Journal of Applied and Natural Science 9 (1): 508 - 519 (2017)

Plant secondary metabolites (PSMs) of Brassicaceae and their role in plant defense against insect herbivores – A review

Sarwan Kumar

Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana - 141004 (Punjab), INDIA
E-mail: sarwanent@pau.edu

Received: March 13, 2016; Revised received: November 6, 2016; Accepted: February 18, 2017

Abstract: The genus *Brassica* includes economically important oilseed and vegetable plants. A number of insect pests are known to infest these crops and cause significant losses in yield. The plants in the family Brassicaceae have multiple defense mechanisms to overcome or reduce the damage by these pests including defensive biochemicals. These Plant Secondary Metabolites (PSMs) involve myrosinase-glucosinolate system, different volatile compounds, lectins, phytoalexins and phytoanticipins. While some of the compounds are always present in the plant system, the others are synthesized after herbivore attack. These compounds can either directly protect the plant by having effect(s) on insects' biology/behaviour or indirectly by attracting the natural enemies of the pests. Because of these secondary compounds, *Brassicas* have the potential to be used in pest management such as biofumigation against soil pests, as trap crops and cover crops and hence, can be a part of push-pull strategy. An attempt has been made to review these compounds in *Brassicas*, their role in defense against insects and potential in pest management.

Keywords: Biocontrol, Biofumigation, *Brassica*, Defense, Plant secondary metabolites

INTRODUCTION

Plants constitute one of the largest group of autotrophs on this planet. They are the good source of food for a number of organisms such as bacteria, fungi, invertebrates and vertebrates. If such a large group of organisms depends on plants for their survival, it is fascinating that plants exist at all. But still plants survive on this earth and some of them in very hostile environments. They possess a diversity of mechanisms to ward off any herbivore or attacker. This ability to defend themselves is important not just for plants in their natural environments but also for plants under cultivation (Agrawal, 2006; Walters, 2011; War *et al.*, 2012; Kumar and Singh, 2015).

Among the cultivated plants, the *Brassicas* commonly known as crucifers are grown the world over for food, oil and feed purposes. The cultivated species of Brassicaceae include rapeseed, mustard, cabbage, cauliflower, broccoli, turnip and other leafy vegetables. They are among the oldest cultivated plants known (Snowdon *et al.,* 2007). Among the *Brassicas,* oilseed *Brassicas* are an important source of oil and protein (Font *et al.,* 2003). India is the third largest producer of rapeseed-mustard after China and Canada (FAOSTAT, 2009) and produces about 11.3 per cent of the world's total rapeseed-mustard production (Chattopadhyay *et al.,* 2005). *Brassica juncea* is the major winter season oilseed crop cultivated in India (Damodaram and Hegde, 2002) while, *B. napus* is important oil crop in other countries of the world (Dubuis *et al.,* 2005). Though, these crops are important source of oil, food and feed, in the recent years their significance has also increased further as an important source of biodiesel. However, in a developing country like India, these energy rich crops are largely grown under energy deprived conditions on marginal lands with little inputs. Further, a range of biotic and abiotic factors are also responsible for losses in the yield and very little effort is made by farmers to address these problems especially the biotic factors. Several pathogens, nematodes and insects use *Brassica* plants as hosts. The major challenge with Brassicaceae production is the high susceptibility to insect-pests (Joshi *et al.,* 1989; Ratanpara *et al.,* 1992). Insect pests cause enormous yield losses in *Brassica* crops year after year. To overcome these insect-pests, *Brassica* species use multiple defense mechanisms which can be constitutive, inducible, direct or indirect depending upon the insect or degree of attack. Some of the important insects that attack *Brassicas* are:

Insect-pests

The aphids complex: Aphids are important pests in both oilseed and vegetable *Brassicas* and due to their prolific breeding and short generation time cause enormous damage to the crop if management operations are not carried out well in time. They cause direct damage by sucking large quantities of water and nutrients from plants and thus rendering the plant weak. Feeding damage also leads to curling and crumpling of leaves and other plant parts (pods) (Mossler, 2005; Kumar *et al.,* 2011; Atri *et al.,* 2012; Kumar, 2015; Kumar and Singh, 2015). Both the adults and nymphs suck sap from leaves, stem, flower and pods resulting in poor pod formation and reduced oil content in grains. Failure to manage at proper time can result 75-83 % loss in yield (Sekhon and Ahman, 1993; Sekhon, 1999) and sometimes complete crop failure.

The mustard aphid, *Lipaphis erysimi,* is the most important pest of oilseed *Brassicas*, especially on *B. juncea* in India causing upto 83 per cent yield loss (Sekhon and Ahman, 1993; Kular and Kumar, 2011; Chattopadhyay *et al.,* 2005). It is highly host specific feeding exclusively on *Brassica* phloem sap. Retarded growth, poor seed formation and low oil content are the prominent manifestations of parasitic feeding and consequent resource restrictions in *Brassica* oilseeds. Parthenogenesis and fast growth results in nymphs attaining reproductive age in less than 10 days. Such an enormous propagation rate gets manifested in abnormally high aphid population under favorable conditions. Since, the generation time is very short, about 45 generations are completed in a year.

The cabbage aphid, *Brevicoryne brassicae*, is global threat to *Brassica* crops especially the vegetable *Brassicas.* Like *L. erysimi*, it also has parthenogenetic viviparity. On vegetable *Brassicas* it is being controlled by multiple insecticidal treatments (Kift *et al.,* 2000). While these above mentioned two species are specialist feeders, the green peach aphid, *Myzus persicae*, is a generalist reported to feed on more than 400 species as host plants (Francis *et al.,* 2001).

Aphids produce at a higher rate during the early vegetative stage of plants (Agarwala and Datta, 1999). Parthenogenesis eliminates the need for females to mate with males and thus helping them conserve energy which is very crucial for these small delicate creatures. Further, viviparity allows the females to directly give birth to young ones, thus, eliminating the egg stage which helps to shorten the generation time. The development of an aphid starts even before the birth of its mother aphid. This is referred to as telescoping of generations. These inherent characters contribute significantly to the pest status of aphids which grow and multiply very fast (Thompson and Goggin, 2006).

Cabbage butterflies: The cabbage butterflies, *Pieris brassicae, P. rapae* and *P. napi* are specialist feeders predominantly on the plants of family Brassicaceae. *P. brassicae* is an important pest on vegetable *Brassicas* in India and is reported to cause extensive damage to oilseed *Brassicas* for the last few years (Bhalla *et al.,* 1997). *P. rapae* occurs in temperate regions around the world (Capinera, 2004). Though, the damage caused by caterpillars is slight, it can be high in years with high infestation (Hern *et al.,* 1996). *P. napi* is distributed throughout the northern hemisphere ranging from North America, Europe and Asia to North Africa.

Diamondback moth: The diamondback moth, *Plutella xylostella*, is one of the most damaging pests of *Brassica* crops especially vegetable *Brassicas* the world over. It has been a limiting factor in *Brassica* cultivation in many countries inflicting up to 90 % losses (Charleston and Kfir, 2000). It attacks almost at all the crop growth stages and economic damage occurs due to larval feeding on leaves. The pest is very difficult to control as it has developed resistance to all the major groups of insecticides.

Mustard sawfly: The mustard sawfly, *Athalia lugens proxima*, feeds on leaves, buds, flowers and pods. Another species *A. rosae* is also reported to feed on white mustard (*Sinapis alba*), turnip *(Brassica rapa*) and rape (*B. napus*) (Barker *et al.,* 2006).

In addition to these important pests, other pests like cabbage looper (*Trichoplusia ni*), cabbage moth *(Mamestra brassicae*), leaf miner (*Chromatomyia horticola*), cabbage root fly (*Delia radicum* syn., *brassicae*), flea beetle (*Phyllotreta cruciferae*), Brassica pod midge (*Dasineura brassicae*) also cause varied level of damage in *Brassica* crops in one or other part of the world.

Plant defenses: A general understanding: Plants have developed different ways to ward off insect herbivores such as toxic chemicals, volatiles to attract natural enemies of insect herbivores, physical barriers such as trichomes, waxes etc. These act as constitutive defenses against herbivores. On the other side, there are defenses that are either formed or activated after attack/ damage by an insect. These defenses are costly in terms of fitness as they divert resources from other process. Therefore, inducible defenses are important when the defense is metabolically expensive and the attack is unpredictable but frequent (Haukioja, 1999). Induced plants had relatively higher fitness (seed production) than uninduced controls in the presence of herbivores and relatively lower fitness than controls in the absence of herbivores (Agrawal, 1998; 1999a,b; Agrawal, 2000a) demonstrating trade off of resources. The general/constitutive defenses may lack the precision of specific/induced defenses and thereby may make the plant more susceptible to particular attackers than the plants with specific defenses (Agrawal, 2000b). The defenses that affect insect herbivores directly, such as through production of toxic metabolites, are called direct defenses. On the other hand, defenses that do not directly affect the insect but lead to attraction of natural enemies of herbivore are called indirect defenses (Mattiacci *et al.,* 2001). Plants release volatiles into the environment that attract natural enemies of insect herbivores (predators and parasitoids) that reduce the damage by herbivore insect. Such type of release of volatiles into the environment to attract natural enemies of the insect herbivores is

Table 1. Different plant volatiles of Brassicaceae and their role in plant defense.

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 mono- and sesquiterpenes	Whole plant	Plant-plant signalling, induction of plant defenses
Terpenes	Mono- and sesquiterpenes	Flowers, leaves, roots	Pollinator attraction, predator attraction, 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 defense, herbivore attraction
Sulphur containing compounds	Sulphides, elemental sulphur	Probably whole plant	Plant defense

(Rohloff and Bones, 2005)

considered as cry or call for help by the host plant.

The secondary metabolites have been used against insect herbivores for centuries. This has been achieved by plant breeders selecting plants with resistance properties or by including plants with desired chemical properties (attractants and repellents) in production strategies such as intercropping (Buckles *et al.,* 1998) and crop rotations.

Different chemical defenses in *Brassica* plants

Phytoalexins and phytoanticipins: Plants, unlike animals, are sessile organisms that cannot flee their predators. Through the course of evolution, plants have become nature's organic chemists *par excellence*, and collectively synthesize a plethora of secondary metabolites to defend themselves against herbivores and adapt to different types of abiotic environmental stresses. Traditionally, plant defense compounds are grouped into preformed defense compounds i.e. constitutive defenses (phytoanticipins) forming first chemical barrier to herbivore and pathogen attack and defense compounds synthesized in response to herbivore or pathogen attack i.e. inducible defenses (phytoalexins) (Vanetten *et al.,* 1994; Morant *et al.,* 2008).

Phytoalexins are low molecular weight antimicrobial compounds or secondary metabolites that are synthesized *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). Glucosinolates and the glucosinolate-myrosinase system represent an example of such a type of anticipin since myrosinase and glucosinolates are already biosynthesized as precursors before the insect attack. Isothiocyanates produced after glucosinolate hydrolysis play crucial role in protecting plants against various pests. Therefore, isothiocyanates are part of a group of basic plant chemical defenses known as phytoanticipins (Pedras *et al.,* 2007a). Phytoalexins from Brassicaceae family are the only sulfur containing and nitrogen containing phytoalexins (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 recognized as important pesticides and herbicides and until know crucifers are the only plants known to produce such compounds (Pedras *et al*., 2000).

Glucosinolates: Glucosinolates are the most studied defense related secondary compounds in Brassicaceae. These are amino acid-derived secondary plant products containing a sulfate and thioglucose moiety found almost exclusively in order Capparales (Halkier and Gershenzon, 2006). They are almost a uniform class of naturally occurring hydrophilic, non volatile, mostly water soluble, anionic compounds. When hydrolyzed glucosinolates generally liberate D-glucose, sulfate and an unstable aglucone, which undergo rearrangement to yield isothiocyanate as the main product or thiocyanate or a nitrile (organic cyanide) as secondary products. Because of presence of the glucose moiety and sulfate group, glucosinolates are hydrophilic and nonvolatile. On the other hand, isothiocyanates are generally volatile and chemically very active. More than 140 glucosinolates have been isolated from plants, 30 of which are present in *Brassica* species (Bellostas *et al.,* 2007). The content and composition of glucosinolates varies depending on *Brassica* species, the cultivar, plant parts within 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 mostly act as defense chemicals against insect-pests, concentration of which increases in response to insect damage and result in varied effects on insects. They can act both as stimulants and deterrents (Bartlet *et al.,* 1999; Agrawal and Kurashige, 2003; Hopkins *et al.,* 2009). They function as part of the plant's defense against insect attack, act as phagostimulants, and may help host plant location and colonization by many phytophagous insects. They also play a role in the location of insects by their parasitoids and predators. Antixenosis and tolerance have been identified as two mechanisms in seedling of *Sinapis alba* (white mustard) that probably account for flea beetle resistance in this species. The insecticidal activity of glucosinolates is the result of changes in the metabolism of the insect, specifically the inhibition of the glycolysis, Krebs cycle by decreasing the total O_2 uptake and CO_2 expired. They also serve as gustatory stimulants especially for specialist cruciferous insect-pests and their cleavage products; isothiocyanates are feeding and oviposition attractants for many insect species. They may also serve as cues for predators and parasitoids of insect pests for insect host/prey location.

Isothiocyanates are generally biocides whose activity results from interaction with proteins (Kawakishi and Kaneko, 1987). They interact non specifically and irreversibly with proteins and amino acids to form stable products.

Glucosinolate-Myrosinase System: the so called 'mustard oil bomb': Glucosinolates themselves are non toxic and non volatile. They are recognized by insects on contact, ingestion and subsequent hydrolysis. Upon hydrolysis they yield an array of physiologically active cleavage products. The cleavage is catalyzed by a thioglucoside glucohydrolase named myrosinase. The myrosinase is also called thioglucosidase.

In the intact plant tissue, myrosinase and glucosinolates are separated from each other. Thus, the two plant defense compounds are stored in a non-active glucosylated form to chemically stabilize and increase the solubility of the defense compound, to render it suitable for storage in the vacuole, and to protect the plant from the toxic effects of its own defense system (Jones and Vogt, 2001). While glucosinolates are present in vacuoles of various types of cells, myrosinases are localized in the myrosin cells (Kissen *et al.,* 2009) scattered throughout the most plant tissues and are also called toxic mines. These myrosin cells can easily be distinguished from neighbouring cells by light, electron and confocal microscopic observations (Bones *et al.,* 1991; Kissen *et al.,* 2009). These cells contain less lipids, a high content of endoplasmic reticulum and harbour smooth-looking protein bodies referred to as myrosin grains and myrosin grains have been shown to form a continuous reticular system called as the myrosin body (Andreasson *et al.,* 2001). Within the cells, the enzyme is stored inside myrosin grains. Damage to the plant tissue, either by insect feeding or otherwise, brings together glucosinolates and myrosinase resulting in rapid release of glucosinolate degradation products (Bones and Rossiter, 1996; 2006). These breakdown products resulting from glucosinolate hydrolysis represent the 'defense active' components and the dual functioning of glucosinolates and myrosinases coming into contact upon tissue disruption is designated as the glucosinolate-myrosinase defense system. This system has been shown to have multiple roles in plant-insect interactions and insect pest management (Rask *et al.,* 2000). Due its defense related properties this system is also called 'mustard oil bomb' (Kissen *et al.*, 2009).

From plant's health point of view, the glucosinolate-myrosinase system is a double-edged sword. On one side it provides defense against generalist feeders that are unable to cope with glucosinolates or their toxic breakdown products (Rask *et al.,* 2000) and on the other side, it makes plants vulnerable to attack by pests that have specialized to feed on *Brassica* plants (Renwick, 2002). Some of the insects such as *B. brassicae* and *L. erysimi* (specialists) actively take advantage of the defense compounds produced by plants. They sequester these toxic compounds from host plant and use them to protect themselves from predators. These insects synthesize thioglucosidase endogenously and when the insect is crushed or fed upon by predator, the enzyme leads to hydrolysis of sequestered glucosinolates to produce toxic products (Bridges *et al.,* 2002; Rossiter *et al.,* 2003). These crushed insects smell as well as taste badly and release volatiles, alarming other aphids in the colony. It is because of this behaviour that the mustard aphid is also called 'the walking mustard oil bomb' (Bridges *et al.,* 2002, Jones *et al.*, 2001 and 2002, Kazana *et al.*, 2007, Kissen *et al.,* 2009).

The glucosinolates are also known to stimulate larval feeding and oviposition by adults in the large white butterfly, *Pieris brassicae* and small white butterfly, *P. rapae* (David and Gardiner, 1966; Renwick *et al.,* 1992; Smallegange *et al.,* 2007; Thorsteinson, 1953). These are also known to stimulate oviposition by *P. xylostella* (Renwick *et al.*, 2006). Several insects have become well adapted to use the isothiocyanates to their advantage for example host location (Renwick, 2002). Studies have shown the presence of receptor neurons that can detect isothiocyanates in many specialist insects such as *B. brassicae* (Nottingham *et al.,* 1991) and *P. xylostella* (Renwick *et al.,* 2006).

But this does not mean that these secondary compounds are of adaptive advantage to insect-pests only. They play positive role from plants health perspective also. These compounds also play an important role of attracting the natural enemies of the insect-pests, for example, isothiocyanates emitted from damaged plants are used by natural enemies of insect-pests for host finding (Pope *et al.,* 2008). The infested plants are known to produce greater variety and amount of volatiles than the uninfested ones (Geervliet *et al.,* 1997).

Some of the specialized insects have developed ways to cope with the 'glucosinolate-myrosinase' system. For example, *P. xylostella* (Ratzka *et al.,* 2002) and the desert locust, *Schistocerca gregaria* (Falk and Gershenson, 2007) produce a glucosiolate sulfatase enzyme (GSS) which removes sulfur from glucosinolates to produce desulfoglucosinolates that are not hydrolyzed by myrosinase, thus, preventing the formation of toxic isothiocyanates and enabling the insects to feed on glucosinolate containing plants (Ratzka *et al.,* 2002; Falk and Gershenson, 2007). On the other hand, *P. rapae* redirects the glucosinolates hydrolysis reaction from the formation of toxic isothiocyanates to the formation of less toxic nitriles through a specific gut protein (nitrile specifier protein) (Wittstock *et al.,* 2004).

Since, glucosinolates play a defensive role in plants against herbivorous insects, it raises the question that double zero ('00') canola plants which are exceptionally low in these compounds might be susceptible to many insects. However, practically this is not so. These low glucosinolate plants may be less attractive to specialist insects for which these compounds serve as attractants and feeding stimuli (Gabrys and Tjallingii, 2002; Mewis *et al.,* 2002). This is again supported by the work of Giamoustaris and Mithen (1995) who reported that increase in the content of glucosinolates in *B. napus* resulted in increased feeding damage by specialist insects, flea beetles (*Psylliodes chrysocephala*) and greater incidence of small white butterfly (*Pieris rapae*), while the damage by generalist pests, i.e. pigeons and slugs, was reduced. Further, glucosinolate rich flower tissues are preferred more by *P. brassicae* and sustain higher growth compared to leaf tissues (Smallegange *et al.*, 2007) indicating the selective role of glucosinolates to elicit feeding in this specialist insect and the adaptation of the insect to use these compounds to its advantage.

Volatile compounds: Based on degradation of glucosinolates by myrosinase, *Brassica* plants produce volatile and semi-volatile toxic compounds that directly function in plant defense. Insect attacked plants release volatiles to attract natural enemies of insects that keep a check on the herbivore insect population. This can be equated with the 'call or cry for help' by a plant to the predator/parasitoid of insect herbivore. A detailed account of different plant volatiles and their roles is given in table 1.

Lectins: Lectins are proteins that selectively bind carbohydrates and more importantly the carbohydrate moieties of glycoproteins that are present on surface of most animal cells. They are found in a wide range of plant, microbial and animal tissues (Nachbar and Oppenheim, 1980; Komath *et al.,* 2006). Lectins incorporated in artificial diets have been shown to result in reduced performance of several insect species (Janzen *et al.*, 1976; Shukle and Murdock, 1983; Murdock *et al.*, 1990; Powell *et al.*, 1993; Peumans and van Damme, 1995; Rahbé *et al.,* 1995; Sauvion *et al.*, 2004a; Sadasivam and Thayumanavam, 2003). Lectins that are not efficiently degraded by digestive enzymes and that have an affinity for the surface of gut epithelial cells can be poisonous (Vasconcelos and Oliveira, 2004). They can form complexes with gut proteins (likely glycosylated proteins) with high affinity (Gatehouse *et al.*, 1995; Macedo *et al.*, 2004; Sauvion *et al.,* 2004b). The actual mechanism of insecticidal action is not clear at present. Since lectins interact with mono- and oligosaccharides, the insecticidal activity may involve a specific carbohydrate-lectin interaction with glycoconjugates on the surface of digestive tract epithelial cells (Macedo *et al.,* 2004). Acute symptoms following ingestion include nausea, vomitting and diarrhoea. They lead to membrane disruption of epithelial cell microvilli of insects fed upon diet containing lectin (Hart *et al.,* 1988).

Lectins have been reported to show biological activity against a wide range of insects especially the sap sucking insects (Foissac *et al.*, 2000; Powell, 2001). In *Brassicas*, they are of particular interest as aphids especially the mustard aphid is a limiting factor in successful cultivation of oilseed *Brassicas*. *Brassica fruticulosa* - a wild relative of cultivated *Brassicas* is reported to possess resistance against cabbage aphid, *Brevicoryne brassicae* (Cole, 1994a,b; Ellis and Farrell, 1995; Ellis *et al.,* 2000) and the high concentration of lectins was reported to be responsible for this. An accession of *B. fruticulosa* was also reported to possess resistance against *L. erysimi* in India (Kumar *et al.,* 2011). The results of feeding preference/choice test revealed that *L. erysimi* showed maximum preference for feeding on *B. rapa* cv. BSH-1, while the least preference was shown for *B. fruticulosa*. The antixenosis to feeding in *B. fruticulosa* has earlier been reported for cabbage aphid, *B. brassicae*. Monitoring of feeding behaviour of this species electronically by electrical penetration graph (EPG) showed a large reduction in the duration of passive phloem uptake on *B. fruticulosa* compared to the susceptible *B. oleracea* var. *capitata* cv. 'Offenham Compacta'. There was either quick withdrawl of stylets from sieve elements or disrupted phloem uptake (Cole, 1994a). This wild *Brassica* can serve as a good source of resistance in breeding programmes aimed at development of cultivars resistant to aphids particularly the mustard aphid and attempts have been made to introgress the gene of interest from this wild species to the cultivated plants (Kumar *et al.*, 2011; Atri *et al.,* 2012).

Evidence for defense against insect herbivores: *Brassica juncea* and *B. nigra* are less suitable hosts for *Dasineura brassicae* due to the presence of allyl and phenylethyl glucosinolates (Ahman, 1986). Allyl glucosinolate was the most toxic compound lethal at 10 ppm. This concentration is within the range of corresponding parent allyl glucosinolate in *B. juncea* cultivars. These plant secondary compounds may be feeding/oviposition stimulants or deterrents for insect herbivores. Attraction of a plant to a particular insect due to high concentration of these compounds does not mean that they do not play role in plant defense. Although, specialist insects have managed to utilize them to their benefit, but still these compounds play a role as indirect defenses. Volatiles released due to insect feeding give a cue to their natural enemies for insect host location. *Diaeretiella rapae*, a predominant parasitoid of *Brassica* feeding aphids, attacks the mustard aphid, *L. erysimi* at a greater rate than the generalist feeding aphid, *Myzus persicae* (Blande *et al.*, 2007). Agrawal and Kurashige (2003) analyzed 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 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.* Similarly, Dilawari and Atwal (1987) observed that number of probes increased and feed uptake reduced significantly in an artificial media containing higher level of glucosinolates. Though, glucosinolates are used by these insects for host location, there degradation products prove toxic to them.

Karowe and Schoonhoven (1992) determined the relative suitability of *Brassica* as host plants both for unparasitized *P. brassicae* caterpillars and for *Cotesia glomerata* developing in *P. brassicae.* Of all the *Brassica* plants tested, the host-parasitoid complex attained a lower final weight than unparasitized *P. brassicae* probably due to reduced consumption by the parasitized *P. brassicae*. 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 those from mechanically damaged (Steinberg *et al.*, 1993).

Olfactory attraction of diamondback moth female (*P. xylostella*) to the odours of intact and homogenized 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 which was absent in odours from intact plants.

The chemical potential of glucosinolates and the glucosinolate-myrosinase system has been shown for cabbage and mustard aphids. The cabbage aphid 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 endogenous insect myrosinase, thus mimicking the plant glucosinolate-myrosinase system (Rossiter *et al.,* 2003; Jones *et al.,* 2001 and 2002; Kazana *et al.*, 2007). Similar defense responses exist in important *Brassica* crops. For *L. erysimi,* isothiocyanates together with ά-farnesene have been reported to work as alarm signals (Dawson *et al.*, 1987). It was suggested that the functioning of glucosinolate utilization may be important in understanding the exploitation of biological control agents to control these aphids (Cole, 1997). Electrophysiological studies together with high resolution gas chromatography identified metabolites of glucosinolates in crucifer plants being synergists for alarm pheromone of *L. erysimi*. The most active, allyl isothiocyanate, significantly improved the activity of an aqueous formulation of ά-farnesene (Dawson *et al.*, 1990). The volatile z-jasmone was shown to repel aphids, while being an attractant to parasitoids (Birkett *et al.*, 2000).

Potential in Pest Management: Increasing knowledge of plant defenses has been utilized by man to breed crop plants resistant to insect-pests and other biotic stresses. Attempts are underway to exploit these secondary plant metabolites for breeding plants resistant to pests. Some success has been achieved in the transfer of gene for lectin production from wild *B. fruticulosa* to the *B. juncea* background that offers appreciable level of resistance against *L. erysimi* (Kumar *et al.,* 2011). Though genes for lectin production have been transferred from diverse sources resulting in the production of *Brassica* transgenics (Kanrar *et al.,* 2002; Hossain *et al.*, 2006), but in view of the continuing concerns about the adoption of transgenic food crops and their perceived adverse effects on the environment, this conventional breeding strategy is especially significant.

Though some specialist insects have developed strategies to overcome the adverse effects of glucosinolate-myrosinase system, high concentration of glucosinolates can adversely affect even these specialists (Agrawal and Kurashige, 2003; Siemens and Mitchell-Olds, 1996; Kumar and Sangha, 2013). Wild relatives of *Brassicas* contain more glucosinolates and specialists as well as generalists perform worse on them (Gols *et al.,* 2008; Griffiths *et al.*, 2001). On the other hand, a positive correlation was found between total glucosinolate concentration and plant damage by *P. chrysocephala* and *P. rapae* on *B. napus* (Giamoustaris and Mithen, 1995) suggesting the possible role of other factors in addition to glucosinolates. The success of glucosinolate coping strategies is related to several factors such as levels of individual glucosinolates and myrosinase. For example, 4-methoxy glucobrassicin has been identified as an important glucosinolate acting as anti-aphid component (Kim and Jander, 2007; Kusnierczyk *et al.,* 2008). Thus, this opens up the possibility of breeding for higher levels of pest resistance by manipulating the levels of individual glucosinolates.

Another potential area of use of secondary plant metabolites of Brassicaceae is biofumigation for the management of soil borne pests. Biofumigation is defined as the use of biocidal compounds either as commercial fumigants or released by plants used as green manures or rotation crops for suppression of soil borne pests, pathogens and weeds. Studies have shown that Brassica plants incorporated into soil are effective in controlling nematodes and pathogens (Mojtahedi *et al.,* 1993; Muelchen *et al.,* 1990). Biofumigation results from the production of isothiocyanates after tissue disruption. Thus, high level of tissue disruption and high soil moisture content are important for the production of these volatiles. Simple ploughdown of rapeseed plants yielded very low concentration of isothiocyanates rarely exceeding 1 nmol/g dry weight of soil, which is below the recommended concentration for pest control (Gardiner *et al.*, 1999). However, by thorough pulverization of mustard combined with heavy watering high concentration of 100 nmol/g of soil was achieved (Matthiessen *et al.,* 2004). It should be noted, however, that, low concentration of isothiocyanates released for a prolonged period may decrease damage by soil pathogens (Mattner *et al.,* 2008; Mojtahedi *et al.,* 1993).

The *Brassica* plants can be used in habitat manipulation to reduce the damage, caused by insect-pests such as intercropping, trap cropping and in push-pull strategy. Intercropping helps to increase plant diversity in a field and hence disrupts the host location by the pest and its subsequent colonization. In addition, it provides better diversity of arthropods such as natural enemies of insect pests. However, in the case of *Brassica* plants intercropping studies have yielded variable results. Bukovinszky *et al.* (2005) attributed this to differences in pre- and post-alighting search mechanisms between *Brassica* specialists. For example, there was no effect of intercropping on host searching by *Pieris rapae* due to its better visual and olfactory sense ability, whereas, *Brevicoryne brassicae* was affected to a greater extent due to its limited dispersal ability (Banks, 1998). The trap crop to be used to attract a pest should be highly attractive to the target pest for feeding or oviposition. Previous studies at Ludhiana have indicated *B. carinata* to be highly attractive for oviposition to *P. brassicae* than the main *B. juncea* crop with reports of more than 100 larvae on a single plant (Kumar, 2011 and 2016). Similarly, *B. rapa* var. *brown sarson* cv. BSH 1 is highly attractive to *L. erysimi* and is being used as a susceptible check in screening studies (AICRP, 2011). Growth stage related visual and olfactory stimuli were in part responsible for the effect. The high pest density on the trap crop can be managed by spraying insecticides or mechanical removal and destruction of the pest such as gregarious larvae of *P. brassicae.*

The push-pull strategy has a great potential for insect-pest management than either intercropping or trap cropping. Merging intercropping with trap cropping is called the push-pull strategy. In the push element of the strategy, the target pest incidence on main crop can be reduced by use of stimuli that either deter/repel the pest or mask the apparency of the crop. It can be achieved by intercropping with plants that are not attractive to the pest such as non-host plants. The actual mechanism by which intercropping works is still not clear and the proposed plant-chemistry based hypothesis was recently challenged by Finch and Collier (2012). They suggested that intercrops hypothetically could function as physical barriers and thus hide the target crop from herbivores.

In addition to the use of non host plants, some pheromones such as alarm pheromones or deterrents can also be used to repel the pest. In the pull component, target insects can be attracted either by planting trap crop and/or use of host plant volatiles, attractive pheromones (sex pheromone) and oviposition and gustatory stimuli (Shelton and Badenes-Perez, 2006). Though, a lot of work has been reported on pull element, there is a need for detailed work for thorough understanding of the repellency function in intercrop systems. This will help in making the push-pull approach a more broadly generalized application of chemical ecology in agriculture.

Conclusion

Although there are a number of plant species from various orders which possess defense related compounds, this review has particularly focused on those of *Brassicas* with their role in plant defense as well as insect-pest management. Like any other plant species, these defenses in Brassicaceae have evolved as a result of millions of years of adaptations and counter-adaptations by plants and insects. The ability of some specialized insects to control the breakdown of glucosinolates to yield breakdown products formed via a nitrile specifier protein or to prevent hydrolysis of glucosinolates by a desulfatase activity are some of the examples of how plant adaptations to herbivory are met by counter adaptations from the herbivores.

Detailed knowledge on defense systems of plants including the genes and enzymes of the biosynthetic and catabolic pathways, metabolon formation and metabolic cross talk will lead to exploitation and enhancement of the plants' own defense mechanisms. This can be achieved by molecular breeding approaches which are either based on natural variation for these traits or production of plant species with host plant resistance to insects introduced by transformation of entire pathways. Such approaches will have wider implications as they will result in significant reduction in agricultural production footprint on the environment and will also limit the use of chemical pesticides. Molecular breeding tools have enabled successful transfer of entire dhurrin biosynthetic pathway from sorghum to *Arabidopsis* with resistance to specific target insect (Tattersall *et al.*, 2001) and that too without any inadvertent effect on the metabolome (Kristensen *et al.*, 2005). It is a unique example of a plant engineered to provide insect resistance by production of a new defense compound, while at the same time adhering to the principle of substantial equivalence.

Plant defense systems, in general, and those of *Brassicas*, in particular, present a vast unexplored and hence, unexploited potential of great agricultural, medicinal and industrial importance.

REFERENCES

Agarwala, B.K. and Datta, N. (1999). Life history response of mustard aphid *Lipaphis erysimi* to phonological changes in its host. *J. Biosci.*, 24: 224-231

Agrawal, A.A. (1998). Induced responses to herbivory and increased plant performance. *Sci.,* 279:1201-1202

Agrawal, A.A. (1999a). Induced responses to herbivory in wild radish: effects on several herbivores and plant fitness. *Ecol.,* 80: 1713-1723

Agrawal, A.A. (1999b). Induced plant defense: evolution of induction and adaptive phenotypic plasticity. In: Agrawal, A.A., Tuzun, S. and Bent, L. (eds.) Inducible plant defenses against pathogens and herbivores: Biochemistry, ecology and agriculture. American Phytopathological Society Press, St. Paul, MN, pp. 251-68

Agrawal, A.A. (2000a). Benefits and costs of induced responses to herbivory in *Lepidium virginicum* (Brassicaceae). *Ecol.,* 81: 1804-13

Agrawal, A.A. (2000b). Specificity of induced resistance in wild radish: causes and consequences for two specialist and two generalist caterpillars. *Oikos*, 89: 493-500

Agrawal, A.A. (2006). Macroevolution of plant defense strategies. *Trends Ecol Environ*, 22 (2): 103-109

Agrawal, A.A. and Kurashige, N.S. (2003). A role for isothiocyanates in plant resistance against the specialist herbivore *Pieris rapae*. *J. Chem. Ecol.,* 29: 1403-1415

Ahman, I. (1986). Toxicities of host secondary compounds to eggs of the *Brassica* specialist *Dasineura brassicae*. *J. Chem. Ecol.*, 12: 1481-88

AICRP, (2011). All India Coordinated Research Project on Rapeseed-Mustard. *Proceedings of 18th Annual Group Meeting of Rapeseed Mustard Research Workers*. Aug 05-07, 2011, Assam Agricultural University Khanapara Campus, Guwahati, pp. Ento 1-4.

Andreasson, E., Jorgensen, L.B., Hoglund, A.S., Rask, L. and Meijer, J. (2001). Different myrosinase and idioblast distribution in *Arabidopsis* and *Brassica napus. Plant Physiol.*, 127: 1750-63

Atri, C., Kumar, B., Kumar, H., Kumar, S., Sharma, S. and Banga, S.S. (2012). Development and characterization of *Brassica juncea – fruticulosa* introgression lines exhibiting resistance to mustard aphid, *Lipaphis erysimi* (Kalt.). *BMC Genet.,* 13: 104. doi: 10.1186/1471-2156-13-104

Banks, J.E. (1998). The scale of landscape fragmentation affects herbivore response to vegetation heterogeneity. *Oecologia*, 117: 239-46

Barker, A., Molotsane, R., Muller, C., Schaffner, U. and Stadler, E. (2006). Chemosensory and behavioural responses of the turnip sawfly, *Athalia rosae*, to glucosinolates and isothiocyanates. *Chemoecol.*, 16:209-18

Bartlet, E., Kiddle, G. and Williams, I. (1999). Wound-induced increase in the glucosinolate content of oilseed rape and their effect on subsequent herbivory by a specialist. *Entomol. exp. Appl.*, 91: 163-67

Bellostas, N., Sorensen, A.D., Sorensen, J.C., Sorensen, H., Sorensen, M.D., Gupta, S.K. and Kader, J.C. (2007). Genetic variation and metabolism of glucosinolates. *Adv. Bot. Res.*, 45:369-415

Bhalla, S., Kapur, M.L., Verma, B.R. and Singh, R. (1997). An unusual abundance of cabbage butterfly, *Pieris brassicae* (Linnaeus) on various *Brassica* species in the environs of Delhi and screening for locating sources of resistance among different cultivars. *J. entomol. Res.*, 21: 147-51

Birkett, M.A., Campbell, C.A.M., Chamberlain, K., Guerrieri, E., Hick, A.J., Martin, J.L., Matthes, M., Napier, J.A., Pattersson, J., Pickett, J.A., Poppy, G.M., Pow, E.M., Pye, B.J., Smart, L.E., Wadhams, G.H., Wadhams, L.J. and Woodcock, C.M. (2000). New roles for *cis*-jasmone as an insect semiochemical and in plant defense. *PNAS* (USA), 97: 9329-34

Blande, J., Pickett, J. and Poppy, G. (2007). A comparison of semiochemically mediated interactions involving specialist and generalist *Brassica*-feeding aphids and the braconid parasitoid *Diaeretiella rapae*. *J. Chem. Ecol.*, 33: 767-79

Bones, A.M. and Rossiter, J.T. (1996). The myrosinase-glucosinolate system, its organization and biochemistry. *Physiologia Plantarum*, 97:194-208

Bones, A.M. and Rossiter, J.T. (2006). The enzymic and chemically induced decomposition of glucosinolates. *Phytochem.*, 67: 1053-67

Bones, A.M., Thangstad, O.P., Haugen, O. and Espevik, T. (1991). Fate of myrosin cells – Characterization of monoclonal antibodies against myrosinase. *J. exp. Bot.,* 42:1541-49

Bridges, M., Jones, A.M.E., Bones, A.M., Hodgson, C., Cole, R., Bartlet, E., Wallsgrove, R., Karapapa, V.K., Watts, N. and Rossiter, J.T. (2002). Spatial organization of the glucosinolate-myrosinase system in *Brassica* specialist aphids is similar to that of the host plant. *Proc. Royal Soc. London B,* 269: 187-91

Buckles, D., Triomphe, B. and Sain, G. (1998). Cover crops in hillside agriculture. Farmer innovation with *Mucuna*. International Maize and Wheat Improvement Centre, Mexico. Available at http://www.idrc.ca/openebooks/269-4

Bukovinszky, T., Potting, R.P.J., Clough, Y. and Vet, L.E.M. (2005). The role of pre- and post-alighting detection mechanisms in the responses to patch size by specialist herbivores. *Oikos*, 109: 435-46

Capinera, J.L. (2004). Cabbageworm, *Pieris rapae* (Linnaeus) (Lepidoptera: Pieridae). *Encyclopedia of Entomology*, Kluwer, Dordrecht, The Netherlands. pp. 444-45

Charleston, D.S. and Kfir, R. (2000). The possibility of using

India mustard, *Brassica juncea*, as a trap crop for the diamondback moth, *Plutella xylostella* in South Africa. *Crop Prot.,* 19: 455-60

Chattopadhyay, C., Agrawal, R., Kumar, A., Singh, Y.P., Roy, S.K., Khan, S.A., Bhar, L.M., Chakravarthy, N.V.K., Srivastava, A., Patel, B.S., Srivastava, B., Singh, C.P. and Mehta, S.C. (2005). Forecasting of *Lipaphis erysimi* on oilseed *Brassicas* in India – a case study. *Crop Prot.,* 24: 1042-53

Clossais-Bernard, N. and Larher, F. (1991). Physiological role of glucosinolates in *Brassica napus*: Concentration and distribution pattern of glucosinolates among plant organs during a complete life cycle. *J. Sci. Food Agric.,* 56: 25-38

Cole, R.A. (1994a). Locating a resistance mechanism to the cabbage aphid in two wild *Brassicas*. *Entomol. exp. Appl.,* 71: 23-31

Cole, R.A. (1994b). Isolation of a chitin binding lectin, with insecticidal activity in chemically defined synthetic diets, from two wild brassica species with resistance to cabbage aphid, *Brevicoryne brassicae*. *Entomol. exp. Appl.,* 72: 181-87

Cole, R.A. (1997). Comparison of feeding behaviour of two *Brassica* pests *Brevicoryne brassicae* and *Myzus persicae* on wild and cultivated *Brassica* species. *Entomol. exp. Appl.,* 85: 135-43

Damodaram, T. and Hegde, D. M. (2002). Oilseeds situation: A Statistical Compendium 2002, Directorate of Oilseeds Research, Hyderabad 500 030, India, pp. 471

David, W.A.L. and Gardiner, B.O. (1966). Mustard oil glucosides as feeding stimulants for *Pieris brassicae* larvae in semi-synthetic diet. *Entomol. exp. Appl.,* 9: 247-55

Dawson, G.W., Griffiths, D.C., Merritt, L.A., Mudd, A., Pickett, J.A., Wadhams, L.J. and Wookcock, C.M. (1990). Aphid semiochemicals – A review and recent advances in the sex pheromone. *J. Chem. Ecol.,* 16: 3019-30

Dawson, G.W., Griffiths, D.C., Pickett, J.A., Wadhams, L.J. and Woodcock, C.M. (1987). Plant derived synergists of alarm pheromone from turnip aphid, *Lipaphis* (*Hyadaphis*) *erysimi*. (Homoptera: Aphididae). *J. Chem. Ecol.,* 13:1663-71

Dilawari, V.K. and Atwal, A.S. (1987). Effects of cruciferous glucosinolates on probing pattern and feed uptake by mustard aphid, *Lipaphis erysimi* (Kalt.). *Proc. Indian Acad. Sci. (Animal Sciences),* 96: 695-703.

Dixon, R.A. (2001). Natural products and plant disease resistance. *Nature,* 411: 843-47

Dubuis, P.H., Marrazi, C., Stadler, E. and Mauch, F. (2005). Sulphur deficiency causes a reduction in antimicrobial potential and leads to increased disease susceptibility of oilseed rape. *J. Phytopath.,* 153: 27-36

Ellis, P.R. and Farrell, J.A. (1995). Resistance to cabbage aphid (*Brevicoryne brassicae*) in six Brassica accessions in New Zealand. *New Zealand J. Crop Hort. Sci.,* 23: 25-29

Ellis, P.R., Kiff, N.B., Pink, D.A.C., Jukes, P.L., Lynn, J. and Tatchell, G.M. (2000). Variation in resistance to the cabbage aphid (*Brevicoryne brassicae*) between and within wild and cultivated *Brassica* species. *Genet. Resour. Crop Evol.,* 47: 395-401

Falk, K.L. and Gershenson, J. (2007). The desert locust, *Schistocerca gregaria*, detoxifies the glucosinolates of *Schowia purpurea* by desulfation. *J. Chem. Ecol.,* 33: 1542-55

FAOSTAT (2009). Publicly available databases from: Food and Agricultural Organization of the United Nations (FAO), http://faostat.fao.org/.

Finch, S. and Collier, R. (2012). The influence of host and non-host companion plants on the behaviour of pest insects in field crops. *Entomol. exp. Appl.,* 142: 87-96

Foissac, X., Nguyen, T.L., Christou, P., Gatehouse, A.M.R. and Gatehouse, J.A. (2000). Resistance to green leaf hopper (*Nephotettix virescens*) and brown plant hopper (*Nilaparvata lugens*) in transgenic rice expressing snowdrop lectin (*Galanthus nivalis* agglutinin; GNA). *J. Insect Physiol.,* 46: 573-83

Font, R., Del Rio-Celestino, M., Fernandez, J.M. and De Hardo-Bailon, A. (2003). Acid detergent fiber analysis in oilseed brassicas by near infrared spectroscopy. *J. agric. Food Chem.,* 51: 2917-22.

Font, R., Del Rio-Celestion M., Rosa, E., Aires, A. and De Hardo-Bailon, A. (2005). Glucosinolate assessment in *Brassica oleracea* leaves by near-infrared spectroscopy. *J. agric. Sci.,* 143: 65-73

Francis, F., Lognay, G., Wathelet, J.P. and Haubruge, E. (2001). Effect of allelochemicals from first (Brassicaceae) and second (*Myzus persicae* and *Brevicoryne brassicae*) trophic levels on *Adalia bipunctata*. *J. Chem. Ecol.,* 27: 243-56

Gabrys, B. and Tjallingii, W.F. (2002). The role of sinigrin in host plant recognition by aphids during initial plant penetration. *Entomol. exp. Appl.,* 104: 89-93

Gardiner, J.B., Morra, M.J., Eberlein, C.V., Brown, P.D. and Borek, V. (1999). Allelochemicals released in soil following incorporation of rapeseed (*Brassica napus*) green manures. *J. agric. Food Chem.,* 47: 3837-42

Gatehouse, A.M.R., Powell, K.S., van Damme, E.J.M. and Gatehouse, J.A. (1995). Insecticidal properties of plant lectins: Their potential in plant protection. In: A.J. Pusztai and S. Bardocz (eds.) *Lectins*: *Biomedical Perspectives*, pp. 35-58. Taylor and Francis, London, UK.

Geervliet, J.B.F., Posthumus, M.A., Vet, L.E.M. and Dicke, M. (1997). Comparative analysis of headspace volatiles from different caterpillar-infested or uninfested food plants of *Pieris* species. *J. Chem. Ecol.,* 23: 2935-54

Giamoustaris, A. and Mithen, R. (1995). The effect of modifying the glucosinolate content of leaves of oilseed rape (*Brassica napus* ssp. *oleifera*) on its interaction with specialist and generalist pests. *Annals appl. Biol.,* 126: 347-63

Gols, R., Bukovinszky, T., Van Dam N.M., Dicke, M., Bullock J.M. and Harvey, J.A. (2008). Performance of generalist and specialist herbivores and their endoparasitoids differs on cultivated and wild *Brassica* populations. *J. Chem. Ecol.,* 34:132-43

Griffiths, D.W., Deighton, N., Birch, A.N.E., Patrian, B., Baur, R. and Stadler, E. (2001). Identification of glucosinolates on the leaf surface of plants from the cruciferae and other closely related species. *Phytochem.,* 57: 693-700

Halkier, B.A. and Gershenzon, J. (2006). Biology and biochemistry of glucosinolates. *Annu. Rev. Plant Biol.,* 57: 303-333

Hart, C.A., Batt, R.M., Saunders, J.R. and Getty, B. (1988). Lectin-induced damage to the enterocyte brush border:

An electron-microscopic study in rabbits. *Scandinavian J. Gastroenterol,* 3:1153–59.

Haukioja, E. (1999). Ecology: bite the mother, fight the daughter. *Nature,* 401: 22-23.

Hern, A., Edwards-Jones, G. and McKinlay, R.G. (1996). A review of preoviposition behaviour of small cabbage white butterfly *Pieris rapae* (Lepidoptera: Pieridae). *Ann. Appl. Biol.,* 128:349-71.

Hopkins, R.J., Van Dam, N.M. and van Loon, J.J.A. (2009). Role of glucosinolates in insect-plant relationships and multitrophic interactions. *Annu. Rev. Entomol.,* 54:57-83.

Hossain, M.A., Maiti, M.K., Basu, A., Sen, S., Ghosh, A.K. and Sen, S.K. (2006). Transgenic expression of onion leaf lectin in Indian mustard offers protection against aphid colonization. *Crop Sci.,* 46: 2022-32

Janzen, D.H., Juster, H.B. and Liener, I.E. (1976). Insecticidal action of the phytohemagglutinin in black beans on Bruchid beetle. *Sci.,* 192: 795-96

Jones, A.M.E., Bridges, M., Bones, A.M., Cole, R. and Rossiter, J.T. (2001). Purification and characterization of a non-plant myrosinase from the cabbage aphid *Brevicoryne brassicae*. *Insect Biochem. Mol. Biol.,* 31: 1-5

Jones, A.M.E., Winge, P., Bones, A.M., Cole, R. and Rossiter, J.T. (2002). Characterization and evolution of a myrosinase from the cabbage aphid *Brevicoryne brassicae. Insect Biochem. Mol. Biol.,* 32: 275-84

Jones, P. and Vogt, T. (2001). Glycosyltransferases in secondary plant metabolism: tranquilizers and stimulant controllers. *Planta,* 213: 164-174.

Joshi, M.L., Ahuja, D.B. and Mathur, B.N. (1989). Losses in seed yield by insect pests and their occurrence on different dates of sowing in Indian Mustard (*Brassica juncea* subsp. *juncea*). *Indian J. agric. Sci.,* 59: 166-68.

Kanrar, S., Venkateswari Kirti, P.B. and Chopra, V.L. (2002). Transgenic Indian mustard (*Brassica juncea*) with resistance to the mustard aphid (*Lipaphis erysimi* Kalt.). *Plant Cell Rep.,* 20:976-81

Karowe, D.N. and Schoonhoven, L.M. (1992). Interactions among three trophic levels: the influence of host plant on performance of *Pieris brassicae* and its parasitoid *Cotesia glomerata*. *Entomol. exp. Appl.,* 62: 241-47

Kawakishi, S. and Kaneko, T. (1987). Interaction of proteins with allyl isothiocyanate. *J. agric. Food Chem.,* 35:85-88

Kazana, E., Pope, T.W., Tibbles, L., Bridges, M., Pickett, J.A., Bones, A.M., Powell, G. and Rossiter, J.T. (2007). The cabbage aphid: a walking mustard oil bomb. *Proc. Royal Soc. London B.,* 274: 2271-77

Kift, N.B., Ellis, P.R., Tatchell, G.M. and Pink, D.A.C. (2000). The influence of genetic background on resistance to the cabbage aphid (*Brevicoryne brassicae*) in kale (*Brassica oleracea* var. *acephala*). *Ann. appl. Biol.,* 136: 189-95

Kim, J.H. and Jander, G. (2007). *Myzus persicae* (green peach aphid) feeding on *Arabidopsis* induces the formation of a deterrent indole glucosinolate. *Plant J.,* 49: 1008-19

Kissen, R., Rossiter, J. and Bones, A. (2009). The 'mustard oil bomb': not so easy to assemble?! Localization, expression and distribution of the components of the myrosinase enzyme system. *Phytochem. Rev.,* 8: 69-86

Komath, S.S., Kavitha, M. and Swamy, M.J. (2006). Beyond carbohydrate binding: new directions in plant lectin research. *Organic Biomol. Chem.,* 4: 973-88.

Kristensen, C., Morant, M., Olsen, C.E., Ekstrom, C.T., Galbraith, D.W., Moller, B.L. and Bak, S. (2005). Metabolic engineering of dhurrin in transgenic Arabidopsis plants with marginal inadvertent effects on the metabolome and transcriptome. *PNAS* (USA)*,* 102: 1779-84.

Kular, J.S. and Kumar, S. (2011). Quantification of avoidable yield losses in oilseed *Brassica* caused by insect pests. *J. Pl. Prot. Res.,* 51(1): 38-43.

Kumar, S. (2011). *Cotesia glomeratus*: a potential biocontrol agent of large white butterfly, *Pieris brassicae* in Indian Punjab. *Proc. 13th International Rapeseed Cong.*, Prague, Czech Republic, June 05-09, 2011, pp. 1141-43.

Kumar, S. (2015). Relative abundance of turnip aphid and the associated natural enemies on oilseed *Brassica* genotypes. *J. agric. Sci. Technol.,* 17: 1209-1222.

Kumar, S. (2016). Potential of Ethiopian mustard, *Brassica carinata* as a trap crop for large white butterfly, *Pieris brassicae* infesting mustard, *Brassica juncea. J. Pest Sci.* doi:10.1007/s10340-016-0771-6

Kumar, S., Atri, C., Sangha, M.K. and Banga, S.S. (2011). Screening of wild crucifers for resistance to mustard aphid, *Lipaphis erysimi* (Kaltenbach) and attempt at introgression of resistance gene(s) from *Brassica fruticulosa* to *Brassica juncea. Euphytica,* 179: 461-70.

Kumar, S. and Sangha, M.K. (2013). Biochemical mechanism of resistance in some *Brassica* genotypes against *Lipaphis erysimi* (Kaltenbach) (Homoptera: Aphididae). *Vegetos,* 26(2): 387-395. doi: 10.5958/j.2229-4473.26.2.103

Kumar, S. and Singh, Y.P. (2015). Insect Pests In: Kumar, A., Banga, S.S., Meena, P.D. and Kumar, P.R. (eds.) *Brassica Oilseeds Breeding and Management.* CABI Publishing, Wallingford, UK, pp. 193-232.

Kusnierczyk, A., Winge, P., Jorstad, T., Troczynska, J., Rossiter, J. and Bones, A. (2008). Towards global understanding of plant defense against aphids - timing and dynamics of early *Arabidopsis* Ler defense responses to cabbage aphid (*Brevicoryne brassicae*) attack. *Plant, Cell Environ.,* 31: 1097-1115.

Macedo, M.L.R., de Castro, M.M. and das GraÇas Machado Freire, M. (2004). Mechanisms of the insecticidal action of TEL (*Talisia esculenta* Lectin) against *Callosobruchus maculates* (Coleoptera: Bruchidae). *Arch. Insect Biochem. Physiol.,* 56: 84-96.

Matthiessen, J.N., Warton, B. and Shackelton, M.A. (2004). The importance of plant maceration and water addition in achieving high *Brassica*-derived isothiocyanate levels in soil. *Agroindustria,* 3:277-80.

Mattiacci, L., Rudelli, S., Rocca, B.A., Genini, S. and Dorn, S. (2001). Systemically induced response of cabbage plants against a specialist herbivore, *Pieris brassicae*. *Chemoecol.,* 11: 167-73.

Mattner, S.W., Porter, I.J., Gounder, R.K., Shanks, A.L., Wren, D.J. and Allen, D. (2008). Factors that impact on the ability of biofumigants to suppress fungal pathogens and weeds of strawberry. *Crop Prot.,* 27: 1165-73.

Mewis, I.Z., Ulrich, C. and Schnitzler, W.H. (2002). The role of glucosinolates and their hydrolysis products in oviposition and host plant finding by cabbage webworm. *Hellula undalis*. *Entomol. exp. Appl.,* 105:129-39

Mojtahedi, H., Santo, G.S., Wilson, J.H. and Hang, A.N. (1993). Managing *Meloidogyne chitwoodi* on potato with rapeseed as green manure. *Pl. Dis.,* 77: 42-46.

Morant, A.V., Jorgensen, K., Jorgensen, C., Paquette, S.M., Perez, R.S., Moller, B.L. and Bak, S. (2008). β-Glucosidases as detonators of plant chemical defense. *Phytochem.,* 69: 1795-1813

Mossler, M.A. (2005). Florida Crop/Pest Management Profile: Specialty Brassicas (Arrugula, Bok Choy, Chinese Broccoli, Chinese Mustard, Napa) PI-70, Pesticide Information Office, University of Florida, USA.

Muelchen, A.M., Rand, R.E. and Parke, J.L. (1990). Evaluation of crucifer manures for controlling aphanomyces root rot of peas. *Pl. Dis.,* 74:651-54

Murdock, L.L., Huesing, J.E., Nielsen, S.S., Pratt, R.C. and Shade, R.E. (1990). Biological effects of plant lectins on the cowpea weevil. *Phytochem*., 29:85-89

Nachbar, M.S. and Oppenheim, J.D. (1980). Lectins in the United States diet: a survey of lectins in commonly consumed foods and a review of the literature. *American J. clinic. Nutr.,* 33: 2338–45

Nottingham, S.F., Hardie, J., Dawson, G.W., Hick, A.J., Pickett, J.A., Wadhams, L.J. and Woodcock, C.M. (1991). Behavioral and electrophysiological responses of aphids to host and nonhost plant volatiles. *J. Chem. Ecol.,* 17:1231-42

Pedras, M.S.C., Okanga, F.I., Zaharia, I.L. and Khan, A.Q. (2000). Phytoalexins from crucifers: synthesis, biosynthesis, and biotransformation. *Phytochem.,* 53: 161-176

Pedras, M.S.C., Zheng, Q.A. and Gadagi, R.S. (2007a). The first naturally occurring aromatic isothiocyanates, rapalexins A and B are cruciferous phytoalexins. *Chem. Comm.,* 4: 368-70

Pedras, M.S.C., Gadagi, R.S., Jha, M. and Sarma-Mamillapalle, V.K. (2007b). Detoxification of the phytoalexin brassinin by isolates of *Leptosphaeria maculans* pathogenic on brown mustard involves an inducible hydrolase. *Phytochem.,* 68:1572-78

Peumans, W.J. and Van Damme, E.J.M. (1995). The role of lectins in plant defense. *Histochem. J.,* 27: 253-71

Pivnick, K.A., Jarvis, B.J. and Slater, G.P. (1994). Identification of olfactory cues used in host-plant finding by diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). *J. Chem. Ecol.,* 20: 1407-27

Pope, T., Kissen, R., Grant, M., Pickett, J., Rossiter, J. and Powel, G. (2008). Comparative innate responses of the aphid parasitoid *Diaeretiella rapae* to alkenyl glucosinolate derived isothiocyanates, nitriles and epithionitriles. *J. Chem. Ecol.,* 34: 1302-10

Powell, K.S. (2001). Antimetabolic effects of plant lectins towards nymphal stages of the plant hoppers *Tarophagous proserpina* and *Nilaparvata lugens*. *Entomol. exp. Appl.,* 99: 71-77

Powell, K.S., Gatehouse, A.M.R., Hilder, V.A. and Gatehouse, J.A. (1993). Antimetabolic effects of plant lectins and plant and fungal enzymes on the nymphal stages of two important rice pests, *Nilaparvata lugens* and *Nephotettix cinciteps*. *Entomol. exp. Appl.,* 66: 119-26

Rahbé, Y., Sauvion, N., Febvay, G., Peumans, W.J. and Gatehouse, A.M.R. (1995). Toxicity of lectins and processing of ingested proteins in the pea aphid *Acyrthosiphon pisum. Entomol. exp. Appl.,* 76: 143-55

Rangkadilok, N., Nicolas, M.E., Bennett, R.N., Premier, R.R., Eagling, D.R. and Taylor, P.W.J. (2002). Developmental changes of sinigrin and glucoraphanin in three *Brassica* species (*Brassica nigra, Brassica juncea* and *Brassica oleracea* var. *italica*). *Sci. Hort.,* 96: 11-26

Rask, L., Andreasson, E., Ekbom, B., Eriksson, S., Pontoppidan, B. and Meijer, J. (2000). Myrosinase: gene family evolution and herbivore defense in Brassicaceae. *Pl. Mol. Biol.,* 42: 93-113

Ratanpara, H.C., Patel, J.R., Borad, P.K., Mehta, D.M., Patel. A.M. and Shah, B.R. (1992). Relationship between insect damage and yield of cabbage (*Brassica oleracea* convar *capitata* var *capitata*) transplanted during different times. *Indian J. agric. Sci.,* 62: 88-90

Ratzka, A., Vogel, H., Kliebenstein, D.J., Mitchell-Olds, T. and Kroymann, J. (2002). Disarming the mustard oil bomb. *PNAS* (USA)*,* 99: 11223-228

Renwick, J. A. A., Haribal, M., Gouinguenè, S. and Städler, E. (2006). Isothiocyanates stimulating oviposition by the diamondback moth, *Plutella xylostella. J. Chem. Ecol.,* 32: 755-66

Renwick, J.A.A. (2002). The chemical world of crucivores: lures, treats and traps. *Entomol. exp. Appl.,* 104: 35-42

Renwick, J.A.A., Radke, C.D., Sachdev-Gupta, K. and Städler, E. (1992). Leaf surface chemicals stimulating oviposition by *Pieris rapae* (Lepidoptera: Pieridae) on cabbage. *Chemoecol.,* 3: 33-38

Rohloff, J. and Bones, A.M. (2005). Volatile profiling of *Arabidopsis thaliana* – Putative olfactory compounds in plant communication. *Phytochem.,* 66: 1941-55

Rossiter, J.T., Jones, A.M. and Bones, A.M. (2003). A novel myrosinase-glucosinolate defense system in cruciferous specialist aphids. *Recent Adv. Phytochem.,* 37: 127-42

Rouxel, T., Kollmann, A., Boulidard, L. and Mithen, R. (1991). Abiotic elicitation of indole phytoalexins and resistance to *Leptinotarsa maculans* within Brassicaceae. *Planta,* 184: 271-78

Sadasivam, S. and Thayumanavan, B. (2003). Lectins. In: Molecular Host Plant Resistance to Pests. Marcel Dekker Inc., New York. pp. 61-83

Sang, J.P., Minchinton, I.R., Johnstone, P.K. and Truscott, R.J.W. (1984). Glucosinolate profiles in the seed, root and leaf tissue of cabbage, mustard, rapeseed, radish and swede. *Can. J. Pl. Sci.,* 64: 77-93

Sauvion, N., Charles, H,, Febvay, G. and Rahbé, Y. (2004a). Effects of jackbean lectin (ConA) on the feeding behaviour and kinetics of intoxication of the pea aphid, *Acyrthosiphon pisum. Entomol. exp. Appl.,* 110: 31-44.

Sauvion, N., Nardon, C., Febvay, G., Gatehouse, A.M.R. and Rahbé, Y. (2004b). Binding of the insecticidal lectin Concanavalin A in pea aphid, *Acyrthosiphon pisum* (Harris) and induced effects on the structure of midgut epithelial cells. *J. Insect Physiol.,* 50: 1137–50.

Sekhon, B.S. (1999). Population dynamics of *Lipaphis erysimi* and *Myzus persicae* on different species of Brassica, 10th International Rapeseed Congress, Canberra, Australia.

Sekhon, B.S. and Ahman, I. (1993). Insect resistance with special reference to mustard aphid. In: Labana, K.S., Banga, S.S., Banga, S.K. (Eds.), Breeding Oilseed Brassicas, Springer-Verlag, Berlin, Germany, pp. 206-217.

Shelton, A.M. and Badenes-Perez, F.R. (2006). Concepts and applications of trap cropping in pest management. *Annu. Rev. Entomol.,* 51: 285-308

Shukle, R.H. and Murdock, L.L. (1983). Lipoxygenase, trypsin inhibitor and lectin from soybeans: effects on larval growth of *Menduca sexta* (Lepidoptera: Sphingidae). *Environ. Entomol.,* 12: 787-91

Siemens, D.H. and Mitchell-Olds, T. (1996). Glucosinolates and herbivory by specialists (Coleoptera: Chrysomelidae, Lepidoptera: Plutellidae): consequences of concentration and induced resistance. *Environ. Entomol.,* 25: 1344-53

Smallegange, R., Van Loon, J., Blatt, S., Harvey, J., Agerbirk, N. and Dicke, M. (2007). Flower vs. leaf feeding by *Pieris brassicae*: glucosinolate rich flower tissues are preferred and sustain higher growth rate. *J. Chem. Ecol.,* 33: 1831-44

Snowdon, R.J., Luhs, W. and Friedt, W. (2007). Oilseed rape. In: Kole, C. (Ed.) Genome mapping and molecular breeding in plants. Volume 2 Oilseeds, Springer-Verlag Berlin Heidelberg, Germany, pp. 55-114

Steinberg, S., Dicke, M. and Vet, L.E.M. (1993). Relative importance of infochemicals from first and second trophic level in long-range host location by the larval parasitoid *Cotesia glomerata*. *J. Chem. Ecol.,* 19: 47-59.

Tattersall, D.B., Bak, S., Jones, P.R., Olsen, C.E., Nielsen, J.K., Hansen, M.L., Hoj, P.B. and Moller, B.L. (2001). Resistance to an herbivore through engineered cyanogenic glucoside synthesis. *Sci.,* 293: 1826-28

Thompson, G.A. and Goggin, F.L. (2006). Transcriptomics and functional genomics of plant defence induction by phloem-feeding insects. *J. exp. Bot.*, 57(4): 755-766

Thorsteinson, A.J. (1953). The chemotactic responses that determine host specificity in an oligophagous insect (*Plutella maculipennis* (Curt.) Lepidoptera). *Can. J. Zool.,* 31: 52-72

Tripathi, M.K. and Mishra, A.S. (2007). Glucosinolates in animal nutrition: A review. *Animal Feed Sci. Technol.,* 132: 1-27

Vanetten, H.D., Mansfield, J.W., Bailey, J.A. and Farmer, E.E. (1994). 2 classes of antibiotics – phytoalexins vs phytoanticipins. *Pl. Cell,* 6:1191-92

Vasconcelos, I.M. and Oliveira, J.T. (2004). Antinutritional properties of plant lectins. *Toxicon,* 44:385-403

Walters, D.R. (2011). Plant defense: Warding off attack by pathogens, herbivores and parasitic plants. Blackwell-Publishing Ltd., UK, ISBN: 9781405175890, 243p.

War, A.R., Paulraj, M.G., Ahmad, T., Buhroo, A.A., Hussain, B., Ignacimuthu, S. and Sharma, H.C. (2012). Mechanisms of plant defense against insect herbivores. *Pl. Signal. Behav.* 7(10): 1306-1320. doi: 10.4161/psb.21663

Wittstock, U., Agerbirk, N., Stauber, E.J., Olsen, C.E., Hippler, M., Mitchell-Olds, T., Gershenzon, J. and Vogel, H. (2004). Successful herbivore attack due to metabolic diversion of a plant chemical defense. *PNAS* (USA), 101: 4859-64