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Chapter

Perspective Chapter: Capitalizing on the Host Suitability of Brassica Biofumigant Crops to Root-Knot Nematodes (*Meloidogyne* spp.) in Agroecosystems - A Review on the Factors Affecting Biofumigation

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Abstract

The use of brassica biofumigant crops for the management of plant-parasitic nematodes in agroecosystems has been extensively studied. However, the effects of biofumigation against root-knot nematodes (*Meloidogyne* spp.) remain inconsistent, owing to the factors including but not limited to biofumigant crops, edaphic factors, termination methods, cultural practices, and sensitivity of *Meloidogyne* life stages to biofumigation. This review chapter argues that ‘host suitability’ or the susceptibility of biofumigant brassica crops, which is often considered an important management challenge, could in actuality maximize the performance of biofumigation against *Meloidogyne*. Each of these factors has been reviewed with an emphasis on the host’s suitability as an opportunity to capitalize on to maximize the biofumigation effect. This can be achieved by synchronizing the termination time in relation to the nematode development and *Meloidogyne* degree-days. The logic is that the cultivation of susceptible biofumigant crops would stimulate *Meloidogyne* egg hatch and the resulting infective juveniles would be at the most vulnerable stage to biofumigation kill. From a plethora of published research and a myriad of information available on biofumigation, and integration with host suitability, it trickled down to six steps as necessary to maximize biofumigation effects to successfully manage *Meloidogyne* spp. in agroecosystems.

Keywords: cover crops, glucosinolates, isothiocyanates, management, susceptibility

1. Introduction

1.1 Root-knot nematode

More than 4100 species of plant-parasitic nematodes are known worldwide, collectively posing an important threat to global food security [1]. Globally, crop losses

inflicted by plant-parasitic nematodes are estimated at \$125 billion annually, with at least \$10 billion in the United States [1, 2]. Those nematodes in the genus *Meloidogyne*, the root-knot nematodes, are ranked among the most serious plant-parasitic nematodes estimated based on their economic and scientific significance [3]. To date, 98 species of *Meloidogyne* have been described including the major species—*M. incognita*, *M. javanica*, *M. arenaria* and *M. hapla* [4]. Root-knot nematodes are sedentary endoparasites and obligatory biotrophs, infecting a wide range of crops [5]. Second-stage juveniles (J2s) are infective, thus mobile and actively seek hosts (**Figure 1**). In doing so, the J2s are attracted to growing root tips by exudates, enter roots intercellularly behind the root cap, and migrate to the cell elongation region, where they initiate feeding sites by secreting effector proteins synthesized in esophageal glands [6, 7]. The effector proteins hijack routine cellular functions and expedite nuclear division but without cell division (cytokinesis). These events lead to the formation of feeding sites, the multinucleated and hypertrophied giant cells, which are active metabolic sinks diverting photosynthates away from storage organs [8]. The infection of the root system by root-knot nematodes results in characteristic gall formation. Root galling interferes with water and nutrient uptake, resulting in water stress, nutritional deficiency, and stunting of infected plants. The infected plants are predisposed to opportunistic soil-borne pathogens that can exacerbate the severity of the disease.

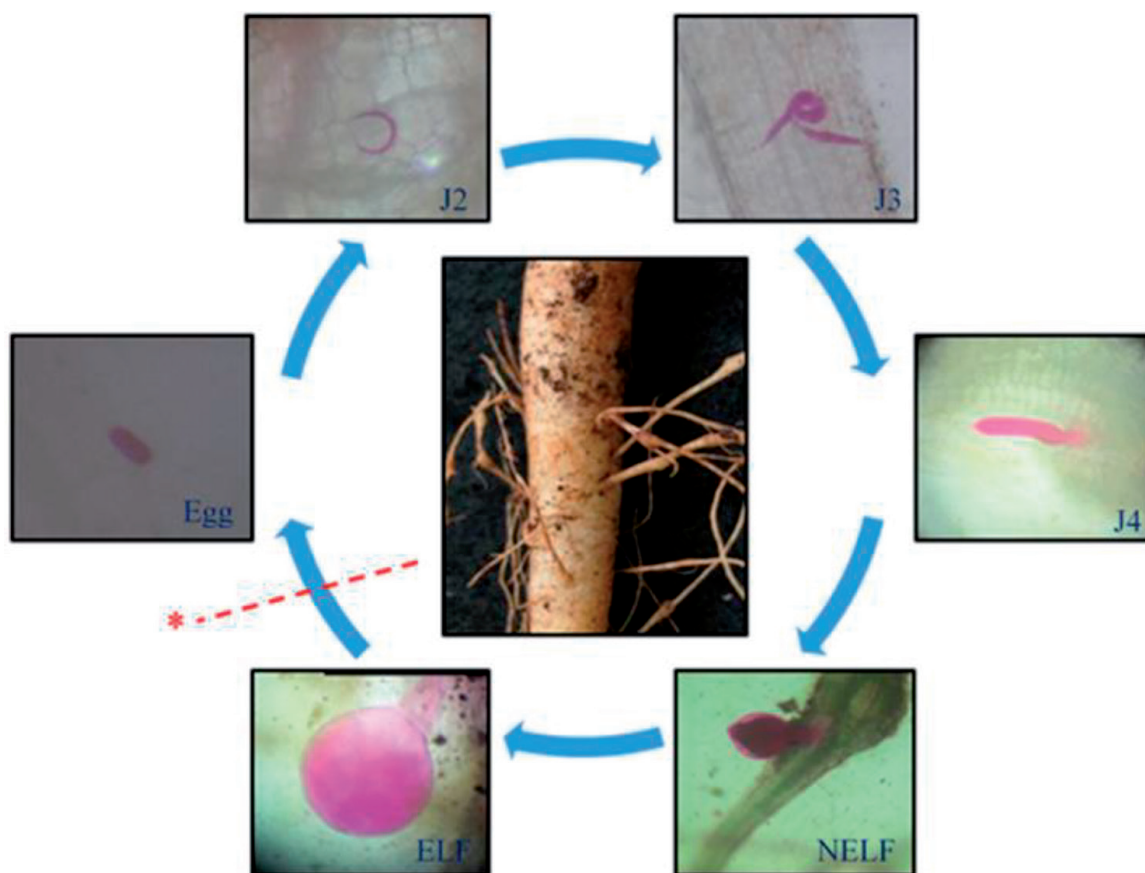


Figure 1. The life cycle of a root-knot nematode. J2 = second-stage infective juvenile; J3 = third stage juvenile; J4 = fourth stage juvenile; NELF = non-egg laying female or mature female; ELF = egg-laying female. Red perforated line and asterisks indicate when biofumigant crops can be terminated to stop egg production.

1.2 Management

Management of root-knot nematodes relies primarily on the use of synthetic nematicides. Since the onset of the Green Revolution, soil fumigation has been an effective and non-discriminant approach to combat soil-borne pests and pathogens, including plant-parasitic nematodes, in agroecosystems. However, fumigants such as methyl bromide have been banned and the use of other effective nematicides is being restricted as with restricted-use pesticides such as Vapam (metam sodium) and Telone (1,3-dichloropropene) [9]. The banning and restricted use of effective nematicides have led to a worldwide search for nematicide alternatives.

Cover crops with allelopathic compounds offer an alternative to managing plant-parasitic nematodes in a user-friendly and environmentally sound manner. Some examples of allelopathic compounds being investigated include monocrotaline in sunn hemp, *Crotalaria juncea* [10], α -tertienyl in French marigold, *Tagetes* spp. [11], dhurrin in sorghum-sudangrass, *Sorghum* \times *drummondii* [12], L-dopa in velvet bean, *Mucuna pruriens* [13], and glucosinolates in members of Brassicaceae [14–18].

This review focuses on the factors affecting the effectiveness of biofumigation against root-knot nematodes, highlighting host suitability as an opportunity to maximize biofumigation effect in agroecosystems.

2. Biofumigation

Biofumigation is a collective term used for all plant-derived volatiles utilized in pest and disease management. The term biofumigation was originally coined by Kirkegaard et al. [19] to refer to the use of plant-derived volatiles exclusively by the members of Brassicaceae for pest and disease management in agroecosystems. In particular, glucosinolates (GLs), β -d-thioglucose thioglycosides, are the naturally occurring secondary metabolites synthesized by members of Brassicaceae, and are stored in vacuole of sulfur-rich S-cells (**Figure 2**). The GLs are spatially separated from myrosinase (Myr) enzymes, β -thioglucosidases, which are stored as myrosin grains in the vacuole of a particular idioblast known as myrosin cell (**Figure 2**) [20–22]. To date, at least 200 GLs have been identified from plants, of which more than 80% occur in members of Brassicaceae [22–25]. Each GL constitutes a β -thioglucose moiety ($C_6H_{12}O_6S$), a sulfonated oxime moiety, and a thiohydroximate-O-sulfonate moiety (**Figure 3**) [26]. Glucosinolates are categorized as aliphatic, aromatic or indole, if the amino acid side chain denoted as R, is methionine, phenylalanine, or tryptophan, respectively (**Figure 3**) [27]. Upon tissue damage during termination or by herbivory, Myr comes in contact with GL and hydrolyzes the thioglucoside linkage (carbon-sulfur bond), yielding D-glucose and an aglycone, thiohydroximate-O-sulfonate, an unstable intermediate (**Figure 3**). Being unstable, the aglycone spontaneously undergoes a non-enzymatic rearrangement to form volatile products including isothiocyanates (ITCs), nitriles, and thiocyanates as well as non-volatile products including sulfate and sulfur [26, 28]. Isothiocyanates have biocidal properties [29] like the synthetic counterpart, methyl ITC from metam sodium in Vapam and Dazomet [30]. Thus, a successful biofumigation partly depends on cultural and termination practices that favor more ITC production.

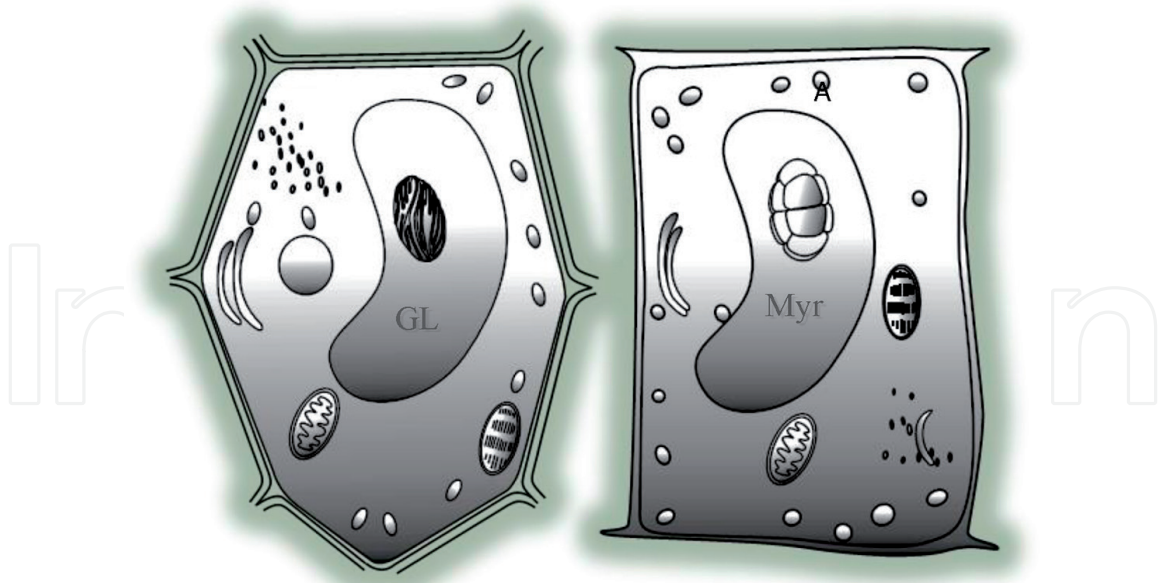


Figure 2. Sulfur-rich S-cell contains glucosinolate (GL), and B) myrosin cell contains myrosinase (Myr) [20].

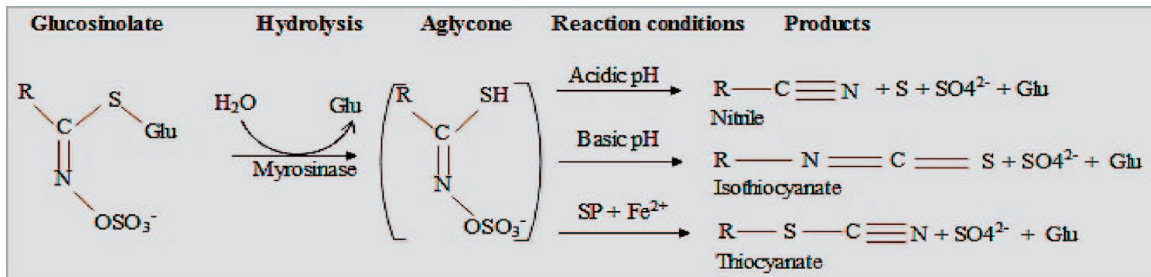


Figure 3. Glucosinolate hydrolysis pathway modified from Kirkegaard [19]. Glu = glucose; R-N=C=S is isothiocyanate; R-C≡N is nitrile; SP = specifier proteins; R-S-C≡N is an ionic thiocyanate.

The effectiveness of biofumigation broadly depends on (1) brassica cover crops, (2) edaphic factors, (3) termination methods, (4) cultural practices, and (5) nematode species and life stages. In addition, this chapter argues that ‘host suitability’ to root-knot nematodes is another critical factor that has become evident in recent years, which is associated with stimulating egg hatch and open-end trap cropping.

3. Brassica cover crops

Members of Brassicaceae constitute some 350 genera and 3500 species [31]. Brassica biofumigant crops that are commonly utilized for biofumigation purposes include brown mustard (*Brassica juncea*), yellow or white mustard (*Sinapis alba*; Syn. *Brassica hirta*), rapeseed (*Brassica napus*), field mustard (*Brassica rapa* var. *rapa*), and oil radish (*Raphanus sativus*) [29]. The selection of biofumigant crop species and cultivars or accessions is crucial because the types and concentrations of GLs vary among species, cultivars, and even tissues within a cultivar [15, 32]. Sinigrin (allyl GL) is a dominant GL in *B. juncea* and *B. nigra*, and varies by cultivar and tissues [29]. For example, total GL and allyl GL levels of *B. juncea* ‘Terrafit’, ‘Terratop’, ‘Terraplus’, and ‘ISCI99’

Biofumigant crop				Total (ITC-generating) GL		Nematode		
Species	Cultivar/accession	Form ^a	Amendment rate ^b	$\mu\text{mol g}^{-1} \text{dw}^c$	$\text{nmol g}^{-1} \text{soil}^d$	Species	Suppression ^e	References
<i>B. carinata</i>	Acc. 94044	GM	2.0%	21.7 (21.5)	86.8 (85.3)	<i>Pratylenchus neglectus</i>	32.6%	[37]
	BRK-147A	GM	na	30.6	135.4	na	na	[32]
	BRK-147A	S	na	116.0	na	na	na	[34]
	ISCI7	SM	2.5 t/ha	163.4 (160.1)	na	<i>Meloidogyne chitwoodi</i>	>80.0%	[38]
	ISCI7	SM	3.0 t/ha	150.7 (147.7)	na	<i>M. incognita</i>	<RGI	[39]
	na	LF	6.0% (v/v)	90.0	na	<i>M. incognita</i>	81.0%	[40]
<i>B. hirta</i>	Martegena	GM	na	73.1	na	<i>M. javanica</i> , <i>T. semipenetrans</i>	na	[41]
<i>B. juncea</i>	Acc. 99Y11	GM	2.0%	20.4	81.6	<i>P. neglectus</i>	40.9%	[37]
	Caliente 99	GM	230.0*	62.5 (49.2)	na	<i>Globodera pallida</i>	Effective	[35]
	Caliente 61	GM	0.1 t/ha	49.1 (36.3)		<i>M. incognita</i>	No effect	[42]
	Cutlass	GM	na	11.7	135.4	na	na	[32]
	ISCI99	GM	9.9 t/ha	29.0 (25.0)	100.5 (91.4)	<i>Trichodorus</i> , <i>Tylenchorynchus</i>	No effect	[33]
		GM	1.1 t/ha	72.1 (58.4)	na	<i>M. incognita</i>	No effect	[42]
	JR049	GM	5.6 t/ha	6.7 (4.9)	44.6 (40.4)	na	na	[15]
	Nemfix	GM	10.3 t/ha	22.5 (20.2)	169.9 (161.6)	<i>M. javanica</i>	9.0 fold	[15, 43]
	Nemfix	SM	2.0 t/ha	na	na	<i>M. javanica</i>	9.0 fold	[43]
	Pacific Gold	SM	1.2 t/ha	153.2 (152.0)	na	<i>M. incognita</i> , <i>P. penetrans</i>	>90.0%	[17]
		GM	1.2 t/ha	57.7 (45.9)	na	<i>M. incognita</i>	No effect	[42]
Pacific Gold	SM	>2.2 t/ha		na	<i>G. pallida</i>	100.0%	[17, 18]	
Pacific Gold	SM	>4.5 t/ha			<i>G. ellingtonae</i>	>92.1%	[18]	

Biofumigant crop				Total (ITC-generating) GL		Nematode		
Species	Cultivar/accession	Form ^a	Amendment rate ^b	$\mu\text{mol g}^{-1} \text{dw}^c$	$\text{nmol g}^{-1} \text{soil}^d$	Species	Suppression ^e	References
	Pacific Gold	S	na	61.0	na	na	na	[34]
	Pacific Gold	SME	1.1 t/ha	278.0 (278.0)		<i>G. ellingtonae</i>	100.0%	[18]
	TerraFit	GM	6.9 t/ha	22.2 (19.3)	61.1 (55.8)	<i>Trichodorus,</i> <i>Tylenchorynchus</i>	No effect	[33]
	TerraPlus	GM	7.5 t/ha	20.1 (15.4)	63.4 (54.5)	<i>Trichodorus,</i> <i>Tylenchorynchus</i>	No effect	[33]
	TerraTop	GM	8.4 t/ha	16.7 (13.1)	61.8 (52.5)	<i>Trichodorus,</i> <i>Tylenchorynchus</i>	No effect	[33]
<i>B. napus</i>	BQ Mulch	GM	7.0 t/ha	25.7	164.5 (91.9)	na	na	[15]
	Dunkeld Acc. 94713	GM	2.0%	7.5 (6.8)	28.8 (24.0)	<i>Pratylenchus neglectus</i>	44.5%	[37]
	Dwarf Essex	SM	5.0 t/ha	41.9 (35.6)	na	<i>M. incognita</i>	90.0%	[17]
	Dwarf Essex	SM	50.0 t/ha	41.9 (35.6)	na	<i>P. penetrans</i>	90.0%	[17]
	MaximaPlus	GM	7.7 t/ha	16.6 (9.0)	78.1 (21.3)	na	na	[15]
	Sunrise	SM	15.0 t/ha	14.8 (3.0)	na	<i>M. incognita,</i> <i>P. penetrans</i>	No effect	[17]
<i>B. nigra</i>	Acc. 95067	GM	2.0%	16.4 (16.4)	65.4 (65.4)	<i>P. neglectus</i>	28.1%	[37]
	Giebra	GM	na	22.5	647.6	na	na	[32]
	Giebra	S	na	193.0	na	na	na	[34]
<i>B. oxyrrhina</i>	Acc. 95060	GM	2.0%	34.0 (33.4)	136.1 (133.8)	<i>P. neglectus</i>	71.8%	[37]
<i>B. rapa</i>	Harmoni	GM	na	3.6	15.7	na	na	[32]
	Harmoni	S		<30.0	na			[34]
	na	GM	2.0%	3.2 (2.9)	12.9 (11.4)	<i>P. neglectus</i>	33.1%	[37]
<i>E. sativa</i>	Nemat	GM	77.7 t/ha*	61 (36)	na	<i>G. pallida</i>	No effect	[35]

Biofumigant crop				Total (ITC-generating) GL		Nematode		
Species	Cultivar/accession	Form ^a	Amendment rate ^b	$\mu\text{mol g}^{-1} \text{dw}^c$	$\text{nmol g}^{-1} \text{soil}^d$	Species	Suppression ^e	References
<i>R. sativus</i>	Bento	GM	124.7 t/ha*	31.7 (27.8)	na	<i>G. pallida</i>	No effect	[35]
<i>S. alba</i>	IdaGold	SM	20.0 t/ha	163.9 (156.8)	na	<i>P. penetrans</i>	65.0%	[17]
	IdaGold	SM	20.0 t/ha	163.9 (156.8)	na	<i>M. incognita</i>	90.0%	[17]
	IdaGold	SM	100.0 t/ha	163.9 (156.8)	na	<i>P. penetrans</i>	90.0%	[17]
	Zlata	GM	30.7 t/ha	na	na	<i>G. rostochiensis</i>	na	[44]

^aGM = green manure; S = intact seed; SM = defatted seed meal; SME = defatted seed meal extract in powder; LF = liquid formulation (prepared from defatted seed meal and liquid phase) mixed in water; na = data not available.

^bTissue amendment is based on dry weight unless indicated with * which is identified as fresh weight.

^cValues outside of parentheses are the average of total GL in dry shoot and root tissues of biofumigant crops, and values inside of parentheses are GL that only generate ITC.

^dValues outside the parentheses are determined based on total GL in root and shoot per dry weight of soil (based on 10-cm soil depth, and 1.08 g cm⁻³ soil bulk densities). Values inside the parentheses are GL that only generate ITC.

^e<RGI = reduced root gall index; effective = nematode suppression was statistically significant; na = data not available; No effect = nematode suppression was not significant.

Table 1.

Nematode suppressive effects of different biofumigant crop species affected by their cultivars/accessions, a form of application, amendment rates, glucosinolate concentration, and target nematodes.

were different among cultivars and tissues [33]. The cultivar 'ISCI99' generated more biomass and accumulated higher concentrations of both total and allyl GLs in roots than in foliage [33]. The concentration of GL in roots and stems decreased gradually as the plant develops; it increased in the leaves and reproductive organs of *B. juncea* [34]. The growing season also affected the concentration of GL in brassica crops [35]. The highest GL production was achieved in summer followed by spring growing seasons, indicative of higher growing degree-days and corresponding biomass production [35, 36]. Hence, the selection of brassica crops is important for successful biofumigation. **Table 1** shows brassica biofumigant crop species and cultivars or accessions, forms of application, amendment rates, GL concentration, and target plant-parasitic nematodes.

4. Edaphic factors

Edaphic factors play an important role in the performance of biofumigation against plant-parasitic nematodes in agroecosystems. The edaphic factors include soil's physical, chemical, and biological properties. The impact of each soil property has on the effectiveness of biofumigation are discussed.

4.1 Soil physical properties

Soil moisture, texture, and temperature are recognized as the main players affecting biofumigation processes in the soil. Soil moisture mediates GL hydrolysis, impacts ITC half-life, and renders GL prone to leaching. The half-life of benzyl GL, for example, increased from 6.8–15.5 hours at a 1:1 soil to water ratio to 17.5–19.5 hours at 8–11.6% soil moisture levels [45]. Excessive soil moisture can cause GL to leach from the biologically active rhizosphere because GL adsorbs weakly to soil particles [46, 47]. Soil moisture is recommended to be maintained at optimum levels to achieve desired outcome [48]. When it comes to soil texture, GL degrades more rapidly in clay topsoil than in sandy topsoil. However, in the clay subsoil, GL degradation reduced due to the lack of biological activities to an extent of no degradation in sandy subsoil [15]. In terms of soil temperature, volatility of ITC increases with temperature, especially short-chained aliphatic GLs are more prone to volatilization loss if proper measures are not taken to contain them in the soil [49–51].

4.2 Soil chemical properties

Soil pH, the redox states of iron, and soil organic matter (SOM) are regarded as important soil chemical properties known to influence ITC production in the soil [52]. Aglycone, an unstable intermediate of GL hydrolysis, undergoes a non-enzymatic rearrangement and depending on the occurrence of these chemical properties, either ITCs, nitriles or thiocyanates are produced. The rearrangement is regulated by these soil chemical properties (**Figure 3**). Low pH favors nitrile production whereas high pH favors ITC production [53, 54]. At soil <pH 6, the aglycone undergoes proton (H^+) dependent desulfuration to yield nitrile and elemental sulfur [52, 55]. In contrast, aglycone experiences a concerted loss of sulfate (SO_4^{2-}) at soil \geq pH 6, which is independent of H^+ in Lossen rearrangement and produces ITC [52]. Thus, maintaining soil \geq pH 6 is desirable for the purposes of biofumigation. With regards to redox states of iron, ferrous (Fe^{2+}) and ferric (Fe^{3+}) irons promote nitrile production [56, 57], thus reduces ITC production. Hanschen et al. [57] autoclaved soil to increase Fe^{2+} content,

and they observed an antagonistic effect on the performance of biofumigation. The presence of Fe^{3+} can nearly terminate both allyl nitrile and allyl ITC production [52, 54, 58]. In terms of SOM, hydrophobic ITCs are adsorbed to SOM, thus reducing their biofumigation activities [46, 59]. Sorption of ITC to SOM increases with their non-polar nature [45]. Price et al. [49] incorporated *B. juncea* tissue in sandy soil with less SOM and found less ITC in the headspace than in clay soil with high SOM. Matthiessen and Shackleton [59] also noted that higher SOM at a low temperature significantly reduced ITC volatility, resulting in a low biofumigation effect.

4.3 Soil microbiota

Some soil microorganisms produce Myr, the enzyme that catalyzes GL hydrolysis. For example, *Aspergillus niger*, a ubiquitous soil-borne facultative pathogen [60, 61], and *Enterobacter cloacae*, a bacterial antagonist of *Fusarium oxysporum* and *Pythium* spp. [62], produce Myr when GL was added to the soil. One reason these microbes produce Myr could be to break down GL to obtain glucose, as glucose is one of the hydrolysates of GL hydrolysis (**Figure 3**). Albaser et al. [63] found a strain of soil-borne bacterium, *Citrobacter* WYE1, to possess an inducible β -glucosidase capable of transforming GL into ITC. Soils treated with γ -irradiation, that did not inactivate Myr enzyme, degraded benzyl GL whereas autoclaved soils, where Myr enzymes were denatured, arrested the GL degradation [15]. This suggests that biofumigation in soils treated by solarization, fumigation, or sterilization could compromise its effectiveness.

5. Termination methods

Method of termination is how the brassica crop residues are terminated for biofumigation purposes. Different termination methods generate different regimes of biofumigation efficacy. At least nine biofumigation methods are described in the literature. These methods are presented from low to high efficacy levels in **Figure 4**. These include (1) intercropping, (2) crop rotation, (3) soil incorporation, (4) soil incorporation + solarization, (5) tissue maceration + soil incorporation, (6) tissue maceration + soil incorporation + watering, (7) tissue maceration + soil incorporation + plastic mulch, (8) tissue maceration + soil incorporation + rolling soil surface or compaction, (9) open-end trap crop + tissue maceration + soil incorporation + plastic mulch [64]. Waisen et al. [65] alluded to the fact that using biofumigant crops which are susceptible to root-knot nematodes can in fact stimulate egg hatch, thus making biofumigation of these crops more effective. This concept is also known as the “open-end trap crop” approach where targeted nematodes are allowed to infect the biofumigant crops prior to being trapped and fumigated.

The incorporation of brassica biofumigant crop tissues in the soil by tillage is a popular method of biofumigation, where ITCs are generated from the mechanical damage of tissues during soil incorporation [35, 66, 67]. During the growth of brassica crops either in rotation or intercropping scenarios, negligible quantities of ITCs are generated through leaf washings, root exudates, or through physical damage by herbivorous pests, which have shown promise to suppress soil-borne pathogens [22, 35]. Oil radish roots released ITC in the rhizosphere following feeding damage by cabbage root fly larvae (*Delia radicum*), which was claimed to be toxic to encysted eggs of potato cyst nematode (*Globodera pallida*) [35]. As the research on biofumigation expands, knowledge of the mechanism of ITC production becomes apparent,

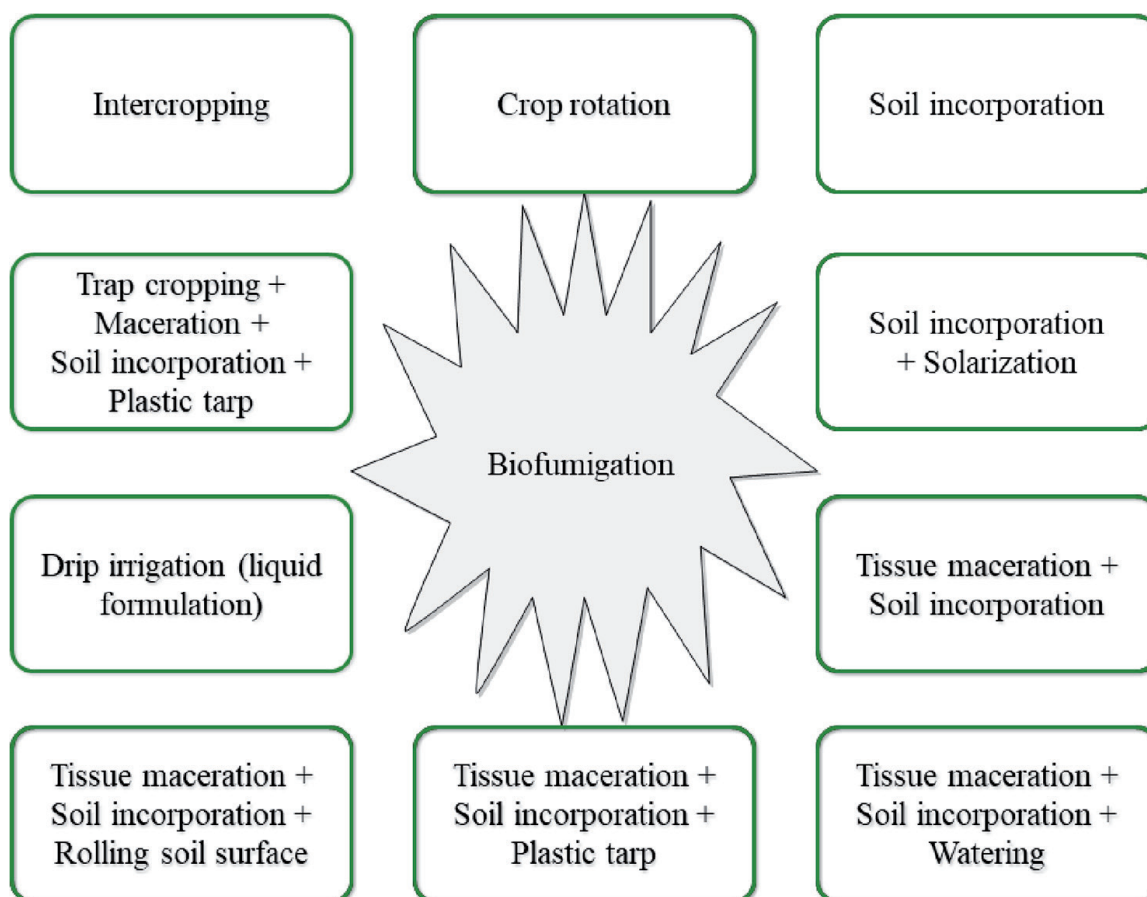


Figure 4.
Biofumigation methods using brassica biofumigant crops.

and the conventional method of biofumigation has shifted to include tissue maceration, irrigation, and mulching with an impermeable plastic film. The fact that GL and Myr are spatially separated in intact plant cells (**Figure 2**), tissue maceration would enhance GL hydrolysis, thus maximizing ITC production and biofumigation effect [48, 68]. Effective biofumigation occurs when hydrolysis of GL generates more than 100 nmol of ITC/g soil [46]. In addition, with the knowledge that water mediates GL hydrolysis, it is beneficial to add water after tissue maceration and soil incorporation to maximize hydrolysis while washing the ITC into the rhizosphere to be in contact with target nematodes. It has been reported that irrigation with 34 mm in a field after pulverizing *B. juncea* tissues produced 100 nmol/g soil of propenyl ITC [48], with a biofumigation effect equivalent to the 200 nmol methyl ITC/g soil from metam sodium [30]. Furthermore, with the understanding that aliphatic ITCs are volatile [4], maximum biofumigation effectiveness requires sealing the soil with impermeable plastic film immediately after tissue maceration and soil incorporation [69]. Mulching with black plastic was shown to be more advantageous than clear solarization mulch because of its low solar radiation transmittance, which would be less destructive to Myr and beneficial to soil microorganisms [60]. Stapleton and Duncan [70] also recommended to tarp the soil for no more than 7 days to avoid anaerobic soil disinfestation [71, 72]. This is because under anaerobic soil conditions, redox potential decline and generate Fe^{2+} as well as organic acids that would interfere with ITC production [73].

6. Cultural practices

The application of sulfur (S) and nitrogen (N) fertilizers to brassica biofumigant crops is important because N and S are integral elemental constituents of GL (**Figure 3**) [74, 75]. Low N and high S fertilizer application enhanced aliphatic GL in *Brassica rapa* [76, 77]. Li et al. [78] noted that while total GL concentration was not affected by fertilizer inputs, individual GL concentration was affected by S or N supply. Nitrogen-containing tryptophan-derived indole GL was directly proportional to N supply whereas S-containing methionine-derived aromatic GL was inversely proportional to N supply [78]. Application of N-containing fungicide, metconazole increased total GL concentration in *B. juncea* and *R. sativus* [35]. In addition, cultivation of biofumigant brassica crops can recruit microorganisms that produce Myr enzymes to break down GL. It is important to be mindful of when to cultivate brassica biofumigant crops as they are photosensitive and flower when the day length is long. This means brassicas intended for biofumigation will quickly flower before sufficient biomass production necessary for biofumigation. In temperate climates such as in California, grow brassica biofumigant crops during winter months and not during spring or summer months. For example, ‘Caliente 199’ brown mustard planted for biofumigation in Coachella Valley in Southern California prematurely flowered at 5-6 weeks barely producing any biomass (**Figure 5**).



Figure 5. Showing brown mustard (*Brassica juncea*) ‘Caliente 199’ field planted in Spring of 2022 bolting prematurely in Coachella Valley (Southern California, USA).

7. Nematode life stages

Sensitivity to ITC varies by species and developmental stages of nematodes [41, 50]. Mojtahedi et al. [50] observed J2s of *M. chitwoodi* were more vulnerable to biofumigation than their egg counterparts. In another study, J2s of *M. incognita* were more sensitive to defatted seed meals of brassicas compared to a mixed stage of root lesion nematode, *Pratylenchus penetrans* [17]. The J2s of root-knot nematodes are more mobile, and their metabolic or respiration rates are elevated and the likelihood of ITC intake is higher than any later other developmental life stages. Fumigation with metam sodium (methyl ITC) is more effective against the target pest when it is actively respiring [79], suggesting that biofumigation would be most effective when the nematodes are active. Thus, J2s are more prone to biofumigation than egg stage or when the nematodes are in survival stage. Thus, the cultural practices aimed at triggering nematode egg hatch are crucial.

8. Host suitability

Most brassica crops that are utilized for biofumigation purposes are good hosts for root-knot nematodes. Thus, the use of susceptible biofumigant crops as a pre-plant cultural nematode management tactic has been cautioned or their use has been considered an important management challenge because of the high likelihood of increasing the target nematode population before planting cash crop [80–82]. The cultivars of *B. juncea* and *B. rapa* were reported to be good hosts of root-knot nematodes while that of *Eruca sativa* ‘Nemat’ and *R. sativus* ‘Boss’ including ‘TerraNova’ were ranked among the poorest hosts [80, 81, 83]. Host suitability of a list of *Brassica* species and cultivars to root-knot nematodes is presented in **Table 2**. The use of biofumigant crops that are good hosts of root-knot nematodes has been advised against in attempts to address undesired nematode reproduction. Instead, the use of brassica cultivars that are poor or non-hosts to root-knot nematodes has been recommended [4, 16, 81]. Alternatively, cultivating nematode-susceptible brassica crops during winter to limit nematode development and delay egg production was recommended [83]. However, this approach would be impractical in tropical climatic regions where temperatures remain above the nematode development thresholds all year round.

In the past, the host suitability has perceived negative implications for biofumigation associated with increasing the target nematode population and compromising the performance of biofumigation. This review argues that host suitability could, in fact, be beneficial, especially when it comes to stimulating egg hatch and trapping J2s as an open-end trap crop [65]. The hatchlings or J2s are now at the most sensitive or vulnerable stage to be killed by ITC through biofumigation. Melakeberhan et al. [87] found that *M. hapla* accumulated 450–500 degree-days (with a base temperature of 10°C) to develop from undifferentiated eggs to egg-laying females on oil radish and proposed that terminating the crop before completion of the nematode’s life cycle might be best used as a trap crop. Waisen et al. [65] found *M. incognita* J2s accumulated 283 degree-days to reach egg-laying females on *B. juncea* ‘Caliente 199’ in greenhouse conditions, and reduced soil population of *Meloidogyne* spp. in two field trials.

The key to maximizing biofumigation kill is to grow root-knot nematode susceptible biofumigant crop with an aim to activate or stimulate egg hatch and subsequently terminate the crop right before the nematode completes its life cycle. The termination time is critical and it must be done based on nematode degree-days or heat units as

Biofumigant crop		Meloidogyne species			References
Species	Cultivar	<i>M. hapla</i>	<i>M. incognita</i>	<i>M. javanica</i>	
<i>Brassica carinata</i>	Bc007	Poor	Moderate	Poor	[81]
<i>Brassica juncea</i>	ISCI99	Good	Good	Good	[81]
	Nemfix	Good	Good	Good	[81, 83]
	Pacific Gold	Moderate/good	Good	Moderate	[80, 81]
<i>Brassica napus</i>	Humus	Poor/moderate	Poor/moderate	Poor/moderate	[81]
	Winfred	Poor	Moderate/good	Good	[81]
<i>Brassica rapa</i>	Rondo	Good	Good	Good	[81]
	Samson	Good	Good	Good	[81]
<i>Eruca sativa</i>	Nemat	Poor	Poor	Poor	[81, 84, 85]
<i>Raphanus sativus</i>	Adagio	Poor	Poor	Poor	[81, 86]
	Adios	Poor/moderate	Moderate/good	Poor/moderate	[81]
	Boss	Poor	Poor	Poor	[81, 84]
	Colonel	Good	Poor	Poor	[81]
	Comet	Poor	Good	Poor	[81]
	Defender	Poor	Poor	Poor	[81]
	TerraNova	Good	Poor	Poor	[81]
<i>Sinapis alba</i>	Abraham	Poor/moderate	Poor	Poor/moderate	[81]
	Absolut	Poor	Moderate	Moderate	[81]
	Accent	Poor	Poor	Poor	[81]
	Achilles	Poor/moderate	Moderate/good	Moderate/good	[81]
	Condor	Poor	Moderate/good	Poor	[81]
	IdaGold	Good	Moderate/good	Moderate	[81]
	Maxi	Moderate	Poor/moderate	Poor	[81]
	Santa Fe	Poor/moderate	Moderate	Poor/moderate	[81]

Table 2.
 Host suitability of common biofumigant crops to major *Meloidogyne* species.

demonstrated by Waisen et al. [65] and Melakeberhan et al. [87]. At the average soil temperatures of 22°C in winter or 29°C in summer in Hawaii, USA, brassica crops were recommended to grow for 5–6 weeks to achieve the dead-end trap cropping effect [64, 65]. At this time, root-knot nematodes will reach mature females but before laying eggs.

9. Conclusions

An important question to address is what is the best possible combination with respect to the abovementioned factors affecting biofumigation to maximize the biofumigation performance against root-knot nematodes in agroecosystems? This chapter highlights that the exploitation of brassica host suitability to root-knot nematodes can enhance the biofumigation effect with a time-sensitive process of stimulating egg hatching and trapping J2s with a subsequent targeted release of ITC at the most vulnerable life stage. Ideally, coupling open end trap crop tactic with an effective termination method that releases maximum ITC would enhance biofumigation effect on target nematodes [88]. Based on the abovementioned factors and the contemporary knowledge on the mechanism of biofumigation, it trickles down to six steps as necessary to maximize biofumigation effects. These include (1) Select a potent and susceptible biofumigant crop - Selecting a cultivar or an accession of *Brassica* species that produce high ITC-generating GL (e.g., *B. juncea* 'Caliente 199'). Most importantly, the selected brassica biofumigant crop must be susceptible to your target plant-parasitic nematode, the root-knot nematode; (2) Field preparation—Till the field, direct seed the selected biofumigant crop (e.g., *B. juncea* 'Caliente 199' at 10–12 kg/ha). In temperate climates such as in California, Grow brassica biofumigant crops in winter but not in spring or summer as they are photosensitive and flower before biomass production necessary for biofumigation. Adjust the soil pH to near neutral (pH 6–7) because lower pH favors nitrile production, instead of ITC. Irrigate and fertilize the biofumigant crops as needed. (3) Termination—Terminate the biofumigant crop 5–6 weeks after planting. Based on field research conducted in tropical climates in Hawaii, termination can be done at 5-week old in summer or 6-week old in winter. Termination involves comprehensive maceration of aerial tissues using a flail mower; (4) Tissue incorporation - Immediately incorporate the macerated tissues to 10–15 cm deep to minimize volatilization losses of ITC and maximize ITC contact with nematodes. Soil incorporation must target rhizosphere where the nematodes are; (5) Sealing the soil—covering the soil with impermeable plastic mulch (opaque or black plastic is recommended as soil is cooler under black plastic mulch and chances of Myr denaturation is minimized) immediately after the tissue incorporation to retain ITC from volatilization loss; and (6) uncover and transplant cash crop—uncover the plastic mulch after 7 days and transplant the cash crop. The one-week time window is recommended to avoid phytotoxicity.

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