

Review

Glucosinolates as an effective tool in plant-parasitic nematodes control: Exploiting natural plant defenses

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ABSTRACT

Plant-parasitic nematodes (PPNs) are an important damaging biotic agent for numerous crops around the world, causing serious losses directly and indirectly. Cultural and chemical control strategies were mainly used to PPNs management. However, the choice of chemical nematicides is strictly limited in the agrosystems due to their toxicity, their impact to the environment and, therefore, banning policies. The main lines of action of biological control strategies for nematode control, are based on the development of antagonist microorganism formulations and the use of plant extracts with nematocidal potential. There are many plant secondary metabolites with effective nematocidal potential. In this sense, glucosinolates (GSLs) and, especially, glucosinolate hydrolysis products (GHPs) show relevant nematocidal activity. The effects through which these compounds control nematodes, both direct and indirect are diverse, such as toxicity, anti-hatching effect or promotion of competing saprophytic nematodes or nematophagous bacteria populations. The present work compiles many of the studies that describe the use of GSLs and GHPs as nematicides in agriculture, through very diverse strategies that range from crop rotation with Brassicales to the direct application of GSLs and GHPs to the soil. The authors present GSLs and GHPs as a more sustainable and suitable alternative in nematode control, remarking the need to further research in the modes of action and the impact on environment.

1. Introduction to glucosinolates

The present work focuses on the utilization of GSLs and GHPs in PPNs control, compiling several studies using different strategies and application range, from crop rotation to the addition of GSLs extracts in the field. With this collection of studies, the authors aim to present a broader perspective on the effectiveness and interest of these compounds, discussing its utilization niches and strategies in PPNs control, but also its challenges and future prospects.

Glucosinolates (GSLs) are plant hydrophilic secondary metabolites, mainly found in the order Brassicales, and composed of an amino acid-derived side chain, a sulfonated oxime group and a thioglucose group (Mitreiter and Gigolashvili, 2021). These compounds are produced in many plant tissues and organs, at different quantities and types (Touw

et al., 2020), and its biosynthesis involves a complex network of transcription factors, hormones, enzymes and multiple genes (Sønderby et al., 2010). The process follows three consecutive stages: first, the chain of certain precursor amino acids may be elongated; second, the core structure is formed; and third, the GSL molecule undergoes secondary modifications such as modifications of the side chain or the glucose moiety, which are responsible for all the GSL diversity in this group (Blažević et al., 2020). GSLs can be classified in three different groups, depending on the amino acid from which they are formed: aliphatic GSLs derive from alanine, valine, leucine, isoleucine or methionine; benzolic GSLs derive from phenylalanine or tyrosine and indolic GSLs derive from tryptophan (Clarke, 2010; Lee et al., 2012).

Many key roles in different physiological processes have been attributed to GSLs and their hydrolysis products, such as auxin signaling

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(Vik et al., 2018), feeding deterrence (Hopkins et al., 2009), flowering time (Jensen et al., 2015), stomatal closure (Hossain et al., 2013), water transport (Martínez-Ballesta et al., 2014), environmental adaptations (Poveda et al., 2021), plant stress alleviation (Variyar et al., 2014) and growth-defense balance (Francisco et al., 2016a, 2016b). However, one of their main roles is the bioprotection due to their antimicrobial and insecticidal activities. Intact GSLs may confer resistance to certain insects, but the main defense activity occurs after those are hydrolyzed by the enzyme myrosinase into bioactive GHPs such as isothiocyanates (Chhajed et al., 2020). GSLs and myrosinases, despite both being present in many tissues and organs of the plant, are spatially separated and stored in different plant cells, GSLs are stored in S-cells and myrosinase in myrosin cells, guard cells or phloem associated cells (Chhajed et al., 2020). Sometimes, both are separated in different compartments within a single cell, GSLs usually in vacuoles and myrosinases in endoplasmic reticulum or cytosol (Bednarek et al., 2009; Mitreiter and Gigolashvili, 2021). Upon tissue damage, myrosinase hydrolyzes GSLs forming glucosinolate hydrolysis products (GHPs), such as isothiocyanates (ITCs), thiocyanates, nitriles, epithionitriles and/or oxazolidine-2-thiones (Wu et al., 2021). The nature of the final product formed depends on several factors, such as pH, side-chain structures or specific proteins that modulate the hydrolysis (Holst and Williamson, 2004; Wu et al., 2021). The influence of these specific proteins and their interaction with myrosinase is still under investigation (Chhajed et al., 2020), but several proteins have shown to affect the formation of different GHPs (Chhajed et al., 2019). For example, the heat sensitive epithiospecifier protein (ESM) favors the formation of ITCs over nitrile and epithionitrile, in contrast with the epithiospecifier protein (ESP), nitrile-specifier protein (NSPs), or thiocyanate-forming protein (TFP), which favor the formation of nitriles (Buw and Wittstock, 2009; Hanschen et al., 2014; Chhajed et al., 2020).

The antimicrobial and antifungal activity of GLSs is well known (Poveda et al., 2020a), causing the mortality of pathogenic bacteria, such as *Pseudomonas syringae* or *Xanthomonas campestris* (Sotelo et al., 2015), pathogenic fungi and oomycetes, such as *Alternaria brassicae*, *Sclerotinia sclerotiorum*, *Fusarium* spp., *Phytophthora* spp. and *Pythium* spp. (Sotelo et al., 2015; Ren et al., 2018). However, there are some specialist pathogens that have adapted to these compounds and successfully infect Brassicaceae plants, not being affected by the GSL defensive system. This is the case of *Alternaria brassicicola*, which is adapted to indolic GSLs and is not affected by their GHPs, probably by manipulating the plant's gene expression to modulate its defense response, resisting the toxic compounds or avoiding recognition by the plant (Buxdorf et al., 2013). Tolerance strategies are also used by endophytic beneficial microorganisms of this group of plants (Poveda, 2021). From an ecological point of view, these compounds also affect the soil biota as a whole. Soil biofumigation may have indirect effects on soil biota such as preservation of soil moisture, temperature regulation, improvement of soil organic matter or suppression of weeds (Ntalli and Caboni, 2017), but GSLs and its degradation products alter bacterial and fungal communities (Hanschen et al., 2015; Hu et al., 2015).

In addition to antimicrobial and antifungal qualities, the toxicity of GSLs and its hydrolysis products to nematodes have also been described previously (Buskov et al., 2002; Lazzeri et al., 1993; Zasada and Ferris, 2003). In contrast, possible negative effects have been described for integrated pest management strategies through the use of seed meal from *B. carinata*, by negatively affecting the populations of entomopathogenic nematodes such as *Steinernema feltiae* and *S. riobrave*, decreasing their action as biological control agents against the Colorado potato beetle (*Leptinotarsa decemlineata*) (Henderson et al., 2009).

2. Plant-parasitic nematodes (PPNs) as pests in modern agriculture

More than 30,000 species of nematodes have been identified, and at least 4100 of them are classified as plant-parasitic nematodes (PPNs)

(Decraemer and Hunt, 2006). These invertebrate biotroph pathogens feed on all plant parts but specially on roots, puncturing the plant tissues with their stylet, and secreting also different molecules which allow them to enter the plant and alter the host cell metabolism to obtain nutrients for life cycle completion (Davis et al., 2004). One of the groups that cause major losses in agriculture are the root-knot nematodes (*Meloidogyne* spp.), the root lesion nematodes (*Pratylenchus* spp.), the cyst nematodes (*Heterodera* spp., *Globodera* spp.) and the stem and bulb nematodes (*Ditylenchus* spp.), which are classified into these categories depending on the type of damage, or the species or tissue that they infect (Phani et al., 2021). Root-knot and cyst nematodes invade the roots and develop a permanent feeding site by altering the metabolism of a group of cells in the vascular system, forming specific feeding structures within the roots called Giant Cells, which enlarge and serve as nurturing cells till nematodes cycle completion. The roots also usually react by swelling, forming galls (root-knot nematode). The cyst nematodes differentiate another kind of feeding cells, called syncytia from fusion of the surrounding cells in the host plant roots (Mitchum et al., 2013; Escobar et al., 2015). The root lesion nematode is a migratory endoparasite that causes damage in roots, which form necrotic lesions (Fosu-Nyarko and Jones, 2016). Stem and bulb nematodes cause damage mainly in the stems and bulbs of affected plants respectively, infecting many plant species including rice, potato, strawberry, cucurbits or ornamentals (Jones et al., 2013).

PPNs severely affect the plant root system by entering and altering host cell metabolism, thus compromising the root efficacy in water and nutrient absorption (Jones et al., 2013). In addition, they can also favor secondary infections and diseases because of the damage caused in roots facilitating fungal and bacterial diseases. Additionally, PPNS can also be vectors of various plant viruses (Jones et al., 2013). Considering both direct and indirect damage caused by PPNS to crops, the estimated annual yield loss ranges from 80 to 173 billion US\$ (Elling, 2013; Youssef et al., 2013; Singh et al., 2015). However, the difficulty in associating the generic symptoms caused by nematodes in crops, the indirect effect of secondary infections and even further damage in form of food quality or visual imperfections, make these estimations likely underestimated (Jones et al., 2013).

The available strategies to control PPNS infestation can be grouped in three broad categories: cultural, chemical and biological. Some cultural methods are known to reduce their effects for quite some time, such as cleaning farm implements, introducing a rotation with crops less targeted by PPNS or organic amendments (LaMondia, 2006). Heat solarization can be effective (Briar et al., 2016), but it also impacts the whole soil biosphere, including non-target organisms. Chemical fumigants have been extensively used in PPNS control, in particular methyl bromide, until it was prohibited in 2005 due to toxic effects in the environment (Zasada et al., 2010). Other pesticides have been studied and tested such as metham sodium, 1,3 dichloropropene, chloropicrin, flusulfone, fluopyram and fluzaindoline. However, in many cases these products lack biosafety data, and often target non intended organisms in the environment (Phani et al., 2021). Since the Green Revolution, global agriculture has shifted its focus from augmenting yields through external inputs, to sustainability, therefore, other measures than synthetic chemical fumigants have been developed in this direction. In this respect, cultural and biological control measures include the use of resistant crop varieties, PPNS antagonist or pathogen organisms, such as the fungal genus *Trichoderma* or the bacteria genus *Pseudomonas* or *Bacillus*, the use of vegetal subproducts, such as neem cake powder or biochar, or the activation of plant defenses through systemic acquired resistance (SAR) or induced systemic resistance (ISR) using elicitors (Poveda et al., 2020b; Phani et al., 2021). The utilization of resistant crop varieties is a very effective and economically viable strategy (Fuller et al., 2008): it's main mechanism is based on the host plant cell death located near the feeding site, the accumulation of reactive oxygen species (ROS) and the reinforcement of the cell wall by a callose deposition (Williamson and Kumar, 2006; Bernard et al., 2017). However, plant-

resistance genes were identified only in a limited number of crops (e.g. *Mi* genes against *Meloidogyne* spp. reviewed in [Saucet et al., 2016](#)) and its durability is questioned as for example, virulent populations of *Meloidogyne* spp. to the *Mi-1* gene were identified in tomato ([Jacquet et al., 2005](#); [Verdejo-Lucas et al., 2009](#)). Hence, the most successful strategy in PPNs control is the integrated management through many combined tools such as resistant crop varieties and cultural measures, chemical pesticides and biological practices ([Fuller et al., 2008](#)). However, this approach faces many challenges: apart from the mentioned limitations of resistant crop varieties, crop rotation has limited utility against species affecting a wide range of hosts such as *Meloidogyne* spp. or *Pratylenchus* spp., many cultural measures affect the beneficial microflora, and chemical pesticides use is being restricted by legislation due to its effects on the environment ([Dutta et al., 2019](#)).

A greater effort in investigating and developing new alternatives for PPNs control is still needed as some of the above-mentioned measures should be locally tailored and economically adjusted.

3. Natural resistance against PPNs in Brassicaceae plants

Resistance to PPNs has been an interesting trait for plant growers since long time ago, and it has been a target trait in plant breeding programs for more than 25 years ([Roberts, 1992](#)). For example, early works with introgression on potato (*Solanum tuberosum*) and wild *Solanum* species were conducted to obtain resistant cultivars to the potato cyst nematodes *Globodera rostochiensis* and *G. pallida* ([Jacobs et al., 1996](#)) and the mentioned *Mi* genes for *Meloidogyne* spp. (see former section).

In this respect, Brassicaceae crops are nematode hosts, but they often suppress nematode development and infestation ([McLeod et al., 2001](#)). There is great variability of tolerance-resistance between the Brassicaceae-*Meloidogyne* interactions that depends basically on the plant and nematode species. In some cases, nematodes are not able to penetrate the roots, as for *Meloidogyne javanica* in *Brassica rapa*, *Brassica oleracea* var. *capitata* and *Raphanus sativus* roots ([McLeod et al., 2001](#)). In other cases, nematodes penetrate the roots but are not able to complete their life cycle and reproduce, as is the case of *M. incognita* in *Rapistrum rugosum* roots ([Curto et al., 2005](#)). There are also several Brassicaceae crops in which nematodes can complete their life cycle, although their reproduction is greatly affected compared to susceptible crops such as sorghum or tomato infected with *M. javanica* as compared to infected *B. juncea*, *B. napus* or *S. alba* roots ([Pattison et al., 2006](#)). In all these cases, it has been determined that the amount and type of GSLs accumulated in the roots of these Brassicaceae plants are key in their resistance to PPNs. Interestingly, *A. thaliana* is a Brassicaceae plant in whose roots *Meloidogyne* spp. and *Heterodera* spp. are able to complete their life cycle and is frequently used as a plant model in the plant-nematode interaction for those groups of nematodes ([Goddijn et al., 1993](#); [Gheysen and Fenoll, 2011](#); [Huang et al., 2020](#); [Tomaz et al., 2021](#)). This is possibly due to the absence of some GSLs in *A. thaliana*, such as glucobrassicin, glucotropaeolin or sinalbin that are widely distributed in other Brassicaceae plants ([Brown et al., 2003](#)). However, no clear studies have determined yet the exact causes of the compatible interaction with *Meloidogyne* spp.

On the other hand, in the Brassicaceae-*Heterodera* interaction, other mechanisms of resistance have been described so far. *Heterodera schachtii*, also called the beet cyst nematode, is a worldwide important pathogen in sugarbeet cropping. In this respect, *B. napus* or *B. oleracea* are susceptible to *H. schachtii*, but *R. sativus* is resistant ([Peterka et al., 2004](#); [Hol et al., 2013](#)). This resistance has been proven to be independent of the content and profile of GSLs in the roots of these plants ([Peterka et al., 2004](#)) as it is based on the degradation of the nematode feeding sites ([Budahn et al., 2009](#)).

The effectiveness of these naturally resistant plants has been known since long time ago, and, therefore, *Brassica* cultures were frequently used in crop rotations, which reduces the nematode population as part of

an integrated pest management. A deep knowledge on the molecular basis of the mechanisms involved in Brassicaceae resistance to PPNs would be crucial to design control strategies compatible with integrated pest management. Some of them, perhaps based on biotechnology by designing plants overexpressing effective GSLs against PPNs, or by the treatment of crops with mixtures of GSLs extracted from the plants as a biocontrol method ([Peterka et al., 2004](#)).

However, other secondary metabolites from plants have also been used for nematode control. Yet, we will acknowledge in two separate sections a small review of plant secondary metabolites used for PPNs control, while the specific utilization of GSLs will be reviewed in a separate section.

4. Use of plant secondary metabolites in PPNs management

The environmental and health risks associated with the intensive use of synthetic pesticides in general, and nematicides in particular, have led to an increasing interest in developing novel and safer alternatives for controlling these plant parasites ([Cavoski et al., 2011, 2012](#)). A promising alternative consists in the use of plant secondary metabolites ([Thoden et al., 2009](#)), which are small organic molecules involved in growth and development of plants, often playing important roles in plant defense and environment adaptation, but not essential for the plant survival ([Stamp, 2003](#); [Sarker et al., 2005](#)). Several thousands of these chemical compounds have been identified, some of them with nematode suppressing or killing potential ([Renčo et al., 2014](#)). Certain plant metabolites exuded from the roots affect nematode behavior, development, reproduction or survival, therefore, reducing damage in plants. Some may even promote nematode antagonistic microbiota in the rhizosphere ([Sikder and Vestergård, 2020](#); [Mathesius and Costa, 2021](#)), although there is still little information on how plants shape the nematode community in the rhizosphere ([Mathesius and Costa, 2021](#)).

Plant secondary metabolites can act as nematicidal, nematode attractants, repellents, hatching stimulants or inhibitors, which allows for different strategies depending on the effect ([Sikder and Vestergård, 2020](#)). Many of them have been studied for long, such as alkaloids, flavonoids, saponins, sesquiterpenes or monoterpenoids ([Chitwood, 2002](#)). Many alkaloids have nematicidal effect, such as the 1,2-dehydropyrrolizidine alkaloids, which are nematotoxic and herbivore repellent ([Chitwood, 2002](#); [Thoden et al., 2009](#)). Some flavonoids, such as kaempferol, quercetin and myricetin, cause different effects on PPNs, they may act as attractants or repellents, inhibit egg hatching, induce quiescence, and even kill them ([Chin et al., 2018](#)). However, it has been observed that flavonoids have different effects depending on the nematode species, even prolonging the life span of the nematode model species *Caenorhabditis elegans*. The authors hypothesized that these differences could be attributed to differences either in the chemosensory receptors of the nematodes, in the flavonoid receptor binding affinities, in the cell signaling cascades or in solute permeability of their cuticle ([Kampkötter et al., 2007, 2008](#)). Saponins are also known to be nematotoxic on juveniles (J2) and eggs of some species of PPNs *in vitro* (*Meloidogyne incognita*, *Globodera rostochiensis*, *Heterodera carotae* and *Xiphinema index*), and some *in planta* assays, were also conducted, all indicating increased resistance ([Argentieri et al., 2008](#); [D'Addabbo et al., 2011](#)). Another group of secondary plant metabolites with nematicidal effect are the tannins, used in aqueous solutions for controlling PPNs such as *M. javanica*, *G. rostochiensis*, *G. pallida* and *H. carotae* ([Maistrello et al., 2010, 2013](#); [Renčo et al., 2012](#); [Renčo and Sasanelli, 2013](#)). Some essential oils showed nematicidal effect against PPNs, as those from plant species such as *Artemisia absinthium*, *Eucalyptus citriodora* or *Mentha arvensis*, as well as some of their isolated components such as carvacrol, thymol, geraniol, eugenol, or linalool were found to suppress nematode population ([Renčo et al., 2014](#); [Ozdemir and Gozel, 2018](#)). The immense variety of compounds found in the plant secondary metabolism could be a promising source for the sustainable management of PPNs and an interesting alternative in reducing their impact in

agriculture. However, its effects in the environment and toxicology still needs to be deeply studied (Renčo et al., 2014).

5. GSLs and GHPs as nematicides

The natural resistance to certain pests of most *Brassica* species, and the suppression effect observed in soilborne pests and pathogens, have linked these crops to biofumigation since long ago (Kirkegaard and Sarwar, 1998). GSLs and GHPs have been described as nematicidal compounds applied directly from different plant sources either *in vitro*, *in planta*, in soil and in field.

5.1. Crop rotation

Historically, rotation with Brassicales crops has been used to reduce crop diseases caused by PPNs (Dutta et al., 2019). Among others, rotation of *R. sativus*, *E. sativa*, *B. juncea*, *B. rapa*, *B. oleracea* var. *acephala*, *B. oleracea* var. *italica* or *B. napus* with crops such as tomato, potato, zucchini, squash, cantaloupe or strawberry caused reductions in gall index and egg masses of up to 90% in *Meloidogyne* spp. (Mojtahedi et al., 1993; Al-Rehiyani and Hafez, 1998; Al-Rehiyani et al., 1999; Monfort et al., 2007; Lopez-Perez et al., 2010; Aydinli and Mennan, 2018). In the case of the lesion nematode of the genus *Pratylenchus*, a reduction in the nematode population of over 90% in tomato and carrot was assessed by rotation with *R. sativus* or *B. napus*. However, their effect was mostly attributed to an increase in the diversity and quantity of nematophagous bacteria on the ground (Al-Rehiyani and Hafez, 1998; Grabau et al., 2017). In contrast, crop rotation with rapeseed, either with vetch or squash, also significantly reduced the root-gall index in vetch and squash, and *M. incognita* was found to be unable to enter, feed or reproduce on rapeseed roots due to the presence of butanyl GSL, pentanyl GSL, hydroxybutanyl GSL, hydroxypentanyl GSL and hydroxybenzyl GSL (Johnson et al., 1992). In many of these cases, it has been possible to determine that this nematicidal capacity was related to the GSLs present in these plants.

5.2. Biofumigation

The application of plant tissues rich in GSLs has also been proven as an efficient strategy against different PPNs in the field, most of the times referred as biofumigation. The most studied strategy of the use of GSLs and GHPs as nematicides, is the direct application of whole plants or crop residues to the soil (Mojtahedi et al., 1991; Walker, 1997), and one indirect mechanism involved in the reduction of the population of PPNs in these soils is believed to be due to the increase in the quantity and diversity of saprophytic nematodes, which may also imply a competitive pressure for PPNs (Roubtsova et al., 2007).

The application of Brassicaceae plant tissues, such as chopped broccoli leaves (Ploeg and Stapleton, 2001), pellets from dry matter (Díaz et al., 2013), crude extracts (Mashela et al., 2013) or plant tissues from *B. napus* or *S. alba* crushed in water and mixed with the soil (Kruger et al., 2015), showed also potent nematicide activity in tomato, pepper or melon, against *M. incognita*, *M. javanica* and *Criconeoides xenoplax*. Chopped leaves from cabbage and cauliflower were also effective in reducing PPNs populations such as root knot nematodes, lance nematodes, spiral nematodes and stunt nematodes close to 80% in *Abelmoschus esculentus* crops (Behera et al., 2020). Similarly, leaves and stems of *E. sativa*, *R. sativus*, *B. oleracea* var. *capitata* or *B. juncea* have been buried in different crops, reducing *Meloidogyne* spp. populations by more than 80% (Anita, 2012; Youssef and Lashein, 2013; Daneel et al., 2018; Youssef, 2019; Waisen et al., 2020).

In soil, the application of Brassicaceae plants tissues involves the release of GHPs as a consequence of the action of myrosinases from microbial or plant origin. *B. hirta* is a plant with a high content of GSL glucotropaeolin, which hydrolyzes to benzyl ITC, and *B. juncea* has a high content of sinigrin, which hydrolyzes to allyl ITC. The burial of

these plants means the release of both ITCs to the soil, reducing the presence of *M. javanica* (Zasada and Ferris, 2004). In tomato plants the application of oil and dry leaf meal from *B. juncea* produced a decrease in gall index by more than 90% and a reduction of the soil populations by more than 60% in *Meloidogyne* species as a consequence of the release to the soil of allyl ITC (Oliveira et al., 2011; Hajji-Hedfi et al., 2018). *B. juncea* and *R. sativus* plants present large amounts of sinigrin and glucoraphanin in their tissues, respectively, reducing the populations of *G. pallida* in potato crops when buried (Ngala et al., 2015a,b). These nematicidal effects of GHPs are not only a consequence of the formation of ITCs, but also some nitriles that have been described as potential nematicides *in planta*.

5.3. Seed meals

Regarding *in planta* effects, the application of GSLs and GHPs as nematicides has been carried out mainly through seed meals from *B. juncea* and *B. carinata*, which suppress the hatching of *Globodera* species in potato crops (Dandurand et al., 2017), the hatching and formation of galls by *Meloidogyne* species in different crops (Yu et al., 2007; Mocali et al., 2015; Handiseni et al., 2017) or reducing the populations of *Pratylenchus* in apple crops (Mazzola et al., 2007, 2009, 2015). Seed meals from *S. alba* have also been applied alone and in combination with *B. juncea* for suppressing *M. incognita* populations in tomato and pepper crops (Meyer et al., 2011, 2015). Similarly, burial of seed meal from *B. napus* suppresses root infection by *P. penetrans*, due to the high content of 3-butenyl (Mazzola et al., 2001), a described GSL with antibacterial capacity (Jang et al., 2010). The ability of allyl ITCs released from Brassicales plant tissues in the field, to act as nematicides has been described, as for example defatted seed meals from *E. sativa*, *Barbarea verna* and *Brassica nigra* in tomato crops (Curto et al., 2016).

5.4. Aqueous extracts

Aqueous extracts of tissues rich in GSLs have also been an alternative as nematicides. Application of aqueous extracts from brassica plants in potato crops against *Globodera* species, reduced the numbers of new cysts by 60%, the reproduction rate less than 1 and final populations of eggs and J2 by 90% (Fatemy and Sepideh, 2016). The application of aqueous macerates of broccoli in tomato plants also reduced gall index by 80% in *M. incognita* as a consequence of the formation of 4-(methylthio) butanenitrile and 5-(methylthio) etanenitrile (Silva et al., 2018). In soybean plants, commercial products have been used that induce the release to the soil of benzyl ITC, significantly reducing the movement of juveniles, hatching and reproduction in *H. glycines* and *M. incognita* (Zasada et al., 2009b; Rogers et al., 2010; Wu et al., 2014). Experiments *in vitro* on different PPNs were the direct evidence demonstrating the nematicidal effect of GHPs from *Brassica* species.

5.5. In vitro experiments

In addition to all of the in-field and in-plant studies shown above, there are numerous *in vitro* studies that have demonstrated the high nematicidal effect of GHPs application on different PPNs. In 1993 and 2004, Lazzeri et al. described how GSLs from seeds of a wide variety of Brassicales crops had no nematicidal effect *in vitro* against *H. schachtii*. However, after adding myrosinase to these GSLs, significant mortality rates of PPNs were reported, due to the formation of GHPs such as allyl ITC, 3-butenyl ITC, benzyl ITC, 4-methylthio-3-butenyl ITC, 2-hydroxy-3-butenyl ITC, 2-phenylethyl ITC or propenyl ITC (Lazzeri et al., 1993, 2004). Similar experiments were carried out with 2-phenylethyl GSL from *Nasturtium officinale* to which 0.25 mg/mL of myrosinase enzyme was added, forming 2-phenylethyl ITC after 8 h of incubation and causing 100% mortality of *G. rostochiensis* juveniles (Serra et al., 2002). From *B. juncea* and *Armoracia rusticana* it has been possible to obtain allyl ITC *in vitro*, which is capable of causing 100% juvenile inactivity in

Table 1
Studies on the use of GSLs as an effective control strategy against plant-parasitic nematodes.

Nematodes	GSLs/GHPs used	GSLs/GHPs origin	Nematode reduction	Type of experiment	References
<i>Criconebella</i> spp.	Allyl ITC	Comercial product	81–84%	In field: tomato	Yu et al., 2019
<i>Criconeboides xenoplax</i>	Unidentified	<i>Sinapis alba</i> <i>Brassica napus</i> <i>Brassica juncea</i>	Positive	In soil	Kruger et al., 2015
<i>Globodera ellingtonae</i>	Unidentified	<i>Brassica juncea</i>	48.3–86.7%	In field: potato	Dandurand et al., 2017
<i>G. pallida</i>	2-Propenyl GSL/2-propenyl ITC	<i>B. juncea</i>	25–97%	<i>In vitro</i>	Lord et al., 2011
	2-Propenyl ITC	<i>B. juncea</i>	95%	In soil	
			>50%	<i>In vitro</i>	Brolsma et al., 2014
			Negative	In soil	
	Sinigrin	<i>B. juncea</i>	Positive	In field: potato	Ngala et al., 2015a
	Glucoraphanin	<i>Raphanus sativus</i>			
	Unidentified	<i>Brassica juncea</i>	99–100%	In field: potato	Dandurand et al., 2017
<i>G. rostochiensis</i>	Allyl ITC	Comercial product	87–100%	<i>In vitro</i>	Wood et al., 2017
	Phenethyl ITC	Comercial product	100% (16–40 h of exposure)	<i>In vitro</i>	Buskov et al., 2002
	Benzyl ITC				
	Propenyl ITC				
	2-Phenylethyl ITC	<i>Nasturtium officinale</i>	80–100% (72 h exposure)	<i>In vitro</i>	Serra et al., 2002
	2-Phenethyl GSL	<i>Brassica rapa</i>	47–93%	Greenhouse: potato	Aires et al., 2009
	2-Propenyl GSL	<i>B. oleracea</i> var. <i>trouchuda</i> <i>Nasturtium officinalis</i>			
	Unidentified	<i>B. oleracea</i> var. <i>botrytis</i>	100%	<i>In vitro</i>	Fatemy and Sepideh, 2016
		<i>S. alba</i> <i>R. sativus</i>	Positive	In field: potato	
	Unidentified	<i>Lepidium sativum</i>	86–100% (3 h–48 h)	<i>In vitro</i>	Fatemy, 2018
			Positive	Greenhouse: potato	
	Unidentified	<i>R. sativus</i> <i>S. alba</i> <i>L. sativum</i> <i>N. officinale</i>	32–75%	In field: potato	Franke et al., 2019
<i>Helicotylenchus dihystra</i>	Unidentified	<i>B. oleracea</i> var. <i>capitata</i> <i>B. oleracea</i> var. <i>botrytis</i>	49–61%	In field: <i>A. esculentus</i>	Behera et al., 2020
<i>Heterodera glycines</i>	Allyl ITC	Comercial product	LC ₅₀ 14,9 µg/mL	<i>In vitro</i>	Yu et al., 2005
	Unidentified	<i>B. juncea</i>	LD ₅₀ 311 µg/mL (bran) LD ₅₀ 265 µg/mL (seed meal)	Greenhouse: potato, strawberry and sweet corn	Yu et al., 2007
	Allyl ITC	Not indicated	LD ₅₀ 1792 µM	<i>In vitro</i>	Schroeder and MacGuidwin, 2010
	Benzyl ITC		LD ₅₀ 60,8 µM		
	Phenyl ITC		LD ₅₀ 661,5 µM		
<i>H. schachtii</i>	Benzyl ITC	Comercial product	84–98% (7 days)	Greenhouse: soybean	Wu et al., 2014
	Allyl ITC	<i>L. sativum</i>	Positive (variable)	<i>In vitro</i>	Lazzeri et al., 1993
	3-Butenyl ITC	<i>Brassica napus</i>			
	Benzyl ITC	<i>B. rapa</i>			
	4-Methylthio-3-butenyl ITC	<i>B. carinata</i> <i>R. sativus</i>			
	2-Hydroxy-3-butenyl ITC	<i>Sinapis alba</i>			
	Allyl ITC	Comercial product	LC ₅₀ 30,8 µg/mL	<i>In vitro</i>	Yu et al., 2005
	Unidentified	<i>B. juncea</i>	LD ₅₀ 409 µg/mL (bran) LD ₅₀ 353 µg/mL (seed meal)	Greenhouse: potato, strawberry and sweet corn	Yu et al., 2007
<i>Hoplolaimus</i> spp.	Allyl ITC	Comercial product	75–85%	In field: tomato	Yu et al., 2019
<i>Hoplolaimus indicus</i>	Unidentified	<i>B. oleracea</i> var. <i>capitata</i> <i>B. oleracea</i> var. <i>botrytis</i>	41–52%	In field: <i>A. esculentus</i>	Behera et al., 2020
<i>Meloidogyne</i> spp.	Allyl ITC	Comercial product	LC ₅₀ 18 mg/kg	In field: tomato	Ren et al., 2018
	Allyl ITC	Comercial product	Negative	In field: tomato	Yu et al., 2019
<i>Meloidogyne arenaria</i>	Unidentified	<i>R. sativus</i> <i>Eruca sativa</i>	Positive	In field: tomato	Aydinli and Mennan, 2018
<i>M. chitwoodi</i>	Unidentified	<i>Brassica campestris</i> <i>B. napus</i>	Positive	In soil	Mojtahedi et al., 1991
	Unidentified	<i>B. napus</i>	Positive	In field: potato	Mojtahedi et al., 1993
	Unidentified	<i>R. sativus</i> <i>B. napus</i>	79–84%	In field: potato	Al-Rehiyani and Hafez, 1998
			Positive		Al-Rehiyani et al., 1999
	Unidentified	<i>B. carinata</i>	Positive	In field: potato	Henderson et al., 2009
				Greenhouse: tomato	
<i>M. graminis</i>	Unidentified		21–100%	In field: bermudagrass (<i>Cynodon dactylon</i>)	Handiseni et al., 2017

(continued on next page)

Table 1 (continued)

Nematodes	GSLs/GHPs used	GSLs/GHPs origin	Nematode reduction	Type of experiment	References
<i>M. hapla</i>	Unidentified	<i>S. alba</i> <i>B. juncea</i> <i>B. napus</i> <i>Brassica campestris</i> <i>B. napus</i>	Positive	In soil	Mojtahedi et al., 1991
	Allyl ITC	Commercial product	LC ₅₀ 24,1 µg/mL	<i>In vitro</i>	Yu et al., 2005
	Unidentified	<i>B. juncea</i>	LD ₅₀ 605 µg/mL (bran) LD ₅₀ 511 µg/mL (seed meal)	Greenhouse: potato, strawberry and sweet corn	Yu et al., 2007
	Unidentified	<i>B. juncea</i>	68%	In field: gerbera	Anita et al., 2011
	Unidentified	<i>B. oleracea</i> var. <i>botrytis</i> <i>B. oleracea</i> var. <i>capitata</i> <i>R. sativus</i>	46–61%	In field: celery	Anita, 2012
	Progoitrin	<i>B. juncea</i> <i>B. napus</i>	71–98%	Greenhouse: tomato	Park et al., 2019
	Gluconapin				
	Sinigrin				
	Allyl ITC	<i>B. juncea</i>	72–100%	<i>In vitro</i>	Dahlin and Hallmann, 2020
	Benzyl ITC		100%		
<i>M. incognita</i>	Butyl ITC		74–100%		
	Ethyl ITC		28–100%		
	Methyl ITC		12–100%		
	Phenyl ITC		96–100%		
	2-Phenylethyl ITC		17–100%		
	Butanyl GSL	<i>B. napus</i>	Positive	In field: hairy vetch (<i>Vicia villosa</i>) and squash	Johnson et al., 1992
	Pentanyl GSL				
	Hydroxybutanyl GSL				
	Hydroxypentanyl GSL				
	Hidroxybenzyl GSL				
	Unidentified	<i>Brassica nigra</i> <i>B. oleracea</i> var. <i>chinensis</i> <i>B. oleracea</i> var. <i>italiensis</i> <i>B. oleracea</i> var. <i>Capitata</i> <i>B. oleracea</i> var. <i>compacta</i> <i>R. sativus</i>	38–100%	In field: tomato	Stapleton and Duncan, 1998
	Unidentified	<i>B. oleracea</i> var. <i>italica</i>	Positive	Greenhouse: melon	Ploeg and Stapleton, 2001
	Benzyl ITC	<i>Carica papaya</i>	13–100%	<i>In vitro</i>	Nagesh et al., 2002
	2-Phenylethyl ITC	<i>B. napus</i>	LD ₅₀ 11 µM	<i>In vitro</i>	Lazzeri et al., 2004
	Benzyl ITC	<i>B. juncea</i>	LD ₅₀ 15 µM		
	4-Methylthiobutyl ITC	<i>R. sativus</i>	LD ₅₀ 21 µM		
	Propenyl ITC	<i>E. sativa</i>	LD ₅₀ 34 µM		
	Allyl ITC	Commercial product	LC ₅₀ 17,0 µg/mL	<i>In vitro</i>	Yu et al., 2005
	Unidentified	<i>B. juncea</i> <i>B. rapa</i> <i>B. napus</i> <i>B. oleracea</i> var. <i>acephala</i>	Positive	In field: zucchini squash, cantaloupe, and tomato	Monfort et al., 2007
Unidentified	<i>B. oleracea</i> var. <i>italica</i>	57–80%	In soil	Roubtsova et al., 2007	
Unidentified	<i>B. juncea</i>	LD ₅₀ 534 µg/mL (bran) LD ₅₀ 474 µg/mL (seed meal)	Greenhouse: potato, strawberry and sweet corn	Yu et al., 2007	
Unidentified	<i>R. sativus</i> <i>E. sativa</i>	Positive	In field: zucchini	Lazzeri et al., 2009	
Progoitrin	<i>B. napus</i> <i>S. alba</i>	90–98%	In soil	Zasada et al., 2009a	
Benzyl ITC	Commercial product	Positive	Greenhouse: soybean	Zasada et al., 2009b	
Unidentified	<i>B. oleracea</i> var. <i>italica</i>	Negative (population) 36% (root galling)	In field: tomato and strawberry	Lopez-Perez et al., 2010	
Benzyl ITC	Commercial product	Positive	Greenhouse: soybean and pepper	Rogers et al., 2010	
Unidentified	<i>B. juncea</i> <i>S. alba</i>	41–100%	Greenhouse: pepper	Meyer et al., 2011	
Allyl ITC	<i>B. juncea</i>	>90%	Greenhouse: tomato	Oliveira et al., 2011	
Allyl ITC	<i>Armoracia rusticana</i>	EC ₅₀ 6,6–52,6 mg/L	<i>In vitro</i>	Aissani et al., 2013	
Unidentified	<i>B. carinata</i>	26–64%	Greenhouse: pepper	Díaz et al., 2013	
Unidentified	<i>B. oleracea</i> var. <i>capitata</i>	80–94%	Greenhouse: tomato	Mashela et al., 2013	
Unidentified	<i>B. oleracea</i> var. <i>capitata</i>	67–88%	In field: tomato	Youssef and Lashein, 2013	
Erucin	<i>E. sativa</i>	EC ₅₀ 3,2 mg/L	In field: tomato	Aissani et al., 2015	
Pentyl ITC		EC ₅₀ 11,1 mg/L			

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Table 1 (continued)

Nematodes	GSLs/GHPs used	GSLs/GHPs origin	Nematode reduction	Type of experiment	References
<i>M. javanica</i>	Hexyl ITC		EC ₅₀ 5,0 mg/L		
	Methyl TC		EC ₅₀ 18,1 mg/L		
	Unidentified	<i>B. juncea</i> <i>S. alba</i>	Positive	Greenhouse: tomato In field: tomato	Meyer et al., 2015
	Unidentified	<i>B. carinata</i>	31–79%	In field: tomato	Mocali et al., 2015
	Aromatic GSLs	<i>B. oleracea</i> var. <i>botrytis</i>	Positive	In field: pepper	Rudolph et al., 2015
	Sinigrin/Allyl ITC	<i>E. sativa</i> <i>Barbarea verna</i> <i>Brassica nigra</i>	93–99%	In field: tomato	Curto et al., 2016
	Unidentified	<i>E. sativa</i>	Positive	In field: tomato	Daneel et al., 2018
	4-(Methylthio)butanenitrile	<i>B. oleracea</i> var. <i>italica</i>	Positive	Greenhouse: tomato	Silva et al., 2018
	5-(Methylthio)etanenitrile				
	Sinigrin	<i>Brassica macrocarpa</i>	50%	Greenhouse: tomato	Argento et al., 2019
	Unidentified	<i>Brassica caulorapa</i> <i>B. oleracea</i> var. <i>capitata</i>	37–81%	In field: cowpea	Youssef, 2019
	Unidentified	<i>B. oleracea</i> var. <i>capitata</i> <i>B. oleracea</i> var. <i>botrytis</i>	40–50%	In field: <i>A. esculentus</i>	Behera et al., 2020
	Unidentified	<i>B. oleracea</i> var. <i>capitata</i> <i>B. oleracea</i> var. <i>botrytis</i>	20–34%	In field: <i>A. esculentus</i>	Patil et al., 2020
	Unidentified	<i>B. juncea</i>	Positive	In field: zucchini	Waisen et al., 2020
	Butanyl GSL	<i>B. napus</i>	Positive	In field: hairy vetch (<i>Vicia villosa</i>) and squash	Johnson et al., 1992
	Pentanyl GSL				
	Hydroxybutanyl GSL				
	Hydroxypentanyl GSL				
	Hidroxybenzyl GSL				
	2-Hydroxy-3-butenyl ITC	<i>R. sativus</i>	Positive	In field: vineyard	McLeod and Steel, 1999
	4-Pentenyl ITC				
	2-Phenylethyl ITC				
	4-Methylthio-3-butenyl ITC				
	Unidentified	<i>B. oleracea</i> var. <i>italica</i>	Positive	Greenhouse: melon	Ploeg and Stapleton, 2001
	Unidentified	<i>B. napus</i> <i>B. campestris</i>	Positive	In field: tomato	Stirling and Stirling, 2003
	Allyl ITC	Comercial product	LC ₅₀ >0,01–0,25 µmol/mL	<i>In vitro</i>	Zasada and Ferris, 2003
	Benzyl ITC				
	Butyl ITC				
	Ethyl ITC				
	Pehyl ITC				
2-Phenylethyl ITC					
4-Methylsulfinyl ITC					
Glucotropeolin/Benzyl ITC	<i>Brassica hirta</i>	Positive	In soil	Zasada and Ferris, 2004	
Sinigrin/Allyl ITC	<i>B. juncea</i>				
Unidentified	<i>B. juncea</i>	19–93%	In field: vineyard	Rahman and Somers, 2005	
Ethyl ITC	<i>Armoracia rusticana</i>	LC ₅₀ 2,53–3,05 µg/mL	<i>In vitro</i>	Wu et al., 2011	
Acryloyl ITC	<i>A. lapathifolia</i>	(<i>In vitro</i>)	Greenhouse: cucumber		
Benzyl TC	<i>Lepidium menziesi</i>	LD ₅₀ 0,49–0,48 mL/kg	In field: cucumber		
Benzyl ITC	<i>C. papaya</i>	soil			
1-phenylethyl ITC	<i>B. juncea</i>				
2-phenylethyl ITC					
Allyl ITC					
Unidentified	<i>Ochradenus baccatus</i>	95–100%	<i>In vitro</i> In soil	Oka et al., 2014	
Unidentified	<i>S. alba</i> <i>B. napus</i> <i>B. juncea</i>	Positive	In soil	Kruger et al., 2015	
Unidentified	<i>R. sativus</i> <i>E. sativa</i>	Positive	In field: tomato	Aydnli and Mennan, 2018	
Unidentified	<i>E. sativa</i>	Positive	In field: tomato	Daneel et al., 2018	
Allyl ITC	<i>B. juncea</i>	62%	Greenhouse: tomato	Hajji-Hedfi et al., 2018	
Sinigrin	<i>B. macrocarpa</i>	50%	Greenhouse: tomato	Argento et al., 2019	
Epiprogoitrin	<i>Crambe abyssinica</i>	72–83%	<i>In vitro</i> Greenhouse: soybean	Tarini et al., 2020	
<i>Pratylenchus</i> spp. <i>Pratylenchus neglectus</i>	Unidentified	<i>B. juncea</i>	Positive	In field: zucchini	Waisen et al., 2020
	Unidentified	<i>B. juncea</i>	56–99%	In field: apple	Mazzola et al., 2007
	Unidentified	<i>R. sativus</i> <i>B. napus</i>	79–84%	In field: potato	Al-Rehiyani and Hafez, 1998
	2-Phenylethyl ITC	<i>B. napus</i> <i>B. oxyrrhina</i> <i>B. nigra</i>	56–95%	In soil	Potter et al., 1998

(continued on next page)

Table 1 (continued)

Nematodes	GSLs/GHPs used	GSLs/GHPs origin	Nematode reduction	Type of experiment	References
		<i>B. campestris</i> <i>B. juncea</i> <i>B. carinata</i>			
	2-Phenylethyl ITC Unidentified	<i>B. napus</i> <i>B. juncea</i>	Positive LD ₅₀ 402 µg/mL (bran) LD ₅₀ 320 µg/mL (seed meal)	Greenhouse: <i>B. napus</i> Greenhouse: potato, strawberry and sweet corn	Potter et al., 1999 Yu et al., 2007
<i>P. penetrans</i>	3-Butenyl Unidentified	<i>B. napus</i> <i>B. juncea</i>	Positive LD ₅₀ 458 µg/mL (bran) LD ₅₀ 393 µg/mL (seed meal)	In field: apple Greenhouse: potato, strawberry and sweet corn	Mazzola et al., 2001 Yu et al., 2007
	Unidentified	<i>B. juncea</i> <i>B. napus</i> <i>S. alba</i>	Positive	Greenhouse: apple	Mazzola et al., 2009
	Progointrin	<i>B. napus</i> <i>S. alba</i>	42–97%	In soil	Zasada et al., 2009a
	Unidentified	<i>B. juncea</i> <i>B. napus</i> <i>S. alba</i>	43–95%	In field: apple	Mazzola et al., 2015
<i>Rotylenchulus reniformis</i>	Unidentified	<i>R. sativus</i>	Negative	In field: carrot	Grabau et al., 2017
<i>Tylenchorhynchus mashoodi</i>	Unidentified	<i>B. juncea</i>	Positive	In field: zucchini	Waisen et al., 2020
	Unidentified	<i>B. oleracea</i> var. <i>capitata</i> <i>B. oleracea</i> var. <i>botrytis</i>	41–51%	In field: <i>A. esculentus</i>	Behera et al., 2020
<i>Tylenchulus semipenetrans</i>	Unidentified	<i>Brassica tournefortii</i>	Positive	In soil	Walker, 1997
	Unidentified	<i>B. juncea</i>	76%	In field: orange	Walker and Morey, 1999
	Allyl ITC	Commercial product	LC ₅₀ >0,01–0,25 µmol/mL	<i>In vitro</i>	Zasada and Ferris, 2003
	Benzyl ITC				
	Butyl ITC				
	Ethyl ITC				
	Pehyl ITC				
	2-Phenylethyl ITC				
	4-Methylsulfinyl ITC				
	Glucotropeolin/Benzyl ITC	<i>B. hirta</i>	Positive	In soil	Zasada and Ferris, 2004
Unidentified	Unidentified	<i>B. napus</i>	Negative	In field: wheat and lupin	Osler et al., 2000
	Unidentified	<i>S. alba</i> <i>B. juncea</i> <i>B. napus</i> <i>R. sativus</i>	Negative	In field	Gruver et al., 2010
	Unidentified	<i>B. juncea</i> <i>B. napus</i>	Negative	In soil	Reardon et al., 2013

Globodera spp. and *Meloidogyne* spp. (Aissani et al., 2013; Broksma et al., 2014; Dahlin and Hallmann, 2020). Allyl ITC has previously been described as a potent antimicrobial compound (Romeo et al., 2018) and is capable of causing 100% mortality in just 72 h of exposure in *Globodera*, *Heterodera* and *Meloidogyne* species (Yu et al., 2005; Wood et al., 2017). Aqueous extracts obtained from roots of *Ochradenus baccatus* were also tested *in vitro*, causing the immobilization of 100% of *M. javanica* second-stage juveniles, while their direct application in the root soil as fresh or dry powder reduced the number of nematodes recovered from the soil by 95–100% (Oka et al., 2014). Nowadays, many of these GHPs tested *in vitro* have been produced and commercialized. For example, the commercially available 2-phenylethyl ITC, a compound widely described as antimicrobial and cytotoxic (Popović et al., 2020) against *M. javanica*, reached LC90 values with nematicidal activity in applications of 0.01–0.03 µmol/mL (Zasada and Ferris, 2003).

5.6. Individual GSLs effect

As is the case against different pathogenic microorganisms and agricultural pests, the metabolites with true toxic activity against PPNs are the derived products from GSLs, the GHPs (Poveda et al., 2020a).

GSLs have been also applied directly in the soil showing nematicidal effects possibly due to its hydrolysis to GHPs by soil microorganisms (Bhat and Vyas, 2019). In this respect, progointrin is a described GSL with antioxidant (Cabello-Hurtado et al., 2012) and antiviral (Nie et al., 2020) capacity. Its application in soil, from *B. napus* and *S. alba* seed meal, caused a suppression of the populations of *M. incognita* and

M. javanica greater than 90% (Zasada et al., 2009a). Its stereoisomer, epiprogoitrin increased juvenile mortality, reduced egg hatching and *M. javanica* reproduction on soybean (Tarini et al., 2020). Sinigrin, allyl GSL or 2-propenyl GSL is an aliphatic GSL described with antibacterial, antifungal, antioxidant and insecticidal activity (Mazumder et al., 2016). Burying leaf flour from *Brassica macrocarpa*, rich in sinigrin (300–650 mol/m² dosage), reduced the root disease index caused by *Meloidogyne* in tomato plants by up to 50% (Argento et al., 2019). Similarly, foliar extracts from *B. rapa*, *B. oleracea* var. *truncuda* or *Nasturtium officinalis*, also with a high content of sinigrin, reduced the formation of cyst by *G. rostochiensis* in potato roots (Aires et al., 2009). Similarly, the field application of commercial allyl ITC products produced a significant reduction in the populations of *Criconebella*, *Hoplolaimus* and *Meloidogyne* species in tomato crops (Ren et al., 2018; Yu et al., 2019).

6. Conclusions

The massive use of chemical pesticides was a serious risk for the environment, as well as toxic for human health. Therefore, the search for new safe and environmentally friendly alternatives to control or cope crop pests, pathogens and diseases is absolutely essential. In this sense, GSLs have been described as a powerful alternative to combat plant diseases caused by nematodes, with several advantages over chemical pesticides such as sustainability, they seem appropriate for organic farming as biopesticides, and potentially safe for human and environment health. Examples of these studies can be consulted in the summary

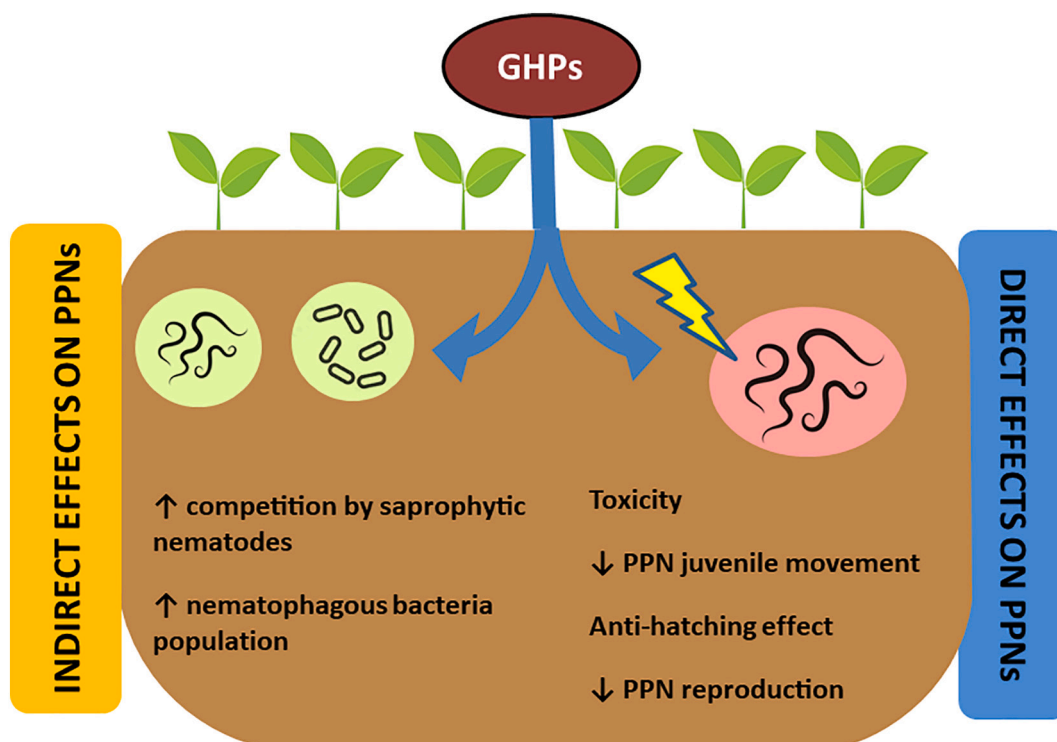


Fig. 1. Direct and indirect effects derived from the addition of glucosinolate hydrolysis products (GHPs) to soil on the plant-parasitic nematodes (PPNs).

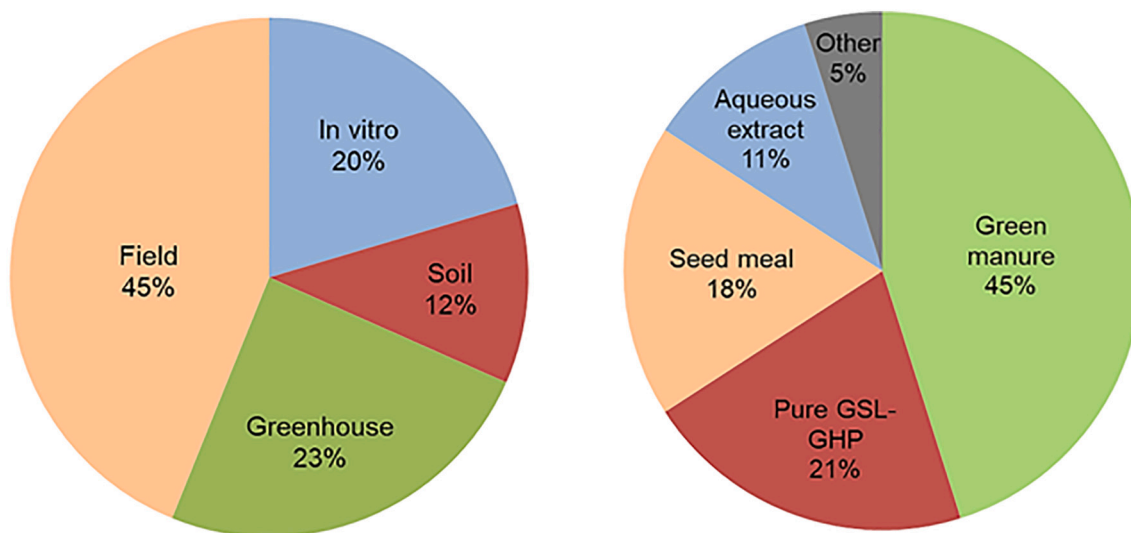


Fig. 2. Percentage of reviewed works divided by type of experiment (left) and mode of GSL-GHP addition (right).

form in Table 1 and Fig. 1.

The information extracted from the analysis of previous works aimed at the reduction of PPNS using GSLs-GHPs, shows a vast majority of studies conducted in field (45%) over studies in greenhouse (23%), *in vitro* (20%) or in soil (12%). In some cases, studies *in vitro* has been conducted to complement field, greenhouse or soil results. As for the mode of GSLs-GHPs application, green manure has been the most used strategy in these studies (45%). Some articles have conducted different approaches such as crop rotation (Osler et al., 2000), Brassica oil addition (Nagesh et al., 2002; Hajji-Hedfi et al., 2018) or Brassica susceptibility assays (Potter et al., 1999), which have been categorized as “Other” (5%) (Fig. 2).

The compilation of studies carried out in this review confirm the use

of GSLs and GHPs as an interesting choice for nematocides in agriculture. Many of the studies carried out to date have focused on the description of the nematicidal effect after their application to crops, but still there is scarce information about their modes of action. It is also known that GSLs influence soil microbiota, both bacterial, fungal and nematode populations, but few studies have focused on this aspect and how do they exert those effects. In this sense, it is urgent to deeply understand the molecular features of their inhibitory effect on the plant-nematodes interaction, and to study putative side effects in the environment, such as their impact on the soil, microbiota or even on the plant's physiology itself. Future lines of research should point in this direction.

On the other hand, despite of the numerous studies on the use of GSLs and GHPs (mainly allyl ITC) as nematocides (Table 1), research is still

required to develop efficient and repetitive application methodologies for different crops. Understanding the biochemical and molecular mechanisms involved in its nematocidal capacity will add crucial knowledge for the development of novel and effective PPN control programs in crops.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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