


Review

The Roles of Cruciferae Glucosinolates in Disease and Pest Resistance

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Abstract: With the expansion of the area under Cruciferae vegetable cultivation, and an increase in the incidence of natural threats such as pests and diseases globally, Cruciferae vegetable losses caused by pathogens, insects, and pests are on the rise. As one of the key metabolites produced by Cruciferae vegetables, glucosinolate (GLS) is not only an indicator of their quality but also controls infestation by numerous fungi, bacteria, aphids, and worms. Today, the safe and pollution-free production of vegetables is advocated globally, and environmentally friendly pest and disease control strategies, such as biological control, to minimize the adverse impacts of pathogen and insect pest stress on Cruciferae vegetables, have attracted the attention of researchers. This review explores the mechanisms via which GLS acts as a defensive substance, participates in responses to biotic stress, and enhances plant tolerance to the various stress factors. According to the current research status, future research directions are also proposed.

Keywords: *Brassicaceae*; glucosinolates; hydrolytic products; pathogen; insect resistance; secondary metabolites



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1. Introduction

Plants are exposed to complex and highly variable environmental conditions in the course of their growth and development, and are often at risk of death or even extinction under the influence of diverse biotic and abiotic stress factors [1–3]. To survive such challenges in their habitats and environments, plants have evolved numerous adaptive mechanisms, including the production of diverse metabolites, which exhibit obvious species specificity [4]. Depending on their structure and type, plant secondary metabolites are mainly divided into terpenoids, phenols, and nitrogen-containing compounds [5–7]. Numerous studies have shown that there are about 90,000–200,000 types of metabolites in plants, and they play essential roles in signal transduction, adaptive regulation, growth and development, and plant defense [8–10]. Since many of the secondary metabolites act as defenses, it is presumed that biological invasion played a primary role in the evolution of the compounds [11,12].

Among the secondary metabolites, glucosinolates (GLS) are a type of anion hydrophilic secondary metabolite containing nitrogen and sulfur; GLS are water-soluble and can easily be dissolved in ethanol, methanol, and acetone [13,14]. GLS are found in 16 species of dicotyledonous angiosperms, and their contents are relatively high in the Cruciferae, Cleomaceae, and Caricaceae, and especially in the genus *Brassica*, such as in *B. rapa* ssp. *pekinensis*, *B. oleracea*, *B. napus*, *B. juncea*, and *B. rapa*, as well as in *Arabidopsis thaliana* [13,15–18]. In addition, the GLS biosynthetic pathway has been extensively studied in the model plant *Arabidopsis*, and the regulatory genes have been comprehensively

described. Such studies have sparked interest in the unconventional metabolites derived from amino acids, with a lot of research focusing on GLS in *Brassica* plants [19–21].

Since the first type of GLS was isolated from mustard seeds, the associated plant species and GLS degradation products have been gradually recognized. Currently, the structures of more than 200 types of GLS have been identified [13,17,18,22], with more than 15 detected in Cruciferae [23]. Naturally occurring GLS have a common chemical structure: the structures are generally composed of β -D-glucosinyl, a sulfide oxime group, and side-chain R groups (including alkyl, hydroxyalkyl, hydroxyalkenyl, alkenyl, methylsulfanylalkyl, methylsulfonylalkyl, methylthioalkyl, arylalkyl, and indolyl) derived from amino acids; furthermore, GLS are generally in the form of potassium or sodium salts [15]. Based on the amino-acid side chain R groups, GLS can be divided into three categories, including aliphatic GLS (side chains are mainly derived from methionine, alanine, valine, leucine, or isopropyl leucine), indole GLS (side chains mainly derived from tryptophan), and aromatic GLS (side chains mainly derived from phenylalanine or tyrosine) [19,24].

GLS are mainly found in plant seeds, roots, stems, and leaf vacuole cells, and are relatively stable in nature with no associated biological activity; conversely, glucosinase (also known as myrosinase), which is responsible for hydrolyzing glucose residues in the GLS core skeleton, is located in specific protein bodies [25–28]. In intact plants, the hydrolytic systems containing GLS and myrosinase are spatially isolated; however, when tissue is damaged, for example following infestation or mechanical injury, the two rapidly combine, which leads to the rapid formation of GLS hydrolytic products [29–33]. In addition, food processing techniques, such as chopping, juicing, chewing, cooking, high temperature treatment, and thawing, can also break down GLS [34]. The hydrolytic products of GLS breakdown include glucose and unstable sugar glycoside ligands, and the glycoside ligands are rearranged to form isothiocyanates, nitriles, oxazolidinethiones, thiocyanate, epithionitriles, and other products, which all exhibit a wide range of biological activity [35–38].

GLS and their degradation products influence the taste and flavor of cruciferous vegetables [39,40], and there were significant difference in GSL content among *Brassica* plants; the total GSL content in the freeze-dried samples ranged from 621.15–42,434.21 $\mu\text{mol kg}^{-1}$, with an average value of 14,050.97 $\mu\text{mol kg}^{-1}$ [41]. The spicy taste in radish is caused primarily by volatile allyl, 3-butane, and 4-methyl thiocyanate (ITC). Furthermore, over the past few decades, it was established that some of the metabolite classes containing nitrogen and sulfur exhibit immunosuppressant and anticancer properties [16,35,42–45]. Sulforaphane, the degradation product of glucoraphanin, exhibits anticancer activity, can relieve neuropathic pain caused by chemotherapy, and has significant inhibitory effects against prostate, rectal, breast, pancreatic, and bladder cancers [46–52]. In contrast, a progoitrin degradation product, goitrin (5-vinylloxazolidine-2-thione), can cause goiter and abnormalities in the internal organs of animals [53].

In the field, the mustard oil bomb is a major defense mechanism deployed against insect herbivory [54–56], pathogen infection [57–61], and various abiotic stress factors (such as drought, low or high temperature, light, and salt stress) [62–70]. The findings of such studies have prompted research on the potential application of GLS extracts and metabolites in crop pest and disease control in recent years [8,71,72].

Cruciferous vegetables are the largest leafy vegetables in the world, and are widely cultivated globally, and the cultivated area is expanding year by year according to the statistics of Food and Agriculture Organization of the United Nations (FAO) (Figure 1). Cruciferous plants in cultivation are often affected by various fungi (*Plasmodiophora brassicae*, *Fusarium oxysporum*, *Peronospora parasitica* (Pers), *Sclerotinia sclerotiorum*) [73–76], bacteria (*Xanthomonas campestris* pv. *campestris*, *Erwinia carotovora* pv. *carotovora* Dye, *Maculicola pseudomonas syringae*) [77–79], and viruses (*Turnip mosaic virus*) [80], which cause club root, Fusarium wilt, downy mildew, sclerotinose, black rot, soft rot, black spot, mosaic, etc. Furthermore, *Plutella xylostella*, aphids, and *Pieris rapae* seriously affect the growth and

development of cruciferous plants, and greatly reduce the productivity of cruciferous vegetable farms [81–83].

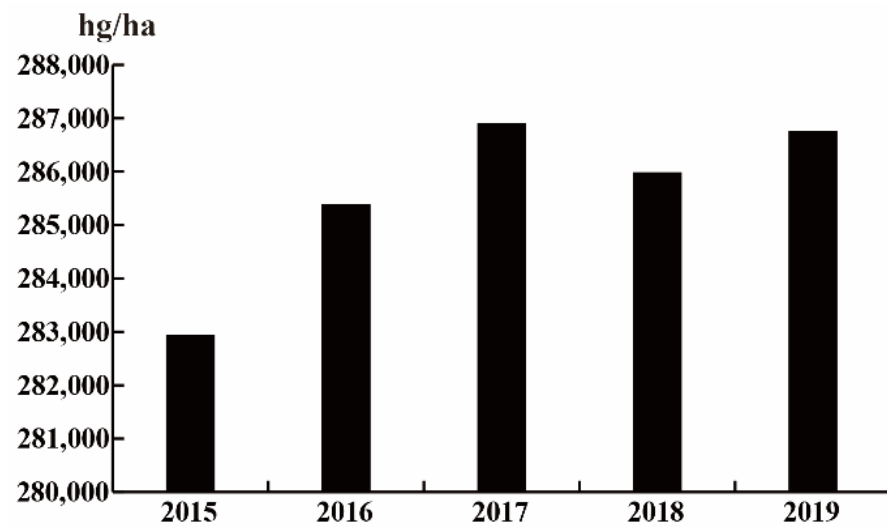


Figure 1. Changes in the cultivated area of cruciferous vegetables in recent years.

Currently, chemical control using pesticides is the primary method used to prevent and manage the diseases and insect pests that impair cruciferous vegetable cultivation and productivity. Despite the agricultural production industry currently advocating reducing pesticide application, the use of pesticides is still high according to the data from the FAO (Figure 2). Mass application of chemical pesticides not only increase production costs and deposit excessive pesticide residues on vegetables, but also pose threats to the environment and human health. Consequently, studies and comprehensive data on the potential of GLS derived from Cruciferae to control diseases are required. This review explores and summarizes the latest research on the disease and insect resistance function of GLS, in addition to the underlying resistance mechanisms, in cruciferous plants and in *Arabidopsis*. The present review could provide a theoretical basis for the application of GLS in disease and pest resistance, and the breeding of resistant cruciferous vegetables.

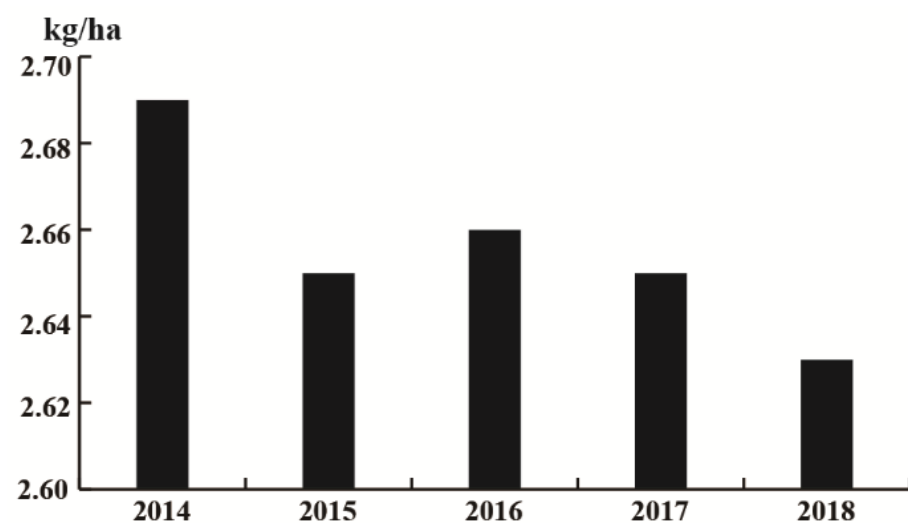


Figure 2. Pesticide application per hectare in recent years.

2. Defense Response of GLS to Fungal Diseases

The main diseases affecting agricultural production are fungal diseases, which have caused serious losses to the production of cruciferous vegetables. Consequently, investigating the potential effects of GLS extracts and enzymolysis products in resistance against

fungal diseases, in addition to their underlying mechanisms of action, could facilitate efforts to improve agricultural productivity in cruciferous crops. Aqueous extracts containing ITC can inhibit the growth of *Alternaria brassicicola* in vitro by 50% [84]. Following exposure to allyl-ITC (Al-ITC), *A. brassicicola* exhibits a response similar to that observed during oxidative stress, based on the results of a study examining the transcriptomic responses of *Arabidopsis* challenged with *A. brassicicola*. In addition, ITCs play major roles in *Arabidopsis* resistance against *Plectosphaerella cucumerina*, *Botrytis cinerea*, *Fusarium oxysporum*, and *Peronospora parasitica* inoculation, demonstrated in a study using a GLS biosynthesis mutant *gsm1-1* and wild-type *Arabidopsis* [85]. Humphry et al. (2010) investigated the accumulation of indole GLS in several insertion lines, and the results suggested that MYB51 participates in the regulation of genes critical for GLS metabolism, which also influences antifungal defense [86]. Meanwhile, S-deficiency in oilseed rape can reduce GLS biosynthesis, which negatively affects resistance against *Leptosphaeria maculans*, *B. cinerea*, and *Phytophthora brassicae* [57].

According to Giamoustaris and Mithen (2010), the levels of *Alternaria* infection are positively correlated with napus GLS contents, and there is no significant relationship between the GLS content and *Leptosphaeria maculans* resistance [87]. In addition, Robin et al. (2020) found that GLS biosynthetic genes were induced following a study carried out on two resistant and two susceptible cabbage in-bred lines after inoculation with two *Leptosphaeria maculans* isolates, and GLS (aliphatic and indolic GLS) accumulation was enhanced [88]. In a study investigating the indolyl-3-acetonitrile, 4-methoxyglucobrassicin, and indole GLS concentrations in *B. rapa* inoculated with *Albugo candida*, Pedras et al. (2008) observed increased levels of indole GLS in inoculated leaves when compared to the control leaves [89]. *B. rapa* indole GLS has also been reported to limit *Colletotrichum gloeosporioides* and *Colletotrichum orbiculare* infection [90], and tryptophan pathway genes involved in indole-GLS biosynthesis are upregulated in *F. oxysporum*-infected plants [91,92].

Based on dynamic transcriptomic analyses of *B. rapus* defense response to *S. sclerotiorum* post-inoculation, Zhao et al. (2004), Borge et al. (2015), and Wu et al. (2016) observed that not only the GLS content but also indolic GLS biosynthesis are associated with *S. sclerotiorum* resistance, and that *S. sclerotiorum* infection can induce GLS biosynthesis [8,93,94]. Unlike in the case of *S. sclerotiorum*, *B. cinerea* does not induce GLS biosynthesis [95]. A comparison of the disease symptoms of wild-type and transgenic *Arabidopsis* lines following inoculating with arbuscular mycorrhizal fungi (AMF), based on the production or enhancement of GLS levels, revealed a previously undocumented role of GLS biosynthesis in reducing AMF colonization [96].

After *Plasmodiophora brassicae* infection, the aliphatic, indolic, and aromatic GLS contents of susceptible *B. napus* exhibit increased accumulation; however, only aromatic GLS contents are significantly increased in resistant *Matthiola incana* L. [97]. The major aliphatic GLS, gluconapin, is significantly increased during secondary infection in *B. napus*, and exogenous jasmonic acid (JA) treatment induces aliphatic GLS in *B. napus* and aromatic GLS in *M. incana*. The expression of *BnMYB28.1*, which regulates the contents of aliphatic GLS in *B. napus*, is significantly increased following both treatment with exogenous JA and *P. brassicae* inoculation. Similarly, after *B. cinerea* infection, the genes involved in indole GLS biosynthesis are upregulated in the *Arabidopsis* UGT80A2 and UGT80B1 double mutant, and the upregulation was correlated with increased levels of JA and the upregulation of two marker genes (PDF1.2 and PR4) of the ERF branch of the JA signaling pathway [98].

3. Defense Responses of GLS to Bacterial Diseases

The bacteria that infect cruciferous plants are all rod-shaped bacteria, which can invade the host through stomata, hydathodes, and wounds, and then be retransmitted by running water, rain, insects, etc. Bacterial diseases in cruciferous have widespread occurrence, are highly destructive, and are challenging to control. Meanwhile, because the pathogens are different from the fungal diseases, the corresponding disease resistance mechanism of host and the GLS involved in resistance may be different. Several studies have demonstrated

that GLS are involved in plant defense against a variety of bacterial diseases. Similar to the case in fungal disease infection, infection by *Burkholderia cepacia*, *Pseudomonas syringae*, and *Xanthomonas campestris* pv. *campestris* (Xcc) led to the upregulation of the GLS biosynthesis [99]. In addition, the introduction of CYP79 influenced *Arabidopsis* disease resistance by increasing the GLS synthesis, and overexpressing the CYP79D2 from cassava increased the accumulation of the aliphatic isopropyl and methylpropyl GLS, which also enhanced resistance against the soft-rot pathogen, *Erwinia carotovora*; however, overexpressing the sorghum CYP79A1 or CYP79A2 increased the accumulation of p-hydroxybenzyl and benzyl GLS, respectively [100].

Mishina et al. (2007) observed that the knockout of PAL1 increased leaf survival after *P. syringae* infection in an analysis conducted on *Arabidopsis* mutants and wild type plants, while Truman et al. (2007) and Aires et al. (2011) observed that indole GLS biosynthesis decreased after *P. syringae* infection [101–103]. Following the transcriptional and metabolic profiling of *A. thaliana* mutants, Clay et al. (2009) reported that the PEN2 and PEN3 genes are necessary for resistance to PtoDC3000 pathogens [104]. Furthermore, Geng et al. (2012) demonstrated that coronatine, a toxin produced by *P. syringae*, suppresses the salicylic acid (SA)-independent pathway, facilitating callose deposition by reducing the accumulation of an indole GLS upstream of the PEN2 myrosinase activity [105]. In addition, a positive correlation has been reported between total GLS content and Xcc disease severity, and Xcc infection enhanced GLS biosynthesis during the early infection period [106,107]. *Pectobacterium carotovorum* ssp. *carotovorum* infection in *B. rapa* can trigger the upregulation of the JA and ethylene (ET) biosynthesis genes in sr gene mutants and increase resistance capacity via GLS accumulation [108].

4. Defense Response of GLS to Pests

With global warming, the loss caused by pests is increasing. Meanwhile, because pests have migration ability, once the control is not effective, it will cause serious damage [109]. Hence, pest control has been a hot spot in agriculture. At present, pest control is mainly focused on chemical agents, but how *Brassicaceae* plants perceive and defend themselves from such threats remain poorly understood. Investigating the mechanisms via which *Brassicaceae* resist insect pests could facilitate efforts to improve crop productivity. Brown and Morra (1997) were the first to report that GLS-containing plants could control soil-borne plant pests [110]. Since then, numerous studies have demonstrated that GLS contents in tissues are positively correlated with damage caused by *Pieris rapae* and *Spodoptera littoralis* [111,112], but negatively correlated with the damage caused by slugs [86]. Furthermore, GLS accumulation induced by *Spodoptera exigua* required functional NPR1 and ETR genes [113].

In another study, the weights of *Trichoplusiani* and *Manduca sexta* on the TGG1 and TGG2 double myrosinase mutants were significantly higher than in wild-type *Arabidopsis* [27]. Similarly, *Mamestra brassicae* larvae gained less weight and exhibited stunted growth when fed on MINELESS (lacking myrosin cells) plants compared to when fed on wild-type plants, with the myrosinase activity in the wild-type seedlings reducing; however, the levels of indol-3-yl-methyl, 1-methoxy-indol-3-yl-methyl, and total GLS in both the wild-type and MINELESS seedlings increased [114]. Conversely, *M. brassicae* and *P. rapae* weighed more on the high-sinigrin concentration plants than in low-sinigrin concentration plants; however, their weights decreased in the high-sinigrin, high-glucoiberin, and high-glucoibrassicin genotypes; furthermore, development time increased under high glucoibrassicin concentrations [115].

By testing the GLS and phenolic concentrations trends in *Brassica nigra* (L.) Koch before and after herbivory by *Pratylenchus penetrans* Cobb and the larvae *Delia radicum* L., Van et al. (2005) observed that the total GLS levels were affected by herbivory by the two root feeders [116]. Besides, *Spodoptera litura* Fabricius was more affected by induced GLS responses than *Plutella xylostella* L. [117]. In addition, following a comparison of GLS levels and the expression profiles of GLS biosynthesis genes before and after *Plutella xylostella*

infestation, Liu et al. (2016) observed a difference in the proportions of stereoisomers of hydroxylated aromatic GLS between G-type (pest-resistant) and P-type (pest-susceptible) *Barbarea vulgaris* [56]. Using m/z 60 as a marker of AI-ITC formation from the sinigrin GLS, Van et al. (2012) analyzed the GLS profiles and volatile organic compound emissions in five *Brassicaceae* species before and after artificial injury or infestation by cabbage root fly larvae (*D. radicum*). According to the results, m/z 60 in *B. nigra*, *B. juncea*, and *B. napus* was primarily emitted directly after artificial injury or root fly infestation, sulfide and methanethiol emissions from *B. nigra* and *B. juncea* increased after infestation, and *B. oleracea* and *Brassica carinata* exhibited increases in fig m/z 60 emissions following larval damage [118].

Long-term feeding on GLS-free *Brassicaceae* diets hardly affects *P. xylostella* oviposition preference and larvae survival; thus, high GLS content varieties are likely to be more susceptible to damage by *P. xylostella* than lower GLS content varieties [119]. Similarly, Chen et al. (2020) generated single or double mutant *gss1* and *gss2* lines using the CRISPR/Cas9 system and analyzed their resistance to *P. xylostella* [120]. According to the results of the bioassays, when fed on their usual artificial diet, there were significant reductions in egg hatching rates and final larval survival rate of the single mutant *gss2* lines when compared with the original strain or mutant *gss1* lines, and the absence of GSS1 or GSS2 reduced the survival rate of *P. xylostella* and prolonged the duration of the larval stage. In addition, feeding by *Spodoptera littoralis*, *Pieris brassicae*, and *P. rapae* led to upregulation of the aliphatic GLS pathway [121–123], and the GLS contents were negatively correlated with *P. brassicae* damage. Furthermore, methyl jasmonate (MeJA) can enhance resistance to *P. brassicae* by inducing GLS accumulation [124,125].

5. Defense Response of GLS to Insects and Aphids

Insects and aphid not only have a wide range of species and rapid reproduction, but also can cause wounds to the plant when feeding, leading to the invasion of pathogenic bacteria, and then cause secondary damage. Moreover, the GLS synthesis and response mechanisms following insect and aphid herbivory are qualitatively and quantitatively different [126]. Agerbirk et al. (2001) observed no correlation between *B. vulgaris* ssp. *arcuata* GLS content and resistance against *Phyllotreta nemorum* [127], while Kroymann et al. (2003) observed a positive correlation between GLS content and damage caused by *Psylliodes chrysocephala* [128]. According to Ulmer et al (2006), total GLS levels did not influence *Ceutorhynchus obstrictus* larval growth or development; however, high levels of specific GLS, such as p-hydroxybenzyl and 3-butenyl GLS, were associated with increased development time or reduced weight [129]. After *Brevicoryne brassicae* herbivory, Myrosinase binding protein (MBP), myrosinase associated protein (MyAP), and myrosinase transcripts, and the synthesis of indolyl and aliphatic GLS, particularly 3-hydroxypropyl and ITC, are induced [103,130,131].

By comparing the larval instar weights and mortality of cabbage stem flea beetle (*P. chrysocephala*) larvae, after feeding on different species, Döring et al. (2020) observed that aliphatic GLS contents increased in the infested turnip rape, and aliphatic and benzenic GLS decreased in infested Indian rape [132]. Although larval weight was not correlated with total GLS, it was positively correlated with progoitrin and 4-hydroxyglucobrassicin contents. Furthermore, decreasing the side chain length of aliphatic GLS and the degree of hydroxylation of butenyl GLS could increase the extent of feeding by adult flea beetles [87].

Numerous intermediate synthetic genes participate in GLS resistance to insects and aphids. For instance, Mewis et al. (2006) observed that GLS accumulation caused by *B. brassicae* and *Myzus persicae* required functional NPR1 and ETR1 genes [113]. After *Myzus persicae* feeding and aphid saliva treatment, a set of O-methyltransferases involved in the synthesis of aphid-repellent GLS were significantly up-regulated based on qRT-PCR analyses of 78 genes. However, ITC production was not correlated with these gene expression level, suggesting that aphid salivary components trigger a defense response in *Arabidopsis* that is independent of the aphid-deterrent GLS [133]. In addition, aphid attack

could increase indolyl GLS concentrations three-fold [134]. Using a combination of QTL fine-mapping and microarray-based transcript profiling methods, CYP81F2 was revealed to facilitate defense against *B. brassicae* but not resistance against herbivory by larvae from four lepidopteran species [135]. By comparing the survival of the *Bemisia tabaci* MEAM1 and *B. tabaci* MED following exposure to sinigrin and myrosinase, Hu et al. (2020) reported that exposure to the toxic hydrolysates of GLS hydrolysates and myrosinase is greater for MED than for MEAM1 [136].

6. Conclusions and Future Research Outlook

Cruciferous vegetables are the most important leafy vegetables; however, the cultivation of cruciferous plants is affected by various fungi, bacteria, aphids, and other pest insects. At present, the prevention and control of these diseases and insect pests mainly focus on chemical agents, and the dosage of the chemical pesticides is also increasing, which not only leads to excessive pesticide residues on cruciferous plants, causing great damage to the environment, but also threatens people's health. Understanding how host-plant characteristics influence the physiological and behavioral responses is essential for the development of resistant cruciferous germplasms. A large number of studies have shown that GLS, esters, and flavonoids are closely related to Cruciferae disease resistance [137,138]. As an important secondary metabolite in cruciferous vegetables, GLS are closely related to biotic and abiotic stresses. Numerous studies have demonstrated a positive relationship between GLS content and disease and insect resistance [57,88,99,106,107,111,112,116,128,134] (Table 1). Consequently, in future cruciferous vegetable breeding activities, varieties with high GLS contents can be selected appropriately to improve plant disease resistance and reduce pesticide use. The degradation products (isothiocyanate and thiocyanate) of GLS are involved in the resistance to a variety of fungi, bacteria, insects, and soil-borne pests [8,71,72]; the aqueous extracts of cruciferous leaves also contain ITC, which can restrict the growth of a variety of fungi, bacteria, and pests [84,85,110]. Moreover, the resistance of these degradation products to pests and diseases is a broad-spectrum resistance, and thus can be used to develop botanical pesticides.

Pest invasion and disease infestation can increase GLS, especially indole GLS, in cruciferous plants [8,9,89–95,105,117,121–123,133,134]. In the case of rapeseed and other species that have low GLS, molecular biology techniques can be used to increase indole GLS production, which could improve resistance to diseases and insect, without increasing total GLS synthesis. Similar to other secondary metabolites, GLS synthesis is regulated by plant hormones. By controlling the amount of sulfur fertilizer applied and exogenous plant hormone treatments, such as JA, ET, MeJA, and SA, GLS synthesis can be modulated, and, in turn, disease resistance [57,105,125,126,139–142]. In addition, pathogen infection and insect herbivory can trigger the upregulation of the JA and ET biosynthesis genes, and increase defensive capacity via GLS accumulation [108]. Therefore, in subsequent cruciferous vegetable production activities, appropriate plant hormones could be sprayed as a novel pest management strategy to improve their stress resistance and minimize pesticide use (Figure 3).

Table 1. Correlation of the GLS components and their metabolites in corresponding pathogen, pest, and insect resistance.

Component	Species	Names	Correlation	References
ITC; Allyl-ITC	Fungal	<i>Alternaria brassicicola</i>	positive	[84–86]
		<i>Plectosphaerella cucumerina</i>	positive	[86]
		<i>Botrytis cinerea</i>	positive	[86]
		<i>Fusarium oxysporum</i>	positive	[86]
		<i>Peronospora parasitica</i>	positive	[86]

Table 1. Cont.

Component	Species	Names	Correlation	References
Total GLS	Fungal	<i>Alternaria brassicicola</i>	positive	[92]
		<i>Leptosphaeria maculans</i>	No; positive	[92,93]
		<i>Sclerotinia sclerotiorum</i>	positive	[7,98,99]
		Arbuscular mycorrhizal fungi	positive	[101]
	Bacteria	<i>Burkholderia cepacia</i>	positive	[104]
		<i>Pseudomonas syringae</i>	positive	[104]
		<i>Xanthomonas campestris</i>	positive	[104,111,112]
		<i>Pectobacterium carotovorum</i>	positive	[113]
	Pest	<i>Pieris rapae</i>	positive	[114]
		<i>Spodoptera littoralis</i>	positive	[115]
		Slug	negative	[93]
		<i>Spodoptera exigua</i>	positive	[116]
		<i>Trichoplusia ni</i>	positive	[117]
		<i>Manduca sexta</i>	positive	[117]
		<i>Manestra brassicae</i>	positive	[118]
		<i>Pratylenchus penetrans</i>	positive	[118]
		<i>Delia radicum</i> L.	positive	[118]
		<i>Spodoptera litura</i> Fabricius	positive	[121]
		<i>Plutella xylostella</i> L.	positive	[121,123,124]
		<i>Pieris brassicae</i>	positive	[128,129]
Insect	<i>Phyllotreta nemorum</i>	No	[131]	
	<i>Psylliodes chrysocephala</i>	positive	[132]	
	<i>Ceutorhynchus obstructus</i>	No	[133]	
Indole GLS	Fungal	<i>Albugo candida</i>	positive	[94]
		<i>Colletotrichum gloeosporioides</i>	Positive	[95]
		<i>Colletotrichum orbiculare</i>	Positive	[95]
		<i>Fusarium oxysporum</i>	positive	[96,97]
	Bacteria	<i>Plasmodiophora brassicae</i>	positive	[102]
Aliphatic GLS	Fungal	<i>Plasmodiophora brassicae</i>	positive	[102]
	Pest	<i>Spodoptera littoralis</i>	positive	[125]
		<i>Pieris brassicae</i>	positive	[125]
		<i>Pieris rapae</i>	positive	[126]
	Insect	<i>Psylliodes chrysocephala</i>	positive	[137]
Aromatic GLS	Fungal	<i>Plasmodiophora brassicae</i>	positive	[102]
	Pest	<i>Plutella xylostella</i> L.	positive	[60]
Benzenic GLS	Insect	<i>Psylliodes chrysocephala</i>	positive	[136]
Indolyl-3-acetonitrile, 4-methoxyglucobrassicin,	Fungal	<i>Albugo candida</i>	positive	[94]
Aliphatic isopropyl; methylpropyl GLS	Bacteria	<i>Erwinia carotovora</i>	positive	[105]

Table 1. Cont.

Component	Species	Names	Correlation	References
Indol-3-yl-methyl; 1-methoxy-indol-3-yl-methyl	Pest	<i>Mamestra brassicae</i>	positive	[118]
P-hydroxybenzyl; 3-butenyl	Insect	<i>Ceutorhynchus obstrictus</i>	positive	[133]
Sinigrin	Pest	<i>Pieris rapae</i>	negative	[119]
Glucobrassicin	Pest	<i>Pieris rapae</i>	positive	[119]

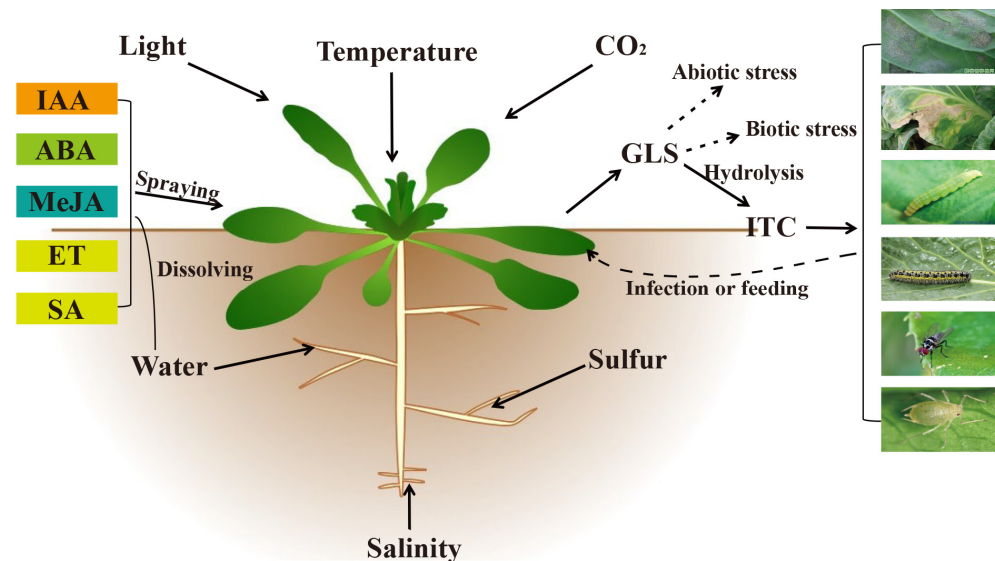


Figure 3. Factors affecting the synthesis of glucosinolate in cruciferous plants.

Some studies have demonstrated that the different stereoisomer structures of hydroxylated aromatic GLS is one of the important factors influencing the varying disease resistance levels between non-cultivars and resistant cultivars [56]. Consequently, by determining and analyzing the GLS responsible for resistance in tolerant materials, chemical synthesis or biotechnology tools can be used to mass-produce the corresponding GLS for widespread application. The present review on the GLS responsible for disease and pest resistance in cruciferous vegetables and their underlying mechanisms could not only offers insights on how cruciferous plants could respond to increased biotic stress in the future but could also facilitate the development of novel disease and pest-resistant plants and the development of safe and high-yield cruciferous vegetable germplasm globally.

Despite there being many research studies on cruciferous plant resistance, which indicated the invasion of the diseases, insects and pests will lead to the synthetic form of the hormones and GLS, and total GLS, especially the indole GLS content, has a positive correlation with cruciferous resistance, but only a few studies have identified the specific resistance due to GLS and other metabolites. This may be related to the determination methods of GLS composition. At present, the conventional determination methods of GLS are HPLC (high performance liquid chromatography) and HPLC-MS; these two methods are not only expensive and difficult, but also often lack some standard samples. So, efficient and accurate GLS determination methods need to be improved or developed in subsequent research. Moreover, the synthesis mechanism and corresponding intermediate pathway of GLS are mainly focused on the model plant *A. thaliana*; studies on other species are thus few. The genomes and cultivation of most cruciferous vegetable patterns are different from *A. thaliana*. Compared with *Arabidopsis*, the genomes and cultivation patterns of Cruciferous plants are more complex. Although the genomes of many cruciferous plants have been sequenced, the genomes of the majority of species are still unknown, which has limited the

study on the anabolism of GLS and other disease-resistance-related substances. With the reduction of the cost of genome sequencing, transcriptome sequencing, and omics analysis, it is believed that people will have a new understanding of the mechanism of GLS against diseases and insects.

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