrolysis represent the 'defence-active' components and the dual functioning of glucosinolates and myrosinases coming into contact upon tissue disruption is designated as the glucosinolate-myrosinase defence system. This system has been shown to have multiple roles in plant-insect interactions and insect pest management (Bones and Rossiter, 1996, 2006; Rask et al., 2000).

It should be noticed that some insects such as *B. brassicae* and *L. erysimi* actively take advantage of the defence compounds produced by their host plants by sequestering toxic compounds from the plant and using these compounds to protect themselves from predators. *B. brassicae* and *L. erysimi* sequester glucosinolates which can be degraded by a thioglucosidase endogenously produced by the insect, when the latter is crushed (Jones et al., 2001, 2002; Bridges et al., 2002;

Table III. The diversity of plant volatiles and signalling compounds in Brassicaceae plants (Rohloff and Bones, 2005).

Compound group	Plant volatiles	Plant organ	Function
Green leaf volatiles	C_6-alcohols, aldehydes and acetates	Green plant parts	Plant-plant signalling, predator attraction, antimicrobial activity
Plant hormones	Jasmonic acid and salicylic acid derivatives, ethylene	Whole plant	Plant-plant signalling, induction of plant defences
Terpenes	Mono- and sesquiterpenes	Flowers, leaves, roots	Flower pollinator attraction, attraction of predators, antimicrobial activity
Aromatics	Benzyl and phenylethyl-derivatives	Mainly flowers	Flower pollinator attraction, antimicrobial activity
Glucosinolate-derived volatiles	Isothiocyanates, thiocyanates, oxazolidine thiones, nitriles, epithionitriles	All plant parts containing myrosinase and glucosinolates	Plant defence, herbivore attraction
Sulphur-containing compounds	Sulphides, elemental sulphur	Probably whole plant	Plant defence

Rossiter et al., 2003; Husebye et al., 2005). These crushed insects likely both smell/taste badly and release volatiles, alarming other aphids in the colony.

2.3. Plant volatiles

Throughout evolution, higher plants have evolved complex mechanisms to be able to communicate with their environment. Based on their capability for gas exchange, plants can release mixtures of plant volatiles having distinct biological functions related to plant-insect, plant-pathogen and plant-plant communication, and adaption to stresses (Kishimoto et al., 2005; Baldwin et al., 2002). Brassicaceae produce volatile and semi-volatile toxic compounds based on glucosinolate degradation upon tissue damage, thus directly functioning in plant defence. However, plant volatile communication is a much more sophisticated process (described in Sect. 3.2) of trophic interactions where, e.g., herbivore-attacked plants release volatile signals to attract predators of the feeding insects. In order to distinguish between the multiple roles and functions of plant volatiles in Brassicaceae, Table III briefly summarises the known chemical structure groups found in different plant parts and tissues.

2.4. Phytoalexins and phytoanticipins

Phytoalexins are low-molecular-weight antimicrobial compounds or secondary metabolites that are synthesised de novo, while phytoanticipins are pre-formed inhibitors of infection (Dixon, 2001; Rouxel et al., 1991). However, the distinction between phytoalexin and phytoanticipin is not always clear as some compounds may be phytoalexins in one species, and phytoanticipins in others (Dixon, 2001). Phytoalexins and phytoanticipins are also referred to as two significant classes of natural pesticides exerting different methods of action (Zukalová and Vašák, 2002). Phytoanticipins emerge from already created precursors, and phytoalexins commence as the result of an external affect due to distinct metabolic activity. Glucosinolates and the glucosinolate-myrosinase system represent an example of such a type of phytoanticipin since myrosinase and glucosinolates are already biosynthesised as precursors before insect attack (Zukalová and Vašák, 2002). The glucosinolate-myrosinase system, which has been throughly investigated in the past decades, is to a large extent considered as a constitutive, as well as inducible type of defence system. It is highly dynamic, interactable with insect pests and a well-established mechanism towards integrated pest management (Bones and Rossiter, 1996, 2006; Rask et al., 2000; Wittstock et al., 2004; Müller and Sieling, 2006). Isothiocyanates produced after glucosinolate hydrolysis by myrosinases play crucial ecological roles in protecting plants against various pests, including insects and microbial systems. Therefore, isothiocyanates are part of a group of basic plant chemical defences known as phytoanticipins (Pedras et al., 2007a). Moreover, phytoalexins from the Brassicaceae family are the only sulphur-containing and nitrogen-containing phytoalexins including an unexpected range of functional groups and indolyl structures (Pedras et al., 2007b). Brassinin, 1-methoxy brassinin, brassilexin and cyclobrassinin are sulphur-containing indole phytoalexins, which have been isolated from different *Brassica* species (Rouxel et al., 1991). Brassinin and 1-methoxybrassinin, which contain a dithiocarbamate group, were the first phytoalexins to be reported. Dithiocarbamates have been recognised as important pesticides and herbicides and until now crucifers are the only plants known to produce such compounds (Pedras et al., 2000).

2.5. Sulphur

The plants of the family Brassicaceae are known to be rich in sulphur (Williams and Cooper, 2004). Sulphur is necessary for plant development and sulphur-containing compounds such as sulphur-rich antifungal proteins, phytoalexins and glucosinolates play an important role in plant defence against pathogens (Dubuis, 2004). *Brassica* plants use sulphur

(S) to synthesise glucosinolates and phytoalexins. Cysteine, the primary product of sulphur assimilation, is incorporated into sulphur-rich proteins (SRPs; including thionins) and glutathione. Furthermore, cysteine is the donor of reduced sulphur for glucosinolate biosynthesis and for the synthesis of phytoalexins (including camalexin) (Rausch and Wachter, 2005). Low sulphate availability has also been shown to induce the expression of myrosinase proteins in *Sinapis alba* plants (Bones et al., 1994; Visvalingham et al., 1998). Pathogen attack and abiotic elicitors lead to the synthesis of sulphur-containing phytoalexins such as brassinin and concentration at the site of pathogen attack. Moreover, leaves of some *Brassica* varieties possess the constitutive elemental sulphur (S^0) that may be related to an alternative process of S^0 biosynthesis, such as from the degradation of certain glucosinolates (see reviews Bones and Rossiter, 1996; Williams and Cooper, 2004). Elemental sulphur as cyclooctasulphur S^8 has been reported to have antimicrobial activity in *Theobroma cacao* (Cooper et al., 1996) and similar inorganic sulphur compounds are also present in Brassicaceae (Rohloff and Bones, 2005).

3. CHEMICAL ECOLOGY AND INSECT BEHAVIOURAL ASPECTS

The chemical ecology of plant-insect interactions deals with chemical signals mediating all aspects of insects' lives, their ecological interactions through identification, and defining the chemicals involved in these interactions (Cardé and Millar, 2004). These chemical signals and ecological interactions include: chemical mediators modifying insect behaviour, plant chemicals to protect from insect herbivores (below- and above-ground), multitrophic interactions among plants-herbivores-parasitoids-hyperparasitoids, oviposition, semiochemical-mediated interactions, and the chemical cues that parasitoids use to find their herbivore hosts. Plant chemicals that elicit immediate behavioural responses in insects are generally categorised as attractants (eliciting oriented movements towards the source), arrestants (causing aggregation), stimulants (eliciting feeding, phagostimulation, oviposition, etc.), repellents (causing oriented movements away from the source) and deterrents (inhibiting feeding or oviposition) (Ryan, 2002).

In an article entitled "Developing sustainable pest control from chemical ecology" (Pickett et al., 1997), the significance of chemical ecological relations is emphasised in order to understand insect/insect and insect/plant interactions, and insect behaviour influenced by pheromones and other semiochemicals. This type of knowledge opens up promising pest control methods as alternative strategies to the exclusive use of broad-spectrum pesticides. In general, insect behaviour results from the integration by its central nervous system of a variety of inputs that derive from stimuli acting on exteroceptors (that sense events external to the insect), enteroceptors (that sense the internal physiological state of the insect), and proprioceptors (that sense the relative positions of parts of the body) (Foster and Harris, 1997).

On the background of chemical ecological and insect behavioural aspects, we have mainly focused on and reviewed regulation of oviposition during insect attack and behaviour of the different herbivore insects that attack brassicas, and their trophic interactions. The oviposition and trophic interaction studies mainly revolve around the response of plant cues and chemicals from *Brassica* plants towards these insects, which have been discussed with special emphasis on glucosinolates, their breakdown products, and blends of plant volatiles that are released during oviposition and multitrophic (second, third or fourth level) interactions. Figures 5 and 6 show the diagrammatic presentation of larvae feeding, oviposition process by adult insects, the trophic interactions of *Brassica* plants as hosts, their herbivore insects and the predators or parasitoids of herbivores.

3.1. Oviposition

The search for an oviposition site by flying insects comprises two phases of behaviour, i.e. pre-alighting and post-alighting (Hopkins et al., 1999). The pre-alighting behaviour of an insect, captivated by a range of visual and odour stimuli, ends up in contact with a potential host plant, and the post-alighting behaviour of the female on the host plant depends upon the balance of the internal physiological condition and external stimuli that she perceives (Hopkins et al., 1999). Olfaction (the sense of smell) has an important role after an insect has landed on a plant, and before it moves to leaves or down to the soil to oviposit. Physical factors such as size, colour and leaf structure characteristics have been shown to influence oviposition behaviour, since bright green surrogate leaves (sprayed with a leaf surface extract of the host plant, with a stem, possessing vertical folds to mimic veins, and with a paraffin cover to mimic the wax layer) received the most eggs (Roessingh and Städler, 1990). Most herbivorous insects firstly attack plants by oviposition. Most lepidopterans do not feed on leaves as adults, but females deposit their eggs on those plants or plant parts where hatching larvae will find suitable food (Hilker and Meiners, 2006). In order to protect themselves against feeding damage, the oviposition-induced plant responses are targeted against eggs laid on the plant, the hatching larvae, or the egg-laying gravid female (Hilker and Meiners, 2002, 2006).

Chemical stimulation of oviposition is a complex process, and specific chemicals are involved in the acceptance of hosts and rejection of non-host plants (Hamilton et al., 2005). Ovipositing females seem to employ plant volatiles as cues for orientation to host plants and the following contact evaluation of plants by means of less- or non-volatile secondary metabolites has a great significance in host recognition (Keiichi, 1995). It was further highlighted that the acceptance or rejection of a particular plant by females is regulated not only by the presence or absence of oviposition stimulants, but by negative stimuli evoked by co-occurring deterrents. Moreover, oviposition-deterring activity has also been observed in leaves without eggs, but adjacent to those carrying eggs, hence indicating a systemic effect (Hilker and Meiners, 2002). Plant

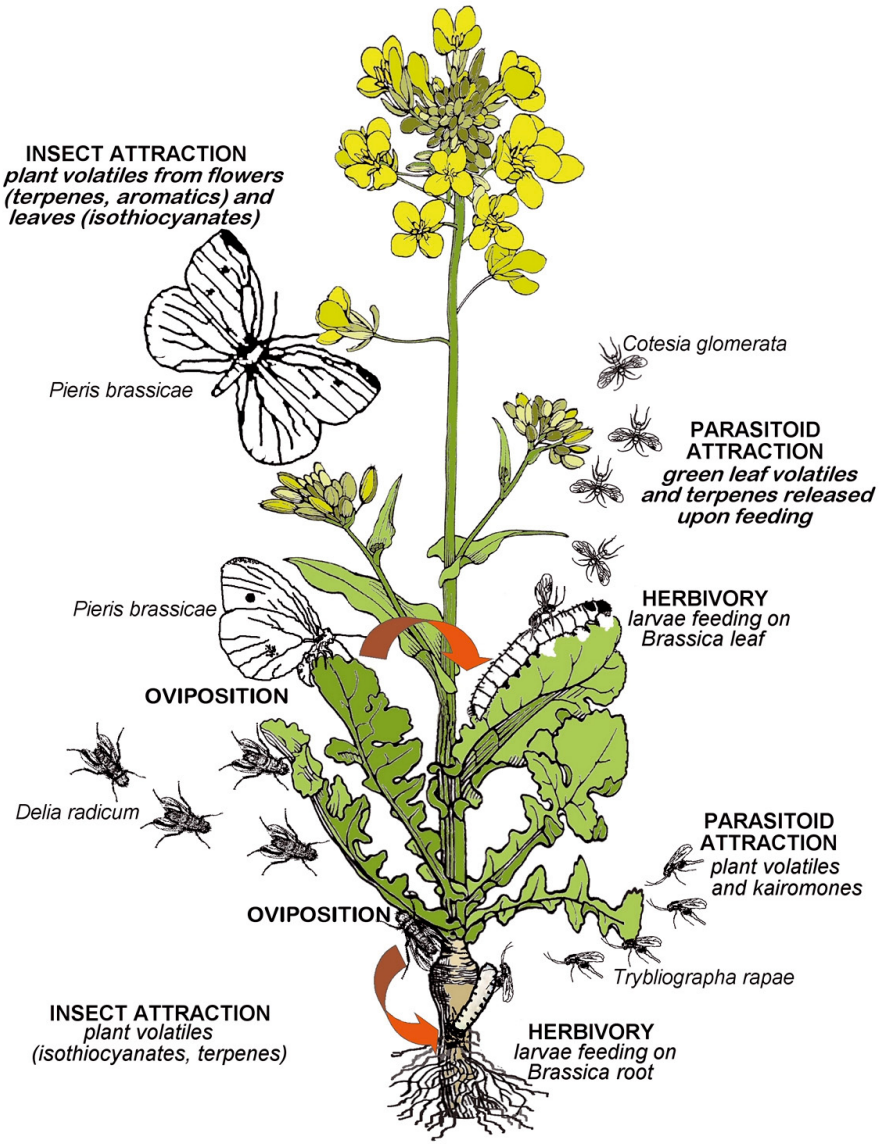


Figure 5. *Brassica* plant as host showing leaf feeding, oviposition and trophic interactions by larvae and adults of *Pieris brassicae* and *Delia radicum* and their parasitoids (modified after Ross-Craig, 1949).

secondary compounds, influencing antixenosis (Tab. IV), are mentioned as a link with oviposition specificity or feeding stimulation of more than 20 insect species (Hopkins et al., 1997). Moreover, plant secondary compounds (or allelochemicals) (Tab. IV) from a particular plant may be oviposition stimulants or deterrents for insects, which feed on that plant (Renwick and Radke, 1981, 1985) and oviposition deterrence by these compounds possibly has significant consequences for crop pest management (Tabashnik, 1987). These chemical deterrents/stimulants evidently play a significant role in the acceptance or rejection of plants as hosts by ovipositing female butterflies.

It has been stated that the induced defence responses both in above-ground and below-ground plant parts are common (Van Dam and Raaijmakers, 2006). Feeding damage by below-ground herbivores may cause a systemic increase in defensive compounds in above-ground parts, hence leading to interactions between above-ground and below-ground herbivores feeding on the same plant. These kinds of above- and below-ground interactions stimulated by induced responses may alter damage patterns and, finally, affect fitness or plant survival (Bezemer and Van Dam, 2005; Van Dam and Raaijmakers, 2006). Furthermore, the root herbivores of oilseed rape, kale, swede and canola have been shown to affect plant performance, commercial yield and plant chemical defence.

Based on oviposition behaviour of different insects and plant defence, we have reviewed essential works that have been conducted on insects that oviposit on *Brassica* plants. In recent years, most of the investigations pertaining to insect oviposition behaviour and related chemical aspects of *Brassica* plants have been focused on white butterflies

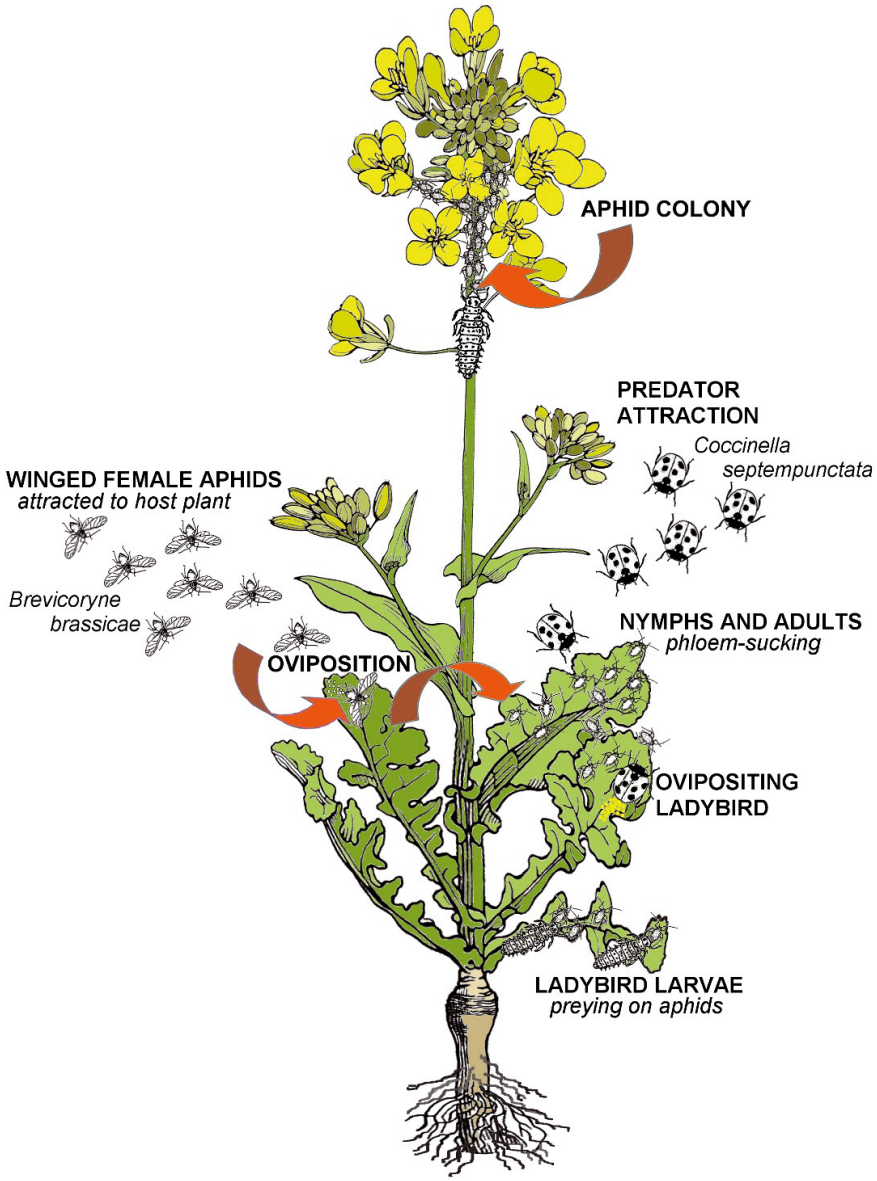


Figure 6. *Brassica* plant as host showing aphid oviposition, colony and trophic interactions between cabbage aphid (*Brevicoryne brassicae*) and its ladybird predators (*Coccinella septempunctata*) (modified after Ross-Craig, 1949).

(*Pieris* spp.), cabbage seed and seedpod weevils (*Ceutorhynchus* spp.), and cabbage root and turnip root flies (*Delia* spp.), with few studies on diamondback moth (*P. xylostella*), cabbage looper (*T. ni*), cabbage moth (*M. brassicae*) and brassica pod midge (*D. brassicae*).

3.1.1. White butterflies (Pieris brassicae and P. rapae)

Almost thirty years ago, it was observed that gravid female *P. brassicae* butterflies show discrimination behaviour in their choice of a plant to oviposit on (Behan and Schoonhoven, 1978). In another study from the 1980s regarding oviposition preferences of field-collected *P. rapae* butterflies towards *B. nigra* plants, leaf water content was considered as a phenotypic characteristic associated with oviposition preference (Wolfson, 1980). Renwick and Radke (1985) further showed that oviposition by *P. rapae* on cabbage was deterred by homogenised cabbage tissue sprayed onto intact plants. Polar as well as non-polar extracts of non-host plants inhibited oviposition. In another investigation, oviposition by *P. rapae* butterflies was deterred by spraying the plant secondary compounds coumarin and rutin on cabbage plants in greenhouse tests. Both coumarin and rutin deterred oviposition primarily by affecting prealighting rather than postalighting behaviour, indicating that deterrence was mediated by non-contact cues

Table IV. Definitions of significant terms mentioned in the article.

Term		Definition	Reference
1	Allelochemical	An infochemical that mediates an interaction between two individuals that belong to different species.	(Dicke and Sabelis, 1992)
2	Antixenosis	A term that is derived from the Greek word 'xeno' (guest) that describes the inability of a plant to serve as host to an arthropod, e.g. insect, represents plant traits conferring non-preference of herbivores, i.e. reduced acceptance for oviposition or feeding.	(Smith, 2005)
3	Deterrent	A chemical that inhibits behaviour, such as feeding or oviposition, when applied to a site where such behaviour normally occurs.	(Blossey and Hunt-Joshi, 2003)
4	Infochemical	A chemical that, in the natural context, conveys information in an interaction between two individuals, evoking in the receiver a behavioural or physiological response.	(Dicke and Sabelis, 1992)
5	Semiochemical	A term that is derived from the Greek word 'semion' (a mark or a signal). Chemicals, which function in communication between and among species, as well as those that serve as messengers between members of the same species.	(Law and Regnier, 1971 as cited by Paré and Tumlinson, 1999)

(Tabashnik, 1987). In a comparative study of oviposition responses of *P. rapae* and *P. napi* to nine crucifers, the results showed that the two *Pieris* spp. have apparently evolved differential sensitivities to the chemical stimuli that trigger or deter oviposition. The balance of positively and negatively interpreted sensory signals generated by plant chemicals obviously plays an important role in acceptance or rejection of a plant by both species. Moreover, in an investigation of leaf volatiles, while the large white butterfly (*P. brassicae*) was laying eggs, it was found that the young cabbage leaves on which *P. brassicae* had laid eggs emitted larger amounts of the monoterpene α-thujene than young clean leaves (Bergström et al., 1994). Furthermore, the oviposition-deterring pheromones (ODPs) of *P. brassicae* and *P. rapae* have been considered to be produced in the female accessory glands, and contain volatile and non-volatile components. Oviposition-deterring pheromones are natural and species-specific compounds that inhibit oviposition, and seem suitable chemicals to reduce crop infestation by insects utilising them, since they produce very low environmental risks (Schoonhoven, 1990).

The potential of glucosinolates in stimulating feeding by larvae and oviposition by adults has been confirmed for *P. brassicae* and *P. rapae* through studies showing that ovipositing *P. rapae* adults respond more strongly to indole glucosinolates, such as glucobrassicin, and less strongly to aliphatic glucosinolates, such as glucocheirolin (Rodman and Chew, 1980; Renwick et al., 1992; Van Loon et al., 1992; Huang and Renwick, 1993; Renwick, 2001). Some of these studies showing response of these insects towards glucosinolates and isothiocyanates are described in more detail below.

Already in 1980, Rodman and Chew showed that the oviposition and larval feeding by *P. napi* is associated with glucosinolate profiles of plant species. Later, Klijnstra and Roessingh (1986) suggested that foretarsal taste hairs of females, apart from the glucosinolate cells, also possess sense cells specifically sensitive to the oviposition-deterring pheromones. These different sense cells are responsible for the sensitivity of tarsal "B-type hairs" to eggwash and glucosinolates. The so-called "B-type hairs" comprise one type of trichoid sensilla which is recognised on the tarsi of *P. brassiace* (Ma and Schoonhaven, 1973). The oviposition by *P. rapae* on cabbage was shown to be stimulated by the glucosinolate glucobrassicin. Other studied glucosinolates were sinigrin, which was slightly active, and glucoiberin, which was completely inactive as a stimulant (Renwick et al., 1992). Another investigation involving oviposition bioassays between cabbage (*B. oleracea*) leaves and *P. brassicae* also identified glucobrassicin as the oviposition stimulant (Van Loon et al., 1992). Moreover, Traynier and Truscott (1991) showed that solutions of glucobrassicin purified from foliage and sinigrin elicited oviposition by the cabbage butterfly, *P. rapae*, at threshold concentrations as low as 10^{-6} M while at higher concentrations, glucobrassicin elicited a faster oviposition rate and a stronger visual response to the substrate through associative learning. In another comparative study on the relative activities of 10 glucosinolates in stimulating oviposition by *P. rapae* and *P. napi,* it was observed that in most cases, *P. rapae* was more sensitive to aromatic and indole glucosinolates than to aliphatic ones (Huang and Renwick, 1994); however, *P. napi* responded strongly to aliphatic glucosinolates.

Bruinsma et al. (2007) investigated the effect of jasmonic acid (a key hormone involved in plant defence responses) on Brussels sprouts (*B. oleracea* var. *gemmifera*) and their acceptability for oviposition by the butterflies *P. rapae* and *P. brassicae*. The investigation showed that both butterfly species laid fewer eggs on leaves of jasmonic acid-treated plants than on leaves of control plants. It was further shown that application of jasmonic acid doubled the

concentration of the glucosinolate glucobrassicin and lowered the concentrations of the glucosinolates glucoiberin and 4-hydroxyglucobrassicin.

3.1.2. *Cabbage seed and cabbage seedpod weevils (Ceutorhynchus assimilis and C. obstrictus)*

In order to develop resistant crop germplasm, it is important to understand how host-plant characteristics affect behavioural and physiological responses of insect herbivores. With this hypothesis, Ulmer and Dosdall (2006) investigated feeding, oviposition preference, larval development and oviposition behaviour of the cabbage seedpod weevil (*C. obstrictus*) on eight Brassicaceae species that differ in their glucosinolate profiles. Among these eight *Brassica* species, the preferred host plant for feeding and oviposition was *B. carinata*, larval development occurred most rapidly on *B. rapa*, and the larval weight was highest on *B. napus*. Total glucosinolate levels did not influence *C. obstrictus* larval growth or development; however, high levels of specific glucosinolates such as sinalbin and gluconapin were associated with increased developmental time or reduced weight.

In a linear track olfactometry test to observe responses of the cabbage seed weevil (*C. assimilis*) to volatiles from oilseed rape (*B. napus*), weevils showed attraction towards the odour of rape during a short period before diapause and for most of their postdiapause life (Bartlet et al., 1993). Apart from that, attraction was also observed for 3-butenyl and 4-pentenyl isothiocyanate, but not for 2-phenylethyl isothiocyanate. A mixture of the three isothiocyanates was more attractive than the individual isothiocyanates. Furthermore, the effects of extracted and artificial oilseed rape odours on the behavioural response of male and female cabbage seed weevils were investigated in a wind tunnel experiment (Evans and Allen-Williams, 1998). Omission of two isothiocyanates from the artificial extract significantly reduced the upwind movement of females.

After oviposition into a pod of oilseed rape, the female cabbage seed weevil marks the pod with oviposition-deterring pheromones by brushing it with her eighth abdominal tergite (Ferguson et al., 1999b). This oviposition-deterring secretion of the cabbage seed weevil was demonstrated to contain iso- and n-alkanes, dimethylalkanes, alkenes, fatty acids, 15-nonacosanone, 15-nonacosanol, and cholesterol (Mudd et al., 1997). Extracts of volatiles entrained from ovipositing weevils failed to inhibit oviposition. The authors evidenced that the oviposition-deterring pheromones of the cabbage seed weevil are sensed primarily by contact chemoreception at the sensilla chaetica of the antennae, and the electrophysiological responses recorded from these gustatory sensilla retain significance as a bioassay to assist identification of the active constituent(s) of the pheromone (Ferguson et al., 1999a). In their previous study, it was reported that the decision of a seed weevil to accept or reject a pod for oviposition to some extent depends upon cues perceived via antennal sensilla. In order to select an oviposition site, a female weevil walks back and forth along the pod, antennating the substrate much more intensively than when walking on the stem or petiole (Ferguson and Williams, 1991).

3.1.3. *Cabbage and turnip root flies (Delia radicum and D. floralis)*

The very first detailed work published on the behavioural responses of cabbage root fly (*D. radicum*) (Traynier, 1967a, b) to host plants specified that the odour stimulates activity and that chemical contact stimulates oviposition (Hawkes and Coaker, 1979). In a visual host finding, and shape recognition study on the cabbage root fly, using four shapes of yellow sticky traps as plant models, Tuttle et al. (1988) indicated that yellow discs or crosses at ground level baited with allyl isothiocyanate effectively monitored female cabbage root fly. The main factors affecting female landing were suggested to be the colour of substrate, height above the ground, presence of host volatiles in the vicinity, visual prominence, and size of the total area of 'attractive' colour. The initial landing phase of turnip root fly (*D. floralis*) (period between landing on the leaf and the first movement across the leaf) was shown to be crucial for host-plant expedition prior to oviposition site selection (Hopkins et al., 1997). The behavioural sequence analysis of individual gravid female turnip root flies showed that during the postalighting behaviour of turnip root fly, the decision to reject a highly resistant plant was predominantly based on plant cues received during a stationary period immediately after landing on the leaf (the leaf contact phase) (Hopkins et al., 1999). The host-plant acceptance by the cabbage root fly seems to result from a synergistic response to simultaneously perceived olfactory and contact chemostimulation (De Jong and Städler, 1999; De Jong et al., 2000). It was elucidated that female flies, after landing on a potential host, explore the plant by walking on the leaf surface and stem. Due to this exploration, the taste receptors located on the tarsi detect the presence of host-specific cues which stimulate the flies to descend to the soil and oviposit.

Glucosinolates, glucosinolate hydrolysis products such as isothiocyanates, and other volatile compounds are important cues for the cabbage root fly in locating and recognising a suitable host, and are involved in the feeding behaviour. Only mated gravid females respond to them (Hawkes and Coaker, 1979; Nottingham and Coaker, 1985; Renwick et al., 1992; Roessingh et al., 1992; Simmonds et al., 1994; De Jong and Städler, 1999; Hurter et al., 1999). In a study examining the role of glucosinolates towards oviposition behaviour of the cabbage root fly using egg counts and electrophysiological recordings from tarsal chemoreceptors, Roessingh et al. (1992) showed that the D sensilla on segments 3 and 4 of the tarsus of cabbage root fly females contain a sensitive receptor cell for glucosinolates. The flies clearly distinguished between model leaves with and without glucosinolates, but a clear dose response curve was only obtained for the indole glucosinolate glucobrassicin, which indicates that glucobrassicin on the cabbage leaf surface stimulates oviposition. Another study involving behavioural and chemosensory responses of the turnip root fly to glucosinolates demonstrated that slight modifications in

chemical composition of glucosinolates resulted in alterations in neural activity (Simmonds et al., 1994). Furthermore, of the eleven glucosinolates tested in these studies, the flies reacted most to glucobrassicanapin, gluconapin and glucobrassicin. Investigation of *B. nigra* and *B. oleracea* plants against cabbage root fly displayed a local increase in indole glucosinolates in the main roots, with *B. oleracea* plants showing a stronger increase in indole glucosinolate levels than *B. nigra*, which was the preferred feeding site of cabbage root fly larvae (Van Dam and Raaijmakers, 2006). Moreover, the increase in indole glucosinolates in *B. nigra* main roots was counterbalanced by a significant decline in aromatic glucosinolates.

Apart from glucosinolates, *Brassica* phytoalexins have been documented as playing a significant role in oviposition (Roessingh et al., 1997; Baur et al., 1996, 1998; De Jong et al., 2000; Hurter et al., 1999; Marazzi et al., 2004a, b). Two compounds, the so-called "Cabbage Identification Factors" (CIFs) are isolated from the surface of *B. oleracea* cv. *botrytis* leaves and identified. These compounds, perceived by a specific receptor neuron in the tarsal sensillum C5 of the female fly (Roessingh et al., 1997), are strong stimulators of oviposition in the cabbage root fly. Spectroscopic data indicated that the main CIF compound (1,2-dihydro-3-thia-4,10,10b-triazacyclopenta[.a.]fluorene-1-carboxylic acid) is a novel compound related to *Brassica* phytoalexins such as brassicanal C and is accompanied by its glycine conjugate. Cabbage (*B. oleracea*) leaves contain these compounds in extremely low concentrations but higher levels were detected in the roots of *B. napus* var. *napobrassica* (rutabaga) (De Jong et al., 2000). Furthermore, surrogate leaves treated with methanolic leaf surface extracts of *B. napus* plants that received three different sulphur fertilisation treatments showed even more marked differences by the oviposition choice of cabbage root fly than the potted plants. The oviposition data was shown to be positively correlated either with CIF or glucosinolates (Marazzi et al., 2004a). Investigation on application of eleven crucifer-specific phytoalexins and related synthetic compounds on surrogate paper leaves, being offered to cabbage root flies in oviposition assays, showed three of them (methoxybrassinin, cyclobrassinin and brassicin) to be significantly stimulatory, whereas the remaining metabolites had no effect, suggesting that the reaction of the fly appears to be structure-specific (Baur et al., 1998). In their previous observations, the authors suggested that the cabbage root fly tends to choose plants infected by suitable bacteria, and thus phytoalexins produced by the infected plant might be providing the specific guiding signal (Baur et al., 1998). The cabbage root fly seems to present another example of a herbivore preferring already attacked plants, which is consistent with the possibility that some phytoalexins act either as a signal for host-plant detection or as a marker for optimally preconditioned plants.

3.1.4. Diamondback moth (Plutella xylostella)

The oviposition preference of *P. xylostella* for cabbage, broccoli and cauliflower was observed in the field (Hamilton et al., 2005). No difference was observed in the number of eggs found on the broccoli or cauliflower cultivars. The eggs that were laid on cultivar *Savoy King* were higher than any of the cultivar tested. Larvae development was more rapid and longer on the cabbage cultivar *Green Coronet* than the cultivar *Savoy King*. It was concluded that in the field, *Savoy King* (cabbage cultivar) is more attractive to oviposition.

Renwick et al. (2006) demonstrated isothiocyanates to be oviposition stimulants for the diamondback moth. Hughes et al. (1997) showed that potent oviposition stimulants for the diamondback moth are extracted from cabbage foliage by soaking the intact leaves in chloroform. Analysis of these extracts revealed the presence of two isothiocyanates, iberin and sulphoraphane. Other isothiocyanates with sulphur in the side chain were also reported to be active.

In 1960, Gupta and Thorsteinson studied the effect of sulphur mineral nutrition on two Brassicaceae species (*S. alba* and *B. nigra*) and demonstrated that the constituents of host plants affected larval feeding and oviposition of *P. xylostella*. In order to observe sulphur perception by the diamondback moth, Marazzi et al. (2004a) raised *B. napus* plants under three different sulphur regimes: sulphur-free, normal field concentration and sulphur-rich (twice the normal field concentration). In addition, they performed dual oviposition assays with the diamondback moth, using either *Brassica* plants or artificial leaves sprayed with methanolic leaf-surface extracts. It was shown that chemical compounds on the leaf surface mediate the oviposition preference and that the female insect can perceive the quality of the host plants in terms of their fertilisation status. Since the leaf content of the volatile isothiocyanates is influenced by sulphur nutrition, the authors analysed the extracts for the presence of these compounds. Eleven glucosinolates were identified, with progoitrin and gluconapoleiferin being the most abundant ones. Sulphur nutrition has also been reported to differentially affect the expression of the glucosinolate-hydrolysing myrosinases (Bones et al., 1994).

3.1.5. The cabbage looper (Trichoplusia ni)

The cabbage looper exhibits a chemical spacing mechanism. This chemical spacing mechanism was noticed as feeding larvae deterred oviposition by gravid females and larval frass, since debris or excrement produced by insects were found to contain the biologically active material (Renwick and Radke, 1980 as cited by Renwick and Radke, 1981). The concept that host-plant chemicals play a role in the spacing of phytophagous insects was introduced by Cirio in 1971 (as cited by Renwick and Radke, 1981). Based on this concept, Renwick and Radke (1981) also demonstrated that the cabbage looper depends on the host plants to avoid overcrowding. Furthermore, the results by Landolt (1993) suggested an important role for damage-induced plant volatiles in host location as well as host acceptance by *T. ni.*

Chow et al. (2005) observed the effects of larval experience with complex plant latex (*Hoodia gordonii*) on subsequent feeding and oviposition by the cabbage looper moth.

The study showed that naïve groups of *T. ni* moths are deterred from feeding and ovipositing on cabbage leaves treated with the *H. gordonii* latex, and that larval feeding experience can lessen or reverse this deterrence. It was further suggested that moths may be acquiring oviposition preferences from larval feeding experience as described by Hopkins' host selection principle (HHSP). This principle, also called theory of larval memory, postulates that the adult females of phytophagous insects will prefer to feed or oviposit on the same plant species upon which they themselves developed as larvae (Hopkins, 1917 as cited by Barron, 2001 and stated by Chow et al., 2005).

3.1.6. The cabbage moth (Mamestra brassicae) and Bertha armyworm (Mamestra configrata)

The cabbage moth (*M. brassicae*) often chooses *Brassica* plants as hosts for oviposition (Ulland et al., 2008). The mortality of eggs, larvae, pupae and larval dispersal of the cabbage moth on white cabbage (*B. oleracea* var. *capitata*) was investigated in a series of small-scale field experiments and in the laboratory (Johansen, 1997). The highest mortality was found in young larvae and in hibernating pupae. The main mortality factor was found to be unfavourable weather conditions, and cold stress.

Furthermore, in other oviposition studies, Rojas and Wyatt (1999) analysed the influence of pre-imaginal (larval conditioning) and post-imaginal experience (adult conditioning) on the orientation, landing and oviposition of the female cabbage moth in a wind tunnel. The females were initially attracted to and landed on chrysanthemum whether or not they fed on this plant species. In addition, the oviposition preference for cabbage plants was not changed by the larval feeding regimen (a regulated system of a diet). Overnight exposure of females to chrysanthemum or cabbage plants decreased the subsequent orientation/landing on the same species offered in non-choice tests. However, it had no effect on subsequent oviposition as females from both treatments oviposited more on cabbage. In another study, Rojas et al. (2000) investigated the orientation and oviposition behaviour of *M. brassicae* on the most preferred host (cabbage) and two other host plants, tomato and chrysanthemum. It was observed that after landing on the plant, the insects were most likely to lay eggs on cabbage and tomato, but the behavioural sequence on these plants was shown to be different. Half of the females laid eggs on tomato only after dragging the ovipositor on the leaf, whereas almost all females laid eggs on cabbage after touching the surface with the ovipositor only briefly. The authors proposed that an understanding of these behaviours could help establish appropriate conditions for future studies on chemical identification of plant semiochemicals mediating host finding of the cabbage moth. The same group also investigated the age at which females begin to lay, the daily pattern of oviposition and the influence of host-plant material on egg-laying, as well as the host preference of *M. brassicae* under laboratory conditions (Rojas et al., 2001). It was observed that the females started ovipositing during the third, fourth and fifth scotophases after emergence. Maximum oviposition occurred during the second hour of scotophase. The females without host-plant material laid fewer eggs than females with host-plant material (*B. oleracea* var. *capitata*). In two-choice tests, the females preferred to oviposit on cabbage rather than chrysanthemum, but there was no difference in the mean number of eggs laid on cabbage and tomato.

Ulland et al. (2008) identified methyl salicylate as primary odorant of a specific receptor neuron type, and showed that it inhibits oviposition by *M. brassicae*. The behavioural effect of methyl salicylate was studied in outdoor test arenas with *B. napus* and artificial plants (Ulland et al., 2008). The experiments indicated that mated *M. brassiace* females avoid plants with dispensers emitting methyl salicylate. It was further pointed out that as methyl salicylate is induced by caterpillar feeding, it may mediate a message to mated *M. brassicae* females that the plant is already occupied.

The oviposition biology of the Bertha armyworm was studied in relation to the effect of conspecific eggs on oviposition site selection (Ulmer et al., 2003). Females strongly preferred to oviposit on leaves with eggs of a different female than on leaves without eggs. Gravid females preferred leaves that were treated with methanol, highlighting that the source of oviposition stimulation is possibly chemical-based.

3.1.7. The Brassica pod midge (Dasineura brassicae)

The oviposition behaviour of the brassica pod midge was compared on a preferred host (*B. napus*) with that of a non-preferred, less suitable host (*B. juncea*) for larval growth (Åhman, 1985). The number of landing females was significantly higher on *B. napus* than on *B. juncea*, indicating host differences in olfactory and/or visual stimuli. After landing, the females showed different behaviour on the two species by staying longer and laying more egg batches on *B. napus* than on *B. juncea* plants (Åhman, 1985). In another study by the same author looking at the toxicities of *Brassica* secondary compounds to the eggs of *D. brassicae*, the nitrile compound 1-cyano-2-phenylethane was shown to be more toxic than a "green leaf alcohol", (*Z*)-3-hexen-1-ol (Åhman, 1986). The author further suggested that a crucifer specialist may be restricted in its use of particular hosts due to the compositions and concentrations of glucosinolate compounds.

3.2. Trophic interactions among *Brassica* crops-herbivores-parasitoids-hyperparasitoids

"Nearly 75% of the world's macroscopic biodiversity is tied up in the look between plants, herbivores, predators and decomposers. In this context, the study of trophic interactions, involving plants, herbivores, and their predators or parasitoids represents a frontier in ecology, and this knowledge can be integrated in environmentally sound agricultural pest management" (Sergio Rasman, Cornell University, USA).

Multitrophic interactions among host plants (first trophic level), herbivores (second trophic level), natural enemies of herbivores/carnivorous arthropods/parasitoids/predators (third trophic level), and hyperparasitoids (fourth trophic level) have been well documented (Agrawal, 2000; Shiojiri et al., 2002; Ode, 2006; Heil, 2008). Parasitoids and predators of herbivores have evolved and generally perform their activities within a multitrophic framework. Plants emit diverse blends of volatile compounds from their leaves, flowers and fruits, which affect a range of organisms in the environment including pollinators, herbivores, neighbouring plants and carnivores (Takabayashi and Dicke, 1996; Neveu et al., 2002; Shiojiri et al., 2002). The emission of these volatiles has mutualistic effects being clearly beneficial for the plant such as in the attraction of pollinators to flowers. Several investigations and documentations from tritrophic level interactions among plants, herbivores, and parasitoids or predators have illustrated that these components are tightly interwoven. Interactions between plants and natural enemies can be antagonistic, additive or synergistic, which illustrates the importance of multitrophic perspectives for effective and sustainable pest management strategies (Wright and Verkerk, 1995; Gange and Brown, 1997; Lewis et al., 1997; Tscharntke and Hawkins, 2002; Gripenberg and Roslin, 2007; De Boer et al., 2008). Apart from bi- or tritrophic, the infochemicals released by an infested plant and/or herbivores are available to other trophic levels. The same information used by the parasitoid to locate the herbivore may be utilised by hyperparasitoids (the fourth trophic level) in order to locate the parasitoids.

Plants under herbivore attack produce chemical cues due to the mechanical damage. These chemical cues are important signals for orientation of both carnivorous enemies and herbivores, including distant host location by arthropods (Karban and Baldwin, 1997; Dicke, 1999; Dicke and Van Loon, 2000; Arab and Bento, 2006). Plants' responses upon damage caused by herbivores occurs through the regulation of several biochemical pathways that lead to the release of chemical compounds, which cause either repellence to herbivore insects or attraction to natural enemies (predators or parasitoids) of herbivore insects (Karban and Baldwin, 1997; Dicke and Van Loon, 2000; Pickett et al., 2003; Arab and Bento, 2006; Gols and Harvey, 2009). Attracted by herbivory-induced plant volatiles, parasitoids of herbivores perform host searching to lay their eggs in or on them as shown in recent studies (Mattiacci et al., 1994; Takabayashi and Dicke, 1996; Dicke, 1999; Hilker and Meiners, 2002; Fatouros et al., 2005b; Heil, 2008). Apart from being chemical cues for parasites and predators, these so-called semiochemical volatiles may induce defence responses in neighbouring plants (Paré and Tumlinson, 1999). Semiochemicals emitted from a diverse group of plants and insects mediate key processes in the behaviour of specific insects.

In addition, several ecological approaches have emphasised the significance of plant traits in plant-insect interactions (Agrawal, 2000), which may vary due to genetic variations among plants and/or induced responses in individual plants upon herbivore attack. These effects are determined mainly by nutritional quality, physical structure, defence-related volatiles and other secondary metabolites. Furthermore, non-lethal exposure of an animal to carnivores, and a plant to herbivores, not only induces a defence, but causes the attacked organisms to produce offspring that are better defended than offspring from untreated parents. This is generally referred to as the transgenerational effect (Agrawal et al., 1999) and likely involves epigenetic modifications. The transgenerational induction of defences has been described as a new level of phenotypic plasticity across generations which might be an important component of predator-prey interactions (Agrawal et al., 1999).

Moreover, the tritrophic role of plant chemistry is a key to various aspects of trophic phenomena (Ode, 2006). This includes top-down effects (controlled by predators) versus bottom-up effects (controlled by resources) and enemy-free space and host choice. The tritrophic effects of plant chemistry are valuable to assess the degree of compatibility between biological control and plant resistance approaches to manage pests (Ode, 2006). Therefore, the study of trophic interactions and their manipulation has the potential to lead to effective ways of biological pest control, and thus reduce pesticide use (Agrawal, 2000; Dicke et al., 1990). Some of the multitrophic (second, third or up to fourth level) studies on *Brassica* species will be reviewed below. Most of these studies revolve around one single herbivore species such as *Pieris* spp., *P. xylostella*, *Delia* spp. and aphids, but studies investigating different herbivore insects simultaneously are also described.

3.2.1. Parasitoids or predators

Cotesia rubecula Marshall is a solitary endoparasitoid of the small white butterfly (*P. rapae*) and *Cotesia glomerata* L., a gregarious parasitoid of both *P. rapae* and *P. brassicae*. *P. rapae* and *P. brassicae* are also the hosts for the egg parasitoid *Trichogramma evanescens* Westwood in cabbage (Noldus and Van Lenteren, 1985a, b). *Cotesia plutellae* Kurdjumov is a dominant solitary koinobiont, larval endoparasitoid of *P. xylostella*, and generally regarded as being highly specific to *P. xylostella* (Talekar and Shelton, 1993; Agelopoulos and Keller, 1994a–c; Geervliet et al., 1994, 1998; Mattiacci et al., 1994, 2001; Harvey et al., 2003; Fatouros et al., 2005b). *Diadegma semiclausum* Hellén is a specialised parasitoid of *P. xylostella* (Bruinsma et al., 2009). *Platygaster subuliformis* Kieffer and *Omphale clypealis* Thompson are among the more than 20 species of hymenopteran parasitoids that attack *D. brassicae* (Murchie et al., 1997). *Lysibia nana* Gravenhorst is a solitary hyperparasitoid of newly cocooned pre-pupae and pupae of several microgastrine braconids, including *C. glomerata* (Harvey et al., 2003). *Adalia bipunctata* L. (predator) is known for its polyphagy against many aphid species (Hodek, 1959, as referred to by Francis et al., 2001). The seven-spot ladybird *Coccinella septempunctata* L. is recorded as the only parasitoid of *B. brassicae* (Acheampong and Stark, 2004). *Diaeretiella rapae* M'Intosh, a predominant parasitoid of *Brassica*-feeding aphids, attacks the mustard aphid *L. erysimi* at a greater rate than the generalist feeding aphid *M. persicae* (Blande et al., 2007). The parasitoid

Trybliographa rapae Westwood is a specialist larval endoparasitoid of *D. radicum* (Neveu et al., 2002). *Phradis interstitialis* Thomson, *Phradis morionellus* Holmgr. and *Tersilochus heterocerus* Thomson are among the most frequent pollen beetle parasitoids (Jönsson et al., 2005). Among these three parasitoids, the parasitoid *P. morionellus* attacks larvae inside oilseed rape buds and flowers and also feeds on the flowers (Jönsson and Anderson, 2007 and references therein). *Microplitis mediator* Haliday is an important parasitoid of early instar larvae of the cabbage moth *M. brassicae* (Lauro et al., 2005). The root-lesion nematode (*Pratylenchus penetrans* Cobb) is a migratory endoparasite with a broad host range (Baldridge et al., 1998 and references therein).

3.2.2. *Host plants (Brassica* spp.*)-herbivores (Pieris* spp.*)-parasitoids-hyperparasitoids*

Among the four different crucifer-specific compounds tested towards perception of *P. rapae*, phenylacetonitrile elicited a higher response than ally1 isothiocyanate, benzyl isothiocyanate and 2-phenylethyl isothiocyanate (Hern et al., 1996). Furthermore, *P. rapae* is considered to be an important pollinator for many plant species, since the butterfly occurs three to four times a year and tends to visit a diversity of flowers (Ômura et al., 1999). As an innate preference, butterflies are attracted by specific aromatic volatiles from rape flowers such as benzaldehyde, phenylacetaldehyde, benzyl alcohol, 2-phenylethanol, phenylacetonitrile and indole, in decreasing order of quantity (Ômura et al., 1999). Moreover, experience-based food consumption studies with larvae of *P. rapae* have shown that plant host preference is dependent on the abundance of glucosinolates in brassicas, independent of the chemical structure of these compounds (aliphatic or aromatic) (Renwick and Lopez, 1999). The role of glucosinolates acting as feeding stimulants for larvae of the large white butterfly *P. brassicae* was recognised long ago (Verschaffelt, 1910) as mentioned by David and Gardnier (1966). David and Gardnier (1966) in their *P. brassicae* and glucosinolate-related study demonstrated that *P. brassicae* reared on fresh cabbage leaf to the end of the fourth instar would not accept diets containing sinigrin (and sucrose) in the fifth instar. Another interesting point is that although glucosinolates act as feeding stimulants for *P. brassicae* larvae, about 50% of unfed, newly hatched larvae will accept a diet which contains no glucosinolates. It was noted that out of the nine effective glucosinolates, four (glucoiberin, glucoerucin, sinigrin and progoitrin) were from cabbage. Agrawal and Kurashige (2003) analysed the classical interaction between *P. rapae* and isothiocyanates. Using whole plants, root extracts and a microencapsulated formulation of allyl isothiocyanate, it was shown that isothiocyanates reduce herbivore survival and growth, and increase development time, each in a dose-dependent manner. Neither the substrate allyl glucosinolate, nor myrosinase negatively affected *P. rapae*, hence presenting strong evidence for a role for isothiocyanates in plant resistance against the specialist herbivore *P. rapae.*

Karowe and Schoonhoven (1992) determined the relative suitability of *Brassica* as host plants both for unparasitised *P. brassicae* caterpillars and for *C. glomerata* developing in *P. brassicae*. Of all these *Brassica* plants (Brussels sprouts, Swedish turnip and rape varieties of *B. napus*), the host-parasitoid complex attained a lower final weight than unparasitised *P. brassicae*, probably due to reduced consumption by the parasitised *P. brassicae*. In contrast, Sato and Ohsaki (2004) elucidated that *C. glomerata*, although a potential parasitoid of *P. brassicae*, did not effectively lower the population density of *P. brassicae* immediately after the first invasion due to its reluctance to parasitise.

The introduction of a new species can alter the attributes of other species within a community, which may affect discontiguous trophic levels via adjacent trophic levels (Tanaka et al., 2007). The exotic large white butterfly *P. brassicae* invaded Hokkaido Island, Japan, and quickly spread throughout the island. Prior to the invasion, the small white butterfly *P. rapae* was the host of the primary parasitoid *C. glomerata*, on which both the larval hyperparasitoid *Baryscapus galactopus* and the pupal hyperparasitoid *Trichomalopsis apanteroctena* depended. At the time of the invasion, *C. glomerata* generally laid eggs exclusively in *P. rapae*. During the five years following the invasion, however, the clutch size (number of eggs laid in a single nesting) of *C. glomerata* in *P. rapae* gradually decreased, whereas the clutch size in *P. brassicae* increased. As a consequence, the invasion of *P. brassicae* changed the host use of the primary parasitoid *C. glomerata* and the pupal hyperparasitoid *T. apanteroctena* within a very short time (Tanaka et al., 2007).

In a study assessing the attractive role of infochemicals originating from either the host, *P. brassicae*, or its food plant, cabbage, it was shown that *C. glomerata* responds to chemical signals emitted from herbivore-damaged plants rather than infochemicals from *P. brassicae* (Steinberg et al., 1993). Geervliet et al. (1997) demonstrated that the parasitoids of *Pieris* species, *C. glomerata* and *C. rubecula*, showed differential responses towards various herbivore-infested food plants. Herbivore-infested plants emit a huge number of compounds to their maximum level, and the parasitoids that search for hosts have to deal with variability in the availability of chemical cues emitted by the food plants and their host. In a tritrophic study with *P. brassicae* and *C. glomerata*, Mattiacci et al. (1994) investigated the significance of herbivory-induced plant volatiles in Brussels sprouts leaves (*B. oleracea*) versus infochemicals released by the larvae. Chemical analysis of the headspace of undamaged, artificially damaged, caterpillar-infested and caterpillar regurgitant-treated leaves showed that the plant responds to damage with an increased release of volatiles. Another tritrophic study revealed that the solitary parasitoid *C. rubecula* discriminated among volatile blends from Brussels sprouts plants treated with regurgitants of unparasitised *P. rapae* or *P. brassicae* caterpillars over blends emitted by plants treated with regurgitant of parasitised caterpillars (Fatouros et al., 2005b). The parasitoid *C. glomerata* discriminated between volatiles induced by regurgitant from parasitised and unparasitised caterpillars of its major host species, *P. brassicae*. Another study of a system comprising

Brassica-Pieris-Trichogramma suggested that egg deposition induces alteration in plant surface chemicals, thus causing the arrest of egg parasitoids by contact cues around the eggs (Fatouros et al., 2005a).

Studies by Blaakmeer (1994) regarding infochemicals in a tritrophic system of *Brassica*, *Pieris* and *Cotesia* identified the glucosinolate glucobrassicin as an oviposition stimulant. In another tritrophic study, Blaakmeer et al. (1994) analysed headspace composition, collected either from intact cabbage plants or cabbage plants infested with either *P. brassicae* or *P. rapae* first instar larvae. They identified twenty-one volatiles in the headspace of intact plants. The major differences between intact and caterpillar-damaged plants regarding the headspace profile were revealed for hexyl acetate, (*Z*)-3-hexenyl acetate, myrcene, sabinene and 1,8-cineole. The larval endoparasitoid *C. glomerata* was attracted by the volatiles released from *B. oleracea* damaged by *P. brassicae* first instar larvae. *C. rubecula*, a specialised larval endoparasitoid of *P. rapae*, was attracted by the volatiles released from the *B. oleracea-P. rapae* plant-host complex. This shows that cabbage plants kept under the conditions of headspace collection produce attractive volatiles for both parasitoids. Furthermore, Harvey et al. (2003) examined the interactions over four trophic levels. The study involved *B. oleracea* and a naturally occurring population of *B. nigra* because of the difference in their glucosinolate content. The concentrations of glucosinolates were more than 3.5 times higher in young shoots of *B. nigra* than in corresponding shoots of *B. oleracea*. The study observed that the cocoon mass of *C. glomerata* was not affected by the host-plant species on which *P. brassicae* fed; however, *L. nana* survival was greater and the body size was larger when *P. brassicae* fed on *B. oleracea*. It was demonstrated that the qualitative differences in herbivore diet can differentially affect the performance of interacting organisms across several trophic levels with a proposition that the bottom-up forces may also play a role in mediating interactions involving plants-herbivores-parasitoids and hyperparasitoids (Harvey et al., 2003).

In a perspective paper, Dicke et al. (2004) presented a tritrophic system comprising host cabbage plants, herbivorous larvae of *P. brassicae* and the parasitoid *C. glomerata*. The damage caused by caterpillars feeding on cabbage plants differentially regulates the expression of various genes in the plants, up-regulates biosynthesis of certain types of glucosinolates, and emits bouquets of volatile organic compounds (VOCs). These VOCs are shown to act as an indirect defence by attracting parasitoids that laid eggs in the caterpillars. Among these volatile organic compounds, the green-leaf volatile (*Z*)-3-hexen-1-ol and the terpenoid 1,8-cineole were shown to be the main volatiles emitted by the cabbage plants. Mumm et al. (2008) investigated the significance of terpenoids in a 'cabbage' system consisting of Brussels sprouts plants, large and small cabbage white butterflies (*P. brassicae* and *P. rapae*), and the larval parasitoid *C. glomerata.* The terpenoid emission was manipulated by treating the plants with fosmidomycin, which inhibits one of the terpenoid biosynthetic pathways, and consequently terpenoid emission. The study demonstrated that inhibitors such as fosmidomycin can be used to investigate the role of terpenoid infochemicals in plant defence mechanisms against herbivores.

3.2.3. Host plants (Brassica spp.*)-herbivore (P. xylostella)-parasitoids*

Olfactory attraction of female diamondback moths (*P. xylostella*) to the odours of intact and homogenised host plants was investigated using behavioural and electrophysiological methods (Pivnick et al., 1994). Allyl isothiocyanate from *B. juncea* and *B. napus* plants was the most attractive component, being absent in odours from intact plants. It was further suggested that certain elements of this fraction, possibly in combination, are important olfactory cues for host-plant finding by the diamondback moth, with isothiocyanates playing an important and synergistic role, particularly when plants are damaged. Van Loon et al. (2002) showed that the diamondback moth larvae employ a combination of biosynthetically distinct categories of feeding stimulants which allows for a higher degree of discriminatory ability than glucosinolates alone.

Karimzadeh and Wright (2008) used a tritrophic cruciferous *P. xylostella-C. plutellae* experimental system in order to test the hypothesis of host-plant effects challenging the innate immune system of an insect host. Using measures of the two principal immune effectors against parasitoids, encapsulation and phenoloxidase activity, it was shown that despite having strong plant effects on parasitism, parasitoidal effects on immune effectors of the host were transitory. These varied levels of parasitism of *P. xylostella* mediated by plant quality are stated to be an outcome of behavioural and fitness factors rather than a reduced immune challenge.

With a consideration that the parasitoids *Trichogramma chilonis* and *C. plutellae*, and the predator *Chrysoperla carnea* are the potential biocontrol agents, Reddy et al. (2002) conducted olfactory response studies with *P. xylostella* on cabbage plants. Among the four larval frass that were tested, only allyl isothiocyanate elicited significant responses in the parasitoids and predator, but *C. plutellae* and *C. carnea* responded well to all four volatiles (dipropyl disulphide, dimethyl disulphide, allyl isothiocyanate and dimethyl trisulphide). The results indicated that the sex pheromone and larval frass volatiles from the diamondback moth and volatile compounds from cabbage may be used as natural enemies to locate diamondback moth (Reddy et al., 2002). Furthermore, the same group performed another study on the host plant-mediated orientation and oviposition by the diamondback moth and its predator *Chrysoperla carnea* in response to four different *Brassica* host plants: cabbage, cauliflower, kohlrabi and broccoli (Reddy et al., 2004). The results indicated that the orientation of female diamondback moths and *C. carnea* females towards cabbage and cauliflower was significantly greater than toward broccoli or kohlrabi plants. Furthermore, in free-choice tests, oviposition by the diamondback moth was significantly greater on cabbage, followed by cauliflower, broccoli and kohlrabi, while *C. carnea* preferred to oviposit on cabbage and cauliflower, followed by broccoli and kohlrabi.

3.2.4. *Host plants (Brassica* spp.*)-herbivores (M. brassicae and P. brassicae)-parasitoids*

Lauro et al. (2005) examined the attack responses of female *M. mediator* to the first three larval instars of *M. brassicae*. Their results suggested that first and second instar larvae of *M. brassicae* are suitable hosts for *M. mediator*. Third instar larvae are suboptimal because of unsuccessful oviposition attempts and immature parasitoids failed to complete development. However, naïve attacking parasitoids exhibited minimal discrimination among instars, although experienced parasitoids most frequently attacked first instar larvae.

In a four-armed airflow olfactometry study with the egg parasiotoid *T. evanescens*, Noldus and Van Lenteren (1985a) observed that the females were attracted by a volatile substance (or substances) released by virgin females of cabbage white butterfly (*P. brassicae*). *T. evanescens* was also observed to be attracted by the volatiles released by calling virgin cabbage moths, *M. brassicae*. The results of the experiments with *M. brassicae* showed that *T. evanescens* is attracted by volatiles which are probably the sex pheromone released by calling virgin females, but not by the main component (Z)-11-hexadecenylacetate, nor by a crude extract of the sex pheromone gland (at the concentrations tested). The study suggested the significance of volatile kairomones for the egg parasite *T. evanescens* in the host-habitat location. In another follow-up study, Noldus and Van Lenteren (1985b) showed that contact kairomones are involved in host location by *T. evanescens*. Indeed, *T. evanescens* females searched significantly longer on cabbage leaves treated with the wing scales of two hosts, *P. brassicae* and *P. rapae.* Furthermore, egg washes of *P. brassicae* containing an oviposition deterrent pheromone for the butterflies were found to have a contact-kairomonal effect on the parasite.

Gardner et al. (2007) performed an oviposition experience study to observe the response of egg parasitoid (*T. vanescens*) towards contact kairomones of two different host species *M. brassicae* and *P. brassicae*. The response of *T. evanescens* was influenced by the number of eggs it had laid, but oviposition did not result in a significant change in behaviour. Parasitoids readily accepted an egg of a second species, and the time spent searching in a particular kairomone area appeared to depend on the reproductive state and expected survival of a parasitoid rather than the development of any host preference. It was further proposed that *T. vanescens* seems to select patches on the basis of reward probability rather than maximising reward size.

3.2.5. *Host plants (Brassica* spp.*)-herbivore (A. rosae)-parasitoids*

Müller and Arand (2007) tested whether adults of *A. rosae* innately prefer the plant species for oviposition that allows the best larval performance with regard to both developmental conditions and (plant-derived) defence efficiency against predators. It was observed that in *A. rosae* innate preferences of ovipositing, females seem to be mainly influenced by the host-plant effects on larval developmental times rather than potential defence efficiency of larvae against predators. The study demonstrated that for preference and performance studies, not only the plant-insect interactions should be considered, but also the biotic determinants (Müller and Arand, 2007). In a previous study by the same group, Müller and Brakefield (2003) tested the role of the *A. rosae* sawflies' haemolymph and of the glucosinolate sinalbin in the defence against wasps by using manipulation assays. The haemolymph released by easy bleeding and its chemical components proved to be in part responsible for the efficient defence of the sawfly against wasps (Müller and Brakefield, 2003).

3.2.6. *Host plants (Brassica* spp.*)-herbivores (Delia* spp.*)-parasitoids*

Birch et al. (1992) showed that different *Brassica* genotypes such as kale, rape and swede after inoculation with turnip root fly (*D. floralis*) eggs showed a similar response in glucosinolate metabolism. Total glucosinolate content in roots increased due to a two- to fourfold increase in indole-based compounds. The largest increase for an individual glucosinolate after attack was found for glucobrassicin. Root damage did not significantly affect stem glucosinolate composition but resulted in an increase in aliphatic glucosinolates with a corresponding decrease in indole-based compounds in leaves. Furthermore, Griffiths et al. (1994) investigated induced changes in the indole glucosinolate content of oilseed and forage rape (*B. napus*) plants in response to either turnip root fly (*D. floralis*) larval feeding or artificial root damage. Larval damage increased the total glucosinolate content of the roots. In contrast, artificial damage reduced the total glucosinolate content of the roots. It was also interesting to note that the concentration of glucobrassicin present in the oilseed rape cultivar *Ariana* was consistently higher in both the larval and artificially root-damaged plants compared with undamaged plants of the same cultivar.

The long-range plant involvement of volatiles in host location of the herbivore *D. radicum* on the parasitoid *T. rapae* was investigated by Neveu et al. (2002). It was shown that the infested turnips systemically emit herbivore-induced plant volatiles that attract the parasitoid *T. rapae,* implying that the production of parasitoid-attracting volatiles appeared to be systemic in this particular tritrophic system.

3.2.7. *Host plants (Brassica* spp.*)-herbivore (D. brassicae)-parasitoids*

The responses of *D. brassicae* and its parasitoids *P. subuliformis* and *O. clypealis* to allyl- and 2-phenylethyl isothiocyanates were investigated using traps in winter oilseed rape (Murchie et al., 1997). In this study it was observed that the traps baited with allyl isothiocyanate caught more male and female *D. brassicae* and more female *O. clypealis* than traps baited with 2-phenylethyl isothiocyanate or unbaited traps. Contrarily, traps baited with 2-phenylethyl isothiocyanate

caught more male and female *P. subuliformis* than traps baited with allyl isothiocyanate or unbaited traps.

3.2.8. *Plants (Brassica* spp.*)-herbivores (Phyllotreta* spp. *and Meligethes aeneus)-parasitoids*

Already in 1956, Görnitz showed that flea beetles are attracted to allyl isothiocyanate, which is a volatile hydrolysis product of the glucosinolate sinigrin. Based on these results, Pivnick et al. (1992) performed trapping experiments to test attraction of crucifer-feeding flea beetles to volatile glucosinolate hydrolysis products released from glass vials. The pattern of attraction was the same for the flea beetle species *P. cruciferae* and *P. striolata.* When captures of the two species were pooled, 3-methylthiopropyl isothiocyanate, methyl isothiocyanate and n-butylisothiocyanate were found to be significantly attractive, while nitriles were the least attractive compounds. Flower and leaf extracts of rape were found to be attractive in the field from at least 20 m, and the pollen beetles were proposed to use odour-mediated upwind anemotaxis to locate oilseed rape plants (Evans and Allen-Williams, 1994). The results from Y-tube olfactometer bioassays indicated that *M. aeneus* is able to locate its host plant by olfactory stimuli in the early bud stage, i.e. the stage at which the infestation begins in the field and when the typical yellow colour and floral scent of oilseed rape are absent (Ruther and Thiemann, 1997). In a field study on the effect of trap design, trap colour and isothiocyanate lures on the capture of the pollen beetle, *M. aeneus* was shown to be attracted to four alkanyl, three alkenyl and 2-phenylethyl isothiocyanate lures (Blight and Smart, 1999). The response of *M. aeneus* to yellow water traps baited with individual lures of 25 floral volatile compounds was also investigated in 17 field experiments with *B. napus* (Smart and Blight, 2000). These compounds comprised seven nitrogenous amino acid derivatives, five non-nitrogenous amino acid derivatives, nine fatty acid derivatives and four isoprenoids. The results showed most compounds to be attractive, but four fatty acid derivatives were repellent. 1-Hexanol was either attractive or repellent, depending on the release rate. It has been further suggested that because of its polyphagous nature, *M. aeneus* responds to a large number of chemically diverse compounds. The attraction to the most effective unbaited yellow traps was enhanced 1.7–3.3 times with the addition of a lure comprising a mixture of allyl, 3-butenyl, 4-pentenyl and 2-phenylethyl isothiocyanate.

Jönsson et al. (2005) analysed behavioural responses in three ichneumonid pollen beetle (*M. aeneus*) parasitoids (*P. interstitialis*, *P. morionellus* and *T. heterocerus*) to volatiles emitted from different phenological stages of oilseed rape. All three parasitoid species were attracted to odours from the bud stage of oilseed rape. *T. heterocerus* was attracted to odours of flowering rape, but the two *Phradis* species avoided the flower odours. However, when the odours of flowering rape were in combination with yellow-coloured flowers, and odours of the bud stage were in combination with green-coloured buds, *P. interstitialis* was equally attracted to both stimuli, and *T. heterocerus* showed an increased preference for flower odours, while no effect of colours could be found in *P. morionellus*. The terpenes sabinene, myrcene, limonene and (*E*, *E*)-α-farnesene were the dominant volatiles in the bud and flower headspace. A group of aromatic compounds including benzaldehyde, methyl benzoate and phenyl acetaldehyde were mainly released from the flowering rape. Furthermore, Jönsson and Anderson (2007) investigated emission of oilseed rape volatiles after pollen beetle infestation by analysing behavioural and electrophysiological responses in the parasitoid *P. morionellus.* It was observed that both starved and fed parasitoids preferred infested rape, but the proportion of responding female *P. morionellus* was significantly lower for the group that was starved. Six of the 20 volatiles identified were released at higher rates from infested than from non-infested rape. The volatiles released at a significantly higher rate from infested rape and detected by *P. morionellus* antennae were (*Z*)-3-hexenylacetate, (*Z*)-3-hexenol, 3-butenyl isothiocyanate and (*E*, *E*)-α-farnesene.

3.2.9. *Plants (Brassica* spp.*)-herbivores (Ceutorhynchus assimilis)*

In a study analysing the peripheral olfactory perception of isothiocyanates, cabbage seed weevil (*C. assimilis*) antennal receptors were able to locate a broad range of compounds associated with the odour of its host plant (Evans and Allen-Williams, 1992). Green leaf volatiles and specific host-related compounds were demonstrated to play a significant role in overall perception and recognition of host odour. In a response study with cabbage seed weevil antenna to volatiles in air entrainment-derived extracts of oilseed rape, using electroantennograms coupled with GC-single cell recording, it was shown that isothiocyanate perception is mediated by three types of olfactory cells, which show differential response to 3-butenyl, 4-pentenyl and 2-phenylethyl isothiocyanate (Blight et al., 1995). The responses of cabbage seed weevil to other electrophysiologically-active volatiles from rape were tested in a linear track olfactometer (Bartlet et al., 1997). Attraction was shown to nitriles (phenylacetonitrile, 4-pentenenitrile and 5-hexenenitrile) and to volatiles emitted by a wider spectrum of plant families, (*Z*)-3-hexen-1-ol and methyl salicylate. The combination of an isothiocyanate mixture with phenylacetonitrile increased attraction, but there was no such increase when the isothiocyanate mixture was combined with methyl salicylate. Furthermore, the response of the cabbage seed weevil to yellow water traps baited with some components of oilseed rape odour was studied in a series of field experiments (Smart and Blight, 1997). Four isothiocyanates, five other amino acid derivatives (aromatic compounds) and two fatty acid derivatives were detected by peripheral olfactory receptors of *C. assimilis.* The results suggested that yellow traps baited with 2-phenylethyl isothiocyanate can be used to monitor immigration into crops in the spring and that phenylacetonitrile may be useful for assessing numbers of weevils colonising the crop throughout the summer. After several field experiment studies on trap design, trap colour, and a mixture of isothiocyanates on the capture of

C. assimilis, Smart et al. (1997) showed that the sticky card trap, mounted at 45° to the vertical and baited with the isothiocyanate mixture, may be useful for monitoring movement of *C. assimilis* during migratory periods.

3.2.10. *Host plants (Brassica* spp.*) – aphids – parasitoids/ predators*

Chemicals that influence aphid behaviour have been studied for many decades, but a major breakthrough occurred in the early 1970s, due to chemical identification of an alarm pheromone for a number of species by several groups (as reviewed by Dawson et al., 1990). This pheromone was shown to comprise the sesquiterpene hydrocarbon (*E*, *E*)-α-farnesene. The chemical potential of glucosinolates and the glucosinolate-myrosinase system has been shown for cabbage and mustard aphids. The cabbage aphid, designated as the walking mustard oil bomb (Bridges et al., 2002; Jones et al., 2001, 2002; Kazana et al., 2007), is not only capable of sequestering harmful glucosinolates but also catalyses the hydrolysis of accumulated glucosinolates upon predator feeding in order to generate biologically active and toxic isothiocyanates. Both *B. brassicae* and *L. erysimi* produce an endogenous insect myrosinase, thus mimicking the plant glucosinolate-myrosinase system and its spatial organisation (Rossiter et al., 2003; Jones et al., 2001, 2002; Bridges et al., 2002; Husebye et al., 2002; Kazana et al., 2007). Recent studies with the model plant *A. thaliana* have shown the induction of aliphatic glucosinolates (Mewis et al., 2006), the contribution of indole glucosinolates towards aphid deterrence of *M. persicae* (Kim and Jander, 2007), and alterations in metabolism and chemical defence by *B. brassicae* (Kuśnierczyk et al., 2007, 2008). It is likely that similar defence responses exist in important *Brassica* crops.

For the mustard aphid (*L. erysimi*), isothiocyanates together with (*E*, *E*)-α-farnesene have been reported to work as alarm signals (Dawson et al., 1987). The sequestration of glucosinolates by the specialist aphid, *B. brassicae*, may provide protective compounds against attack by predators or parasitoids. It was suggested that the functioning of glucosinolate utilisation may be important in understanding the exploitation of biological control agents such as predators and parasitoids to control specialist *B. brassicae* and generalist *M. persicae* aphid species (Cole, 1997). Electrophysiological recordings together with high-resolution gas chromatography identified metabolites of glucosinolate precursors in the cruciferous host plants as being synergists for the alarm pheromone of *L. erysimi*. The most active, allyl isothiocyanate, significantly improved the activity of an aqueous formulation of (*E*,*E*) − α-farnesene (Dawson et al., 1990). The volatile (*Z*)-jasmone was shown to repel aphids while being an attractant to parasitoids (Birkett et al., 2000). Feeding behaviour of the specialist *B. brassicae* and the generalist *M. persicae* on the range of *Brassica* species tested indicated that generalist and specialist aphids are influenced differently by the host plant (Cole, 1997). *M. persicae* did not generally accept or reject *Brassica* species due to the presence of phagostimulants, such as glucosinolates at the leaf surface or along the stylet pathway, unless the concentration was very high.

Francis et al. (2001) performed a tritrophic interaction study on different *Brassica* crops with variable glucosinolate profiles, with *M. persicae* and *B. brassicae* and the predator *A. bipunctata.* It was suggested that the pest management must include both herbivore and plant trophic levels to determine the plant allelochemical impact on the third trophic level, the beneficial entomophagous insects. It was further added that the semiochemicals from plants, directly or through herbivore prey, must be considered as a potential toxin or reliable infochemical in relation to the efficacy of pest control by natural enemies. In another study either *B. nigra* plants (characterised by high levels of sinigrin), or an artificial aphid diet to which sinigrin was selectively added, were used to rear the specialist *B. brassicae* and aphids were provided as a food source to two species of polyphagous ladybirds, *A. bipunctata* and *C. septempunctata* (Pratt et al., 2008). The results indicated that the presence of sinigrin in the diet of *B. brassicae* makes this aphid unsuitable as a food source for *A. bipunctata*, but not for *C. septempunctata*. However, there appear to be costs associated with *C. septempunctata* feeding on aphids that contain this secondary metabolite. Blande et al. (2007) investigated the orientation behaviour of the parasitoid *D. rapae* to the semiochemicals produced when the two aphid species *L. erysimi* (specialist) and *M. persicae* (generalist) were fed on turnip. Isothiocyanates were among the compounds emitted by Brassicaceae plants in response to insect feeding damage, including damage caused by aphids. The results suggested that similar cues may be utilised by *L. erysimi* and *M. persicae* for host location, whereas the acceptance of hosts and their suitability may involve aspects of non-volatile aphid chemistry. In an olfactory perception and orientation behaviour study of the aphid *B. brassicae* and the parasitoid *D. rapae* to alkenyl glucosinolate hydrolysis products, electroantennogram responses indicated peripheral odour perception in *D. rapae* females to all 3-butenylglucosinolate hydrolysis products (Pope et al., 2008). Nevertheless, rearing *D. rapae* either on *B. nigra*, which accumulates 2-propenylglucosinolate, or *B. rapa*, which accumulates 3-butenylglucosinolate, changed the parasitoids' response to 3-isothiocyanatoprop-1-ene and 4-isothiocyanatobut-1-ene.

3.2.11. *Host plants (Brassica* spp.*)-herbivores [(P. xylostella/Pieris) (P. xylostella/M. persicae)]-parasitoids and [P. rapae and two different root feeders]*

Some of the tritrophic studies involving two herbivores documented below are based on the hypothesis suggesting that plants in both natural and cultivated ecosystems are subjected to insect infestation by more than one species and that induced responses occur both locally and systemically throughout the plant (Agelopoulos and Keller, 1994a–c; Shiojiri et al., 2000; Agbogba and Powell, 2007).

The role of volatiles in attracting *C. rubecula* to cabbage infested by the host *P. rapae* was elucidated (Agelopoulos

and Keller, 1994b). The study showed that *C. rubecula* was attracted to cabbage previously infested by *P. rapae*. Additionally, females were also attracted to mechanically damaged cabbage and cabbage previously infested by *P. xylostella* (a non-host lepidopteran herbivore). Furthermore, another tritrophic study by the same group focused on the identification of the volatile compounds that could be involved in the searching behaviour of the parasitoid *C. rubecula* (Agelopouos and Keller, 1994c). The volatiles emitted by the intact cabbage were α-pinene, β-pinene, myrcene, 1,8-cineole, n-hexyl acetate, (*Z*)-3-hexen-1-yl acetate and dimethyl trisulphide. Mechanical damage on an intact plant induced the release of two more compounds, (*E*) – 2–hexenal and l-methoxy-3-methylene-2-pentanone. Feeding by larvae of *P. rapae* induced the plant to release all the compounds upon mechanical damage and additionally 4-methyl-3-pentenal and allyl isothiocyanate. On the other hand, feeding by larvae of *P. xylostella* induced the plant to release all the compounds present after mechanical damage with addition of allyl isothiocyanate. Shijori et al. (2000) performed a comparative study of host-searching behaviour with two parasitoid species (*C. plutellae* and *C. glomerata*) on a cabbage plant, infested by the host larvae *P. xylostella.* It was found that the parasitoids showed their antennal-searching behaviour only on the host-infested site. The searching time of *C. plutellae* on a piece of cabbage leaf infested by host larvae was significantly longer than a piece infested by non-host (*P. rapae*) larvae. Likewise, the searching time of *C. glomerata* on the host (*P. rapae*)-infested piece of cabbage was significantly longer than that on a leaf infested by non-host (*P. xylostella*) larvae. Furthrmore, Shiojiri et al. (2002) conducted another study by using the same system as previously (Shiojiri et al., 2000) confirming that the fitness effects of induced chemical production by plants should be studied in tritrophic interaction webs, because chemicals induced by one herbivore species may indirectly affect oviposition preferences of heterospecific herbivores by altering the effectiveness of their respective parasitoids. Such indirect interactions between host and non-host herbivores are referred to as infochemical-mediated indirect interactions. In a recent study, Bruinsma et al. (2009) showed that feeding by *P. rapae* and *P. xylostella* resulted in increased endogenous levels of jasmonic acid in *B. oleracea* (Brussels sprouts) plants. However, the levels of the intermediate 12-oxophyto-dienoic acid (OPDA) were induced only after *P. rapae* feeding. Moreover, jasmonic acid-induced volatiles of *B. oleracea* attracted parasitoids (*C. glomerata*, *C. rubecula* and *D. semiclausum*) in a time- and dose-dependent application (Bruinsma et al., 2009). In a study using two insects, the peach aphid (*M. persicae*) and the caterpillar (*P. xylostella)* on cabbage plants, Agbogba and Powell (2007) looked at the responses of the aphid parasitoid *D. rapae* by Y-tube olfactometry. Their results indicated that the aphid and the caterpillar induce different changes in the volatile profile of cabbage plants and that *D. rapae* females readily distinguish between the two. In a study, involving *B. nigra* plants, *P. rapae* and two different root feeders (the endoparasitic nematode *P. penetrans* and the larvae of the cabbage root fly *D. radicum*), Van Dam et al. (2005) indicated that root feeding can significantly alter the nutritional quality of shoots by changes in secondary metabolite levels and hence the performance of a specialist shoot feeder. Moreover, it was observed that *P. rapae* larvae grew more slowly and produced fewer pupae on plants that were infested with root feeders, especially on plants infested with the endoparasitic nematode *P. penetrans* and that both glucosinolate as well as phenolic levels were affected by root feeding.

4. BRASSICAS AND THEIR POTENTIAL FOR INTEGRATED PEST MANAGEMENT

Integrated pest management (IPM) is an ecological approach to managing insect pests, by using different pest control methods, that are aimed at the entire pest complex of a crop ecosystem and finally ensures high-quality agricultural production in a sustainable, environmentally safe, and economically sound manner (Bajwa and Kogan, 2002 as cited by Guerena, 2006). The insect pest management strategies include pest monitoring, that allows accurate timing of pesticide applications; combined use of semiochemicals, host-plant resistance and trap crops to manipulate pest behaviour, employing biological control approaches or selective insecticides to reduce pest populations and developing insect-resistant crops (Pickett et al., 1997). From these perspectives of pest management aiming at an ecochemical control, we have briefly reviewed the use of brassicas as biocontrol, cover crops and trap crops in order to control or manipulate the insect-pest complex not only for brassicas, but also insect pests and diseases for other economically important crops. In addition, we have described in brief the role of plant breeding in developing insect resistance in *Brassica* crops.

4.1. Brassicas as biocontrol agents

Brassicas as biocontrol agents generally employ the process of biofumigation. Biofumigation is referred to as the process of suppression of pests and pathogens through release of volatile substances from degradation of biomass into the soil. For the biofumigation process, *Brassica* plants are incorporated into the soil and due to the significant amounts of glucosinolates, toxic breakdown products, especially isothiocyanates, are produced after tissue maceration (Brown and Morra, 1997; Kirkegaard and Sarwar, 1998; Gardiner et al., 1999; Smith et al., 2004). Isothiocyanates carry fumigant properties similar to metham-sodium (Sarwar et al., 1998; Warton et al., 2003). Metham-sodium (sodium *N*-methyldithiocarbamate) is a compound that is used globally to control noxious soil-borne organisms in intensive cropping systems as it generates the wide-spectrum fumigant-like compound methyl isothiocyanate after coming into contact with the wet soil (Matthiessen and Shackleton, 2005). Methyl isothiocyanate (not present in brassicas) is the only isothiocyanate which is used as a pesticide on a commercial basis but other isothiocyanates have also become the subject of interest due to their biofumigation properties (Angus et al., 1994). However, in a cross-enhancement study, Warton et al. (2003) suggested

that in soil suffering from enhanced biodegradation of methyl isothiocyanate, biofumigation using isothiocyanate-producing *Brassica* plants is unlikely to be an effective alternative.

Methyl bromide was used as a soil fumigant with wide-spectrum potential to control soil-borne pests and diseases, nematodes and weeds for economically important crops such as tomato, strawberries and cucurbits (Ploeg, 2008). The phasing out of the ozone-depleting soil fumigant methyl bromide and a higher interest in developing safe and economically viable insect pest management strategies has led to the initiation of alternative approaches. One of these approaches was the process of biofumigation by using macerated *Brassica* tissues as biofumigant agents and as cover crops (Noble et al., 2002; Matthiessen and Shackleton, 2005; Montfort et al., 2007). The biofumigation process potentially fulfils the requirements of a safe and economical pest management strategy and is included as a non-chemical alternative to methyl bromide by the Methyl Bromide Technical Options Committee (MBTOC, 1997), as documented by Ploeg (2008). Novel approaches to disease control, for example incorporating brassicas to biofumigate soil and engineering solutions to disease control has made The Scottish Agricultural College's (SAC) contribution to supporting the potato industry unique (Smith, 2002).

Smith and Kirkegaard (2002) tested the effect of 2-phenylethyl isothiocyanate under in vitro conditions towards a range of fungi, oomycetes and bacteria. *Trichoderma* spp. was the most tolerant, while *Aphanomyces*, *Gaeumannomyces*, *Phytophthora* and *Thielaviopsis* were very sensitive to 2-phenylethyl isothiocyanate. Matthiessen and Shackleton (2005) tested four pure isothiocyanates (methyl, 2-propenyl, benzyl and 2-phenylethyl isothiocyanate), in vapour exposure tests for biological activity against the model soil insect white-fringed weevil both in vitro and in the presence of three contrasting soils and under four temperatures. The results indicated that brassicas rich in aliphatic isothiocyanates are more likely to have the potential to exert stronger isothiocyanate-based biofumigation effects than those similarly rich in aromatic isothiocyanates. The potential of tissue amendments from wild and cultivated *Brassica* species was assessed to kill the root lesion nematode *Pratylenchus neglectus*. The amendment of soils with equimolar levels of purified 2-phenylethyl isothiocyanate resulted in comparable levels of nematode mortality, suggesting that 2-phenylethyl glucosinolate has a role in the suppressive impact of *Brassica* spp. root tissues (Potter et al., 1998). Cox et al. (2006) used *B. juncea* cv. *Pacific Gold* (BSM) to control sting nematodes and observed that BSM seed meal with irrigation provided 92% control, while non-irrigated BSM provided 99.5% control. Monfort et al. (2007) evaluated the potential of *Brassica* species as an alternative control measure for root-knot nematode (*M. incognita*) by using them as green manure amendments prior to planting. The results of their trial, although variable, showed some promise of *Brassica* spp. as a biological control option in vegetable production in Georgia. In another study the effects of soil amendment with rapeseed meal from *B. napus* cv. *Dwarf Essex* (high glucosinolate concentrations) and *Stonewall* (low glucosinolate concentrations) on the biological control activity of *Trichoderma harzianum* towards *Sclerotinia sclerotiorum* and *Aphanomyces euteiches*, Dandurand et al. (2000) demonstrated that both Dwarf Essex and Stonewall meals inhibited colonisation of *S. sclerotiorum* in soil by *T. harzianum*, from 100% to 0% and 8%, respectively. *A. euteiches* was significantly reduced by *T. harzianum* alone (100%), by amendment with *Dwarf Essex* meal alone (77%), and by *T. harzianum* in combination with *Dwarf Essex* meal (100%). Klingen et al. (2002a) analysed the effect of brassicaceous plants on the survival and infectivity of insect pathogenic fungi and their in vitro studies showed that 100 ppm of 2-phenylethyl isothiocyanate completely inhibited growth of *Metarhiziumanisopliae* and *Tolypocladium cylindrosporum*. In a study of oilseed rape *B. napus* extracts in the laboratory for toxicity against adults of *Sitophilus oryzae* and *Rhizopertha dominica* at different concentrations, data showed that the surface treatment of wheat seeds with acetone or petroleum ether extracts of *B. napus* proved to be very effective as they gave 51.8 and 45.0% mortality among *S. oryzae* adults at 4.0% conc. level, respectively (Salem et al., 2007). While all tested extracts *of B. napus* showed various toxicities to *R. dominica* adults, acetone extract was found to have to have the highest effect as it gave 92.4% mortality at 4.0% concentration level, followed by the diethyl ether extract (90%). In a study by Noble et al. (2002), larvae of masked chafer beetles (*Cyclocephala* spp.) were placed in soil amended with *B. juncea* (PI 458934) tissue. Allyl isothiocyanate levels were observed to be positively correlated with larval mortality, with the 8% *B. juncea* treatment resulting in 100% larval mortality with an average allyl isothiocyanate concentration of 11.4 mg L^{-1} of soil atmosphere.

4.2. Brassicas as cover crops

"Cover crops slow erosion, improve soil, smother weeds, enhance nutrient and moisture availability, help to control many pests and bring a host of other benefits to farms, and simultaneously can reduce costs, increase profits, and even create new sources of income" (Clark, 2007).

Brassicaceae cover crops are considered to play a role in controlling nematodes, fungi, weeds and diseases by releasing chemical compounds from decomposing residue with promising but variable results among different species, varieties, geographical locations and differences due to the planting dates (Clark, 2007). *B. hirta*, syn. *S. alba*, *B. juncea*, *Raphanus sativus* and *B. napus* have been used as cover crops with varying success (Boydston, 2004). Mustard cover crops have been used in Europe and the Pacific Northwest to suppress soil-borne nematodes, pathogens and weeds. *Brassica* crops such as *B. juncea* have been reported to improve root health in a subsequent cash crop, such as potatoes, grown after a green incorporated Brassica cover crop (Snapp et al., 2006). Brassica cover crop incorporation as a green manure suppresses some pathogens, including *Verticillium* in potato; *Pythium, Fusarium* and *Rhizoctonia* root rots in beans; *Pythium* in lettuce; pink rot in onion; *Aphanomyces, Pythium, Rhizoctonia* and *Fusarium* root rot in peas; and cavity spot and *Fusarium* in carrot (summarised by Sanders, 2005 as cited by Snapp et al., 2006). *B. juncea*, having high levels of glucosinolates along

with fungal inhibition properties, was the most effective Brassica crop for reducing powdery scab and common scab disease problems in the field trials conducted (Larkin and Griffin, 2007).

4.3. Brassicas as trap crops

The practice of trap cropping, i.e. using a sacrificial resource for the pest to attack, in order to protect a valued resource, has been known for centuries (Foster and Harris, 1997). The use of *Brassica* as trap crops has gained interest in recent years. In order to decrease loss to the main crop from insects, trap crops are deployed to attract or catch targeted insects (Shelton and Badenes-Perez, 2006). The trap crop, bearing highly attractive host plants preferred by pests, is planted close to the main crop to protect it from pests. Being attractive, the trap crop captures pests and concentrates them on itself, where they get destroyed before reaching the main crop (Hokkanen, 1991). Recently, the '*push-pull strategy*' based on an attractive trap crop has been developed to protect oilseed rape (*B. napus*) from its specialist pests (as reviewed by Cook et al., 2007a). The push-pull strategy "*involves the behavioural manipulation of insect pests and their natural enemies via the integration of stimuli that act to make the protected resource unattractive or unsuitable to the pests (push) while luring them toward an attractive source (pull) from where the pests are subsequently removed*" (Cook et al., 2007a). The term push-pull was first accepted in Australia in 1987, as a strategy for insect pest management (IPM) (Pyke et al., 1987 as cited by Cook et al., 2007a).

In order to protect spring-sown oilseed rape from two major inflorescence pests, the pollen beetle (*M. aeneus*) and the seed weevil (*C. assimilis*), Cook et al. (2006) followed a strategy of using *Brassica* as a trap crop. The strategy comprised *Starlight*, an oilseed rape cultivar with relatively low proportions of alkenyl glucosinolates in the leaves and thereby releasing lower levels of attractive isothiocyanates than conventional cultivars as the main crop, and turnip rape as a trap crop. Turnip rape showed good potential as a trap crop for oilseed rape pests, particularly the pollen beetle, as its odour was more attractive to pests than that of oilseed rape (Cook et al., 2006). A study by Barari et al. (2005) examining turnip rape as a trap crop to reduce oilseed rape infestation, and the effects of insecticide treatment on pest incidence and larval parasitism, showed that the turnip rape trap crop borders reduced *P. chrysocephala* but not *C. pallidactylus* infestation of oilseed rape plots. Treatment of the trap crop with insecticide had little effect on either pest or parasitoid incidence in the oilseed rape.

Understanding the mechanisms underlying host-plant preferences of herbivorous pests can lead to improved effectiveness and reliability of the trap crop. With this perspective, Cook et al. (2007b) investigated the behavioural and chemical ecology underlying the success of turnip rape trap crops in protecting oilseed rape from the pollen beetle (*M. aeneus*), which feeds in the flowers and lays its eggs in the buds. Phenylacetaldehyde and (*E*,*E*) – α-farnesene were found to be present in air entrainment samples of both plant species at the flowering growth stage, but only in those of *B. rapa* at the bud stage. The former two compounds were behaviourally active in olfactometer tests. These compounds were suggested to be involved in host location by *M. aeneus* and, at least partially, responsible for the attractiveness of turnip rape and its success as a trap crop to protect oilseed rape from this pest.

Shelton et al. (2008) observed that several types of trap crops have been recommended to control diamondback moth, including *B. oleracea* and *B. juncea*. However, the results varied as populations of *P. xylostella* develop on these trap crops and spill over to the cash crop. In order to overcome this problem, Shelton et al. (2008) sought to develop "dead-end" trap crops that were more attractive for oviposition than the cash crop and on which *P. xylostella* larvae cannot survive. Transgenic collard and Indian mustard lines expressing the *Bt* gene (cry1C) were produced to be used as a "dead-end" trap crop for *P. xylostella*. The use of *Bt* Indian mustard as a trap crop significantly reduced the number of larvae that appeared on a cabbage cash crop, compared with using a non-*Bt* Indian mustard trap crop.

4.4. Plant breeding towards insect resistance in *Brassica* crops

Plant breeding has undergone major changes throughout the past 30 years and moved from the traditional phenotype-based via phenotype-protein-based breeding to the utilisation of so-called molecular markers. The development of PCR techniques has given rise to marker technologies and the generation of detailed molecular maps for selection purposes and breeding programmes for important crop plants, also including crucifers. Additionally, the utilisation of model plants, and in particular *A. thaliana*, has opened up for comparative investigations, not least since *Arabidopsis* is a close relative to *Brassica* species, and thus, facilitated and pushed efforts toward molecular breeding (Snowdon and Friedt, 2004) and state-of-the-art metabolomics-assisted breeding (Fernie and Schauer, 2008). Recent approaches for potential genotype selection and cultivar development in the Brassicaceae (Snowdon, 2007; Duran et al., 2009; Nicolas et al., 2009; Riaño-Pachón et al., 2009) include:

- re-synthesis of *Brassica* species through somatic or interspecific hybridisation;
- genetic markers, mapping and identification of *quantitative trait loci* (QTLs);
- plant model (*Arabidopsis*)-based breeding through intergenome knowledge transfer;
- haploid techniques based on anther and microspore cultures;
- 'omics technologies for global elucidation of genetic, protein and/or metabolite information.

At least two or several of the described approaches are normally applied at the same time, in order to efficiently improve and accelerate the selection process. General breeding goals in *Brassica* crops comprise quite different traits ranging from

morphology and yield, oil content and quality, male sterility, and abiotic stress tolerance, to pathogen and insect resistance (Leckband et al., 2002; Snowdon and Friedt, 2004; Sarfraz et al., 2006).

Nevertheless, today's situation in *Brassica* breeding with regard to insect resistance traits has to be informed on the background of gene modification (GM) of crop plants, on the one hand. Due to successful introduction of genes coding for *Bt* toxins against insect pests in important crops such as cotton, maize and potato (AGBIOS, 2009), R&D activities in GM *Brassica* species toward insect resistance traits have been forced in recent years. In cabbage and oilseed rape, the expression of *Bt* toxins (Jin et al., 2000; Liu et al., 2008), harmful enzymes (Wang et al., 2005; Mulligan et al., 2006) and the regulation of insect gene expression through RNA interference (RNAi) (Baum et al., 2007) have been addressed. However, insect-resistant GM *Brassica* crops are not commercially available so far. On the other hand, biological premises and limitations challenge the breeding efforts toward insect resistance. Evolutionary-evolved plant responses upon feeding insect species have resulted in specific adapted and partly, multitrophic defence mechanisms, depending on whether generalists or specialists are involved. Thus, insect–plant relationships rely on a complex interplay of factors related to attraction, recognition and oviposition, which makes breeding efforts difficult since several traits have to be taken into account. Rather few examples on breeding Brassicaceae toward insect resistance traits exist. Both the (1) biochemical basis of resistance (glucosinolates; host-plant volatiles; other secondary metabolites) and/or the (2) morphological basis of resistance (leaf colour, size and position; epicuticular waxes; trichome density) might be addressed as reviewed by (Sarfraz et al., 2006). In the case of the glucosinolates and derivatives, intensive research in the past decades has led to new knowledge about both the potential toxicity of single biochemical compounds and potential induced resistance and thus, opened up new breeding purposes in the brassicas in general (Lou et al., 2008; Hopkins et al., 2009). Although glucosinolates, and specifically their breakdown products, have been shown to play a major role in defence mechanisms against generalist and specialist insects (stressed in Sects. 2 and 3), such interactions have to be studied on a case-by-case basis for a purposeful plant genotype selection, as pointed out for the diamondback moth in oilseed rape (Sarfraz et al., 2006, 2007). Promising biochemical traits other than glucosinolates have been pointed out by Silverstein and co-authors regarding defensins and smaller cysteine-rich peptides for the establishment of constitutive resistance against insect pests (Silverstein et al., 2005, 2007). Trait selections in less important species, e.g. kale (*B. oleracea* var. *acephala*) and nabicol (*B. napus* var. *pabularia*) (Rodriguez et al., 2005; Picoaga et al., 2003) have shown that the morphological characteristics (glossy leaves) are connected to resistance toward lepidopterous species. In the case of generalist insects, e.g. the cabbage maggot, cross-species approaches using different crucifers might help to identify sources and mechanisms of resistance and thus, to select suitable plant genotypes for hybridisation breeding (Jyoti et al., 2001).

To what extent insect resistance as a newly introduced trait interferes in multitrophic relationships between the host plant, insect pests and their parasitoids has specifically been studied in gene-modified *B. napus* expressing the *Bt* toxin, with negligible effects on beneficial species (Schuler et al., 2001, 2004; Ferry et al., 2006; Mulligan et al., 2006). Recent studies on the glucosinolate content and composition of host plants with differing insect resistance potential have shown that changed plant chemistry possibly impairs parasitoid fitness, underscoring how fine-tuned evolutionary-developed plant herbivore-parasitoid interactions are (Gols et al., 2008b; Bukovinszky et al., 2009; Hopkins et al., 2009).

5. CONCLUSIONS AND FUTURE DIRECTIONS

This review binds together broadly scattered literature on the chemical ecology of *Brassica* plants towards different insects, multiple defence mechanisms of these plants, their role towards the insect-pest complex that attacks brassicas, their potential in insect-pest management and plant breeding towards insect resistance in *Brassica*. Several chemical ecology studies on different *Brassica* plants and insects attacking brassicas emphasise the importance of glucosinolates, breakdown products (isothiocyanates and nitriles), volatile compounds (terpenes, green leaf volatiles, aromatic compounds) and phytoalexins as key components of plant defence against insects. In addition, these studies show that the *Brassica* crops exhibiting multiple defence responses in response to different insects along with insect behaviour represent a complex system. In order to understand this complex system further and to identify differential responses triggered by different insects (herbivores, parasitoids/predators) as well as the underlying regulatory networks and signalling pathways, there is a need to perform gene expression studies on brassicas. Due to the availability of the *A. thaliana* genome, a lot of transcriptional/ecogenomics studies have been performed on *Arabidopsis* in recent years. Using a full genome microarray platform for studying early transcriptional responses in *A. thaliana* against *B. brassicae* infestation, Kuśnierczyk et al. (2008) found strong indications that camalexin is a hitherto unknown insecticide. This finding was further supported by the analysis of camalexin induction and aphid fecundity experiments.

Since *Arabidopsis* and Brassicas belong to the same family, *Arabidopsis* microarrays have been employed for the transcriptional studies in *Brassica* spp. (Dong et al., 2004; Carlsson et al., 2007; Hudson et al., 2007), and can also be used to perform ecogenomics studies to analyse insect infestation responses in *Brassica* crops. Moreover, with the availability of *Brassica* microarrays, it is now possible to perform more complete global transcription profiling studies of insect infestation of *Brassica* plants, providing another gateway towards insect pest management. Future studies could also aim at manipulating plant secondary metabolites such as camalexin, glucosinolates and their breakdown products, volatile compounds, plant allelochemicals or other semiochemicals in order to control pests. This can be applicable through the production of transgenics,

through a combination of breeding methods and tissue culture techniques, and through the exploitation of wild *Brassica* germplasm.

We end this review with a hope that future studies might also discover other aspects of plant-insect interactions, their chemistries in combination with ecogenomics studies, and utilisation of brassicas towards insect-pest management, and will provide us with even more information and clues to understand the plant-insect world and its mysterious trophic interactions. This field of research has gained more and more attention in the past decade and attracted a huge number of scientists, who have spent years exploring the plant-insect world, and have already provided us with excellent information, sources and some natural solutions to overcome insect-pest problems.

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