

GLUCOSINOLATES IN PLANT PROTECTION STRATEGIES: A REVIEW

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Abstract - This review discusses the importance of glucosinolates in plant protection. The Brassicaceae, which are cultivated worldwide, use glucosinolates and their decomposition products to defend themselves against attacks by harmful organisms. The glucosinolate content varies among individual plant species, plant organs and developmental stages. The glucosinolate content in plants is also affected by biotic and abiotic factors, while the type or quantity of glucosinolate determines the susceptibility of the plants to insect pests. These facts can pose a problem when implementing this knowledge in cultivation of the Brassicaceae, especially in regions with moderate climates where Brassicaceae crops are exposed to attacks by a large number of harmful organisms. Under these circumstances, it is essential to research new, or to improve the existing environmentally acceptable methods of protecting Brassicaceae plants against economically important pests.

Key words: Glucosinolates, generalists, specialists, Brassicaceae, insecticidal effect, biofumigation method

INTRODUCTION

For decades, farmers have been attempting to manage the harmful organisms that feed on Brassicaceae crops by application of synthetic insecticides, which in many cases produce negative consequences, such as the development of resistance and negative influences on natural enemies (Hooks and Johnson, 2003). Because of the socio-economic consequences of the excessive use of synthetic insecticides, the use of new, environmentally acceptable methods for plant protection is gaining ground. These practices often involve such strategies as use different dates for sowing/planting, selecting resistant cultivars and cultivating mixed crops (Hooks and Johnson, 2003; Trdan et al., 2005; Ramalho et al., 2012; Bohinc and Trdan, 2012a).

Plants protect themselves from harmful organisms in two ways: via morphological barriers (Smith

et al., 2005; Broekgaarden et al., 2008; Müller, 2008; Trdan et al., 2009) and with chemical substances (secondary metabolites) (Pontoppidan et al., 2003; Broekgaarden et al. 2008; Lucas-Barbosa et al., 2011). For the Brassicaceae, the defense mechanism is predominantly chemical and includes glucosinolates (Björkman et al., 2011) and their decomposition products (Broekgaarden et al., 2008; Pratt et al., 2008). It has been reported that many of the wild plants belonging to the same family as plants of agronomic importance often contain larger quantities of secondary metabolites than their cultivated relatives (Chaplin-Kramer et al., 2011).

The purpose of this report was to collect research findings regarding the influence of individual glucosinolate groups on economically important pests and, as far as possible to promote the use of the natural resistance of Brassicaceae in plant protection and food production.

Versatility of the Brassicaceae

The Brassicaceae (or Cruciferae) comprise 3,200 plant species, including fodder plants, vegetables and ornamental plants; some weed species are also included in this family (Ahuja et al., 2010). Among the Brassicaceae of great agronomic significance are cabbage (*Brassica oleracea* L. var. *capitata*), cauliflower (*Brassica oleracea* L. var. *botrytis*), broccoli (*Brassica oleracea* L. var. *italica*), Brussels sprouts (*Brassica oleracea* var. *gemmifera*), turnip rape (*Brassica rapa* L. ssp. *sylvestris* f. *autumnalis*), different species of mustard (*Brassica juncea*, *Brassica nigra* and *Brassica hirta*) and some other species of leafy vegetables. Production in different climate conditions (Björkman et al., 2011) has enabled the Brassicaceae, which are important from both agronomic (Font et al., 2005; Vaughn and Berhow, 2005; Cartea et al., 2008; Blažević and Mastelić, 2009) and economic aspects (Vaughn and Berhow, 2005), to develop different resistance mechanisms against harmful organisms.

Glucosinolates: characteristic secondary metabolites

Glucosinolates are secondary metabolites (Kliebenstein et al., 2005) that are characteristic of the order Capparales (Al-Gendy et al., 2010; Björkman et al., 2011), primarily represented by the family Brassicaceae (Griffiths et al., 2001; Johnson, 2002; de Villena et al., 2007; Cartea et al., 2007; Blažević and Mastelić, 2009; Al-Gendy et al., 2010; Müller et al., 2010; Björkman et al., 2011; Winde and Wittstock, 2011). These compounds are also produced by 13 other botanical families (Newton et al., 2009). Glucosinolates consist of a β -D-thioglycoside group, a sulfonated oxime functional group and a variable side chain (Beekwilder et al., 2008; Vig et al., 2009; Blažević and Mastelić, 2009; Al-Gendy et al., 2010): based on their side chain, the compounds are divided into aliphatic, indole and aromatic (Cartea and Velasco, 2008; Van Eylen et al., 2009). The presence of glucosinolates varies between individual plant organs (Fahey et al., 2001; Winde and Wittstock, 2011), plant species (Moyes et al., 2000; Chaplin-Kramer et al., 2011), developmental stages (de Villena et al., 2007; Cartea et al., 2008), and also depends on the

weather conditions (Velasco et al., 2007; Winde and Wittstock, 2011).

Glucosinolates affect individual groups of pests, generalists or specialists, differently (Lankau, 2007; Müller, 2010), with the activity of these secondary metabolites either stimulating or deterring feeding. When the plant tissue (cells) is damaged, various biotic or abiotic factors cause the hydrolysis of glucosinolates, resulting in the production of isothiocyanates, thiocyanates and nitriles (Broekgaarden et al. 2008; Müller, 2009). Isothiocyanates and nitriles stimulate specialist pests, whereas their effect on generalists is most often considered repellent (Müller, 2009). The insecticidal effect of isothiocyanates on representatives of the order Lepidoptera can be compared to the effects of synthetic insecticides; conversely, the effects of nitriles are less pronounced, and they primarily serve to attract natural enemies (Schramm et al., 2012).

Influence of glucosinolates on monophagous insect pests of the Brassicaceae

To defend themselves against plant secondary metabolites, herbivores have developed several physiological defense mechanisms (Textor and Gershenzon, 2009). Herbivores can reduce the effects of secondary metabolites primarily by rapid enzymatic decomposition, thereby transforming them into less toxic or non-toxic derivatives (compounds), or by rapidly excreting them (Poelman et al., 2008; Müller, 2009). Interestingly, certain species of herbivores can employ glucosinolates for their own defense. Although these species are primarily a small group of specialists (Pontoppidan et al., 2003; Broekgaarden et al. 2008; Chaplin-Kramer et al., 2011), glucosinolates exert toxic effects on some specialists (Poelman et al., 2008). To defend itself against natural enemies, the cabbage aphid (*Brevicoryne brassicae* [L.]) produces the enzyme myrosinase which degrades plant glucosinolates (Broekgaarden et al. 2008). A similar defense mechanism is used by the mustard aphid (*Lipaphis erysimi* [Kaltenbach]) (Pratt et al., 2008) which occasionally infests oilseed rape and certain mustard plants (Rana, 2005).

Caterpillars of the small white butterfly (*Pieris rapae* [L.]) can degrade glucosinolates through a specific protein found in their intestines. The protein transforms unstable aglycone into nitriles which the larvae then excrete from their bodies. The transformation of these toxic isothiocyanates into less-toxic or non-toxic nitriles also occurs in other species of the genus *Pieris*, *Pieris virginiensis* (Edwards), the green-veined white (*Pieris napi* [L.]), the large white (*Pieris brassicae* [L.]) and also in the orange tip (*Anthocharis cardamines* [L.]). Stimulating effects of glucosinolates on the adult females of the small white (*Pieris rapae* [L.]) and the large white (*Pieris brassicae* [L.]) have also been established in addition to the stimulating effects on the feeding of large white and green-veined white caterpillars (Smallegange et al., 2007). The glucosinolate concentration also significantly influences the duration of the developmental stages of these butterflies (Smallegange et al., 2007).

Caterpillars of the diamondback moth (*Plutella xylostella* [L.]) contain the enzyme sulphatase which transforms the glucosinolates into desulphoglucosinolates; the caterpillars then excrete the desulphoglucosinolates. A similar system of decomposition was found in the desert locust (*Schistocerca gregaria* [Forskål]) (Müller, 2009; Textor and Gershenzon, 2009). Caterpillars of the turnip sawfly (*Athalia rosae* [L.]) use many aliphatic and aromatic glucosinolates to protect themselves against the predatory European paper wasp (*Polistes dominulus* [Christ]), common wasp (*Vespula vulgaris* [L.]) and spined soldier bug (*Podisus maculiventris* [Say]) (Müller et al., 2001; Müller, 2009). Glucosinolates also protect caterpillars of the turnip sawfly against attacks by the European fire ant (*Myrmica rubra* [L.]) (Müller, 2009). Soler et al. (2007) reported on the negative influence of high glucosinolate concentrations on the development of cabbage fly larvae (*Delia radicum* [L.]), whereas the negative influence of isothiocyanates on eggs was detected for the Brassica pod midge (*Dasineura brassicae* [Winn.]) (Åhman, 1985; Björkman et al., 2011) and on the feeding of rape beetle (*Meligethes aeneus* [Fabricius]) imagos (Cook et al., 2006).

The accessibility of different Brassicaceae species within a specific area has also influenced the different extents of damage caused by cabbage stink bugs (*Eurydema* spp.), and it was reported that the glucosinolates in oilseed rape had the greatest stimulating effect on the feeding behavior of cabbage stink bugs (Bohinc et al., 2012).

Influence of glucosinolates on polyphagous insect pests feeding on the Brassicaceae

The influence of individual glucosinolates can significantly affect the feeding behavior of the bertha armyworm (*Mamestra configurata* [Walker]). Indeed, the ability of a plant to defend itself against attacks by this species is affected by the presence of sinalbin and sinigrin (McCloskey et al., 1993; Ulmer et al., 2001): the higher the content of these glucosinolates, the less likely it is that *Mamestra configurata* (Walker) will feed on the plant. One study established that the green peach aphid (*Myzus persicae* [Sulzer]) excretes glucosinolates in its honeydew (Kos et al., 2011) and thus avoids the insecticidal effects of the secondary metabolites; however, this is not the case for all of the glucosinolate groups. Plants that contain only indole glucosinolates are much more resistant to attack by the green peach aphid (*Myzus persicae*) (Kim et al., 2008), which is a very significant pest of peach, tobacco, vegetables and flowers (Vučetić et al., 2008).

Although monophagous caterpillars of the order Lepidoptera can adjust to glucosinolates (they use them for defending themselves), polyphagous caterpillars of the same order have no such adjustment mechanism when feeding (Schramm et al., 2012).

The Brassicaceae are not the most important hosts for the beet armyworm (*Spodoptera exigua* [Hübner]) and the African cotton leafworm (*Spodoptera littoralis*), yet these insects can still complete their developmental cycle. In contrast, the appearance of the cabbage moth (*Mamestra brassicae* [L.]) and the cabbage looper (*Trichoplusia ni* [Hübner]) can represent a serious problem in the cultivation of Brassicaceae (Schramm et al., 2012). It is known that higher glucosinolate content reduces the extent

of cabbage looper (*Trichoplusia ni*) feeding (Kliebenstein et al., 2002). An important factor in the feeding behavior of the cabbage moth (*Mamestra brassicae*) is also the selection of the plant variety, as some Brassicaceae varieties are much more susceptible to attack by these harmful pests (Cartea et al., 2010), an observation that is attributed to the lower glucosinolate content of these varieties.

Influence of glucosinolates on harmful soil organisms (the process of biofumigation)

The term “biofumigation” normally means the suppression of harmful organisms in the soil (herbivores, nematodes and fungi) using plant species (most frequently the Brassicaceae) that contain glucosinolates (Elberson et al. 1996; Matthiessen and Shackleton, 2005; Gimsing and Kirkegaard, 2009). Glucosinolate decomposition products can also influence the ability of weeds to germinate and grow (Bangarwa et al. 2011; Boydston et al. 2011). The influence of products created during the hydrolysis of glucosinolates can successfully be used as an alternative for methyl bromide (Lazzeri et al., 2004).

The effect of biofumigation can be reached in several ways: by ploughing in fresh plant mass or Brassicaceae seed meal (a side-product of the pressing of seeds to produce oil). Biocidal effects can also be achieved by ploughing in dry plant mass, which contains a proportion of the active isothiocyanates of the living plants (Gimsing and Kirkegaard, 2009).

The use of seed meal has proven successful in suppressing wireworms (*Agriotes* spp.) (Elberson et al. 1996; Furlan et al. 2010), and nematicidal (Lazzeri et al., 2009; Zasada et al., 2009) and herbicidal properties have been reported (Noswothy et al. 2005; Handiseni et al., 2011). The nematicidal effects of glucosinolate decomposition products have been reported for the species *Meloidogyne javanica* (Treub [Chitwood]) (McLeod and Steel, 1999, Wu et al., 2011), and a high *in vitro* efficiency against potato nematode (*Globodera rostochiensis* (Woll [Behrens])) has also been confirmed (Serra et al., 2002; Aires et al., 2009).

The results of recent research show that the biofumigation method is also successful in suppressing soil pathogens (Mattner et al., 2008; Motisi et al., 2009), including *Fusarium* spp. (Martínez et al., 2011), Texas root rot (*Phymatotrichopsis omnivora*, [Duggar] Hennebert) (Hu et al., 2011), *Verticillium dahliae* (Kleb.) (Larkin et al., 2011), *Rhizoctonia solani* (Kühn) and take-all (*Gaeumannomyces graminis* var. *tritici* [Walker]) (Motisi et al., 2009).

Influence of glucosinolates on useful organisms

The activities of natural enemies are influenced by both the kind of prey and the plant genotype (Kos et al., 2011). The glucosinolate content in the body of the cabbage aphid can influence natural enemies differently. On the one hand, the negative influence on the predators marmalade hoverfly (*Episyrphus balteatus* [De Geer]) (Kos et al., 2012) and common green lacewing (*Chrysoperla carnea* [Stephens]) (Kos et al., 2011) were described; on the other hand, a stimulating influence of isothiocyanates on the species *Diaeretiella rapae* (M' Intosh) was also reported (Bradburne and Mithen, 2000; Kos et al., 2012).

The vitality of the two-spot ladybird (*Adalia bipunctata* [L.]) and the seven-spot ladybird (*Coccinella septempunctata* [L.]), which feed on cabbage aphid larvae, depends on the sinigrin content (Prat et al., 2008). Sinigrin negatively influences the species *A. bipunctata*, whereas no influence has been detected for the species *C. septempunctata* (Prat et al., 2008).

The application of Brassicaceae seed meal can have a whole spectrum of positive properties that affect harmful organisms in the soil, yet it can also negatively influence non-target organisms, for example, entomopathogenic nematodes of the genus *Steinernema*, as glucosinolate decomposition products prevent the activities of these biotic agents (Henderson et al., 2009).

CONCLUSIONS

Our review has outlined the specificity of the effects of individual glucosinolates on different groups of

harmful and useful organisms (Chaplin-Kramer et al., 2011). Because the number of registered synthetic insecticides is continuously decreasing (Stojanović et al., 2007; The list of registered ..., 2012), more research has been focused on the study of the natural resistance of plants which is manifested by ennobling programs (Müller, 2009; Ban et al., 2006). The utilization of the inherent defense mechanisms of plants will gain more importance in the future.

The fact that the glucosinolate content varies between individual plant species (Moyes et al., 2000; Chaplin-Kramer et al., 2011), between organs of the same plant species and between the developmental stages (de Villena et al., 2007; Cartea et al., 2008) of individual plant species, suggests that the same species and glucosinolate concentration may differentially influence (repel or stimulate) various species of harmful organisms. We believe that all of the listed attributes can represent problems for the implementation of this knowledge in Brassicaceae production, especially in areas with a moderate climate where the Brassicaceae are exposed to attack by numerous harmful insects and other organisms. This situation can undoubtedly be an additional reason to research new methods or to improve the existing methods of the environmentally acceptable protection of Brassicaceae against economically important harmful organisms.

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