Biofumigation to protect oilseed crops: focus on management of soilborne fungi of sunflower

Neïla Ait-Kaci Ahmed1, Grégory Dechamp-Guillaume2 and Célia Seassau3,*

1 Université de Toulouse, INRAE, UMR AGIR, 31320 Castanet-Tolosan, France
2 Université de Toulouse, INRAE, INP-ENSAT Toulouse, UMR AGIR, 31320 Castanet-Tolosan, France
3 Université de Toulouse, INRAE, INP-EIP Toulouse, UMR AGIR, 31320 Castanet-Tolosan, France

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Abstract – Sunflower (Helianthus annuus L.) is one of the three most productive oilseed crops worldwide. Soilborne diseases limit yields and are challenging to manage. The fungi Verticillium dahliae, Sclerotinia sclerotiorum and Macrophomina phaseolina can survive in the soil for many years and spread. Following the ban on fumigants, biofumigation, which consists of growing, chopping and incorporating a Brassicaceae cover crop to allow biocidal compounds production in the soil, may be an alternative. Biocidal effects of the hydrolysis of glucosinolate into active compounds, such as isothiocyanates, have been shown in laboratory studies, but the effectiveness of biofumigation varies more in the field. The present study reviews the main factors that determine effective biofumigation to protect sunflower. Since the toxicity of isothiocyanates to pathogens varies widely among the latter, we reviewed studies that assessed the suppressive effect of products of glucosinolate hydrolysis on V. dahliae, S. sclerotiorum and M. phaseolina. Farmers can use many mechanisms to increase isothiocyanate production, which may protect sunflower crop effectively. Increasing biomass production and chopping the cover crop during mild temperatures and before rainy periods could increase biofumigation effectiveness. Further field experiments are needed to confirm the potential of biofumigation to control soilborne diseases of sunflower and assess potential disservices to beneficial soil communities, given their potential key role in the control of soilborne pathogens.

Keywords: Helianthus annuus / cover crops / Brassicaceae / glucosinolates / agroecological crop protection

Résumé – Protéger les cultures oléagineuses par la biofumigation: le cas de la gestion des champignons telluriques du tournesol. Le tournesol (Helianthus annuus L.) est l’une des trois cultures oléagineuses les plus productives dans le monde. Les pathogènes telluriques limitent sa productivité et leur contrôle est difficile. Les champignons telluriques Verticillium dahliae, Sclerotinia sclerotiorum et Macrophomina phaseolina peuvent survivre plusieurs années dans le sol et sont en recrudescence. Suite à l’interdiction de plusieurs fumigants, la biofumigation, qui consiste en la mise en place, la destruction et l’incorporation de culture intermédiaire de Brassicacées permettant la production de composés biocides dans le sol, pourrait être une alternative. L’effet biocide des produits de l’hydrolyse des glucosinolates, tels que les isothiocyanates, a été démontré au laboratoire, mais l’efficacité de la biofumigation est variable en plein champ. Cette revue a pour objectif de recenser les déterminants majeurs de l’efficacité de la biofumigation pour la protection du tournesol. La toxicité des isothiocyanates étant variable selon les bioagresseurs visés, le second objectif est de recenser les études ayant évalué les effets suppressifs des produits de la dégradation des glucosinolates, contre les champignons telluriques V. dahliae, S. sclerotiorum et M. phaseolina. Les agriculteurs peuvent mettre en place plusieurs leviers afin d’améliorer la production d’isothiocyanates, permettant potentiellement une protection efficace de la culture du tournesol. Maximiser la production de biomasse puis détruire le couvert lors de températures douces et avant une période pluvieuse pourraient améliorer l’efficacité de la biofumigation. Des expérimentations en plein champ

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*Correspondence: celia.seassau@purpan.fr
supplémentaires sont nécessaires pour confirmer le potentiel de la biofumigation pour contrôler les pathogènes telluriques du tournesol et évaluer ses potentiels disservices contre les communautés microbiennes du sol, au regard de leur importance potentielle dans le contrôle des pathogènes telluriques.

Mots clés : Helianthus annuus / cultures intermédiaires multi-services / Brassicaceae / glucosinolates / protection agroécologique des cultures

1 Introduction

1.1 Oiled seed crop production and protection

1.1.1 Factors that limit crop yield

Since 2015, soybean (Glycine max), rapeseed (Brassica napus subsp. napus) and sunflower (Helianthus annuus L.) have been among the three main oilseed crops produced worldwide (FAOSTAT, 2020). In 2018, their worldwide production was ca. 345, 75 and 50 million t/annum, respectively (FAO, 2020). While the global area of these crops is expanding, unfavorable weather conditions threaten their production (FAO, 2018). Despite the moderate water requirements of sunflower, drought is the main environmental factor that limits its growth (Debaeke et al., 2017a), and high temperature can decrease its final production of seeds and oil (Harris et al., 1978). In most European countries that produce sunflower (Romania, Spain, France, Bulgaria, and Hungary), yield gaps of 1.1–2.4 t/ha have been reported, and climate change could be partly responsible for them (Debaeke et al., 2017a). Biotic stress also limits oilseed crop production worldwide. At least 30 sunflower diseases are known. The most damaging and widespread fungal diseases are downy mildew (Plasmopara halstedii), phoma black stem (Phoma macdonaldii), phomopsis stem canker (Phomopsis helianthi), white mold (Sclerotinia sclerotiorum) and Verticillium wilt (Verticillium dahliae) (Seassau, 2010; Vear, 2016; Debaeke et al., 2017b), most of which are soilborne pathogens (P. halstedii, S. sclerotiorum, V. dahliae). More recently, Cadophora malorum has been reported as a new soilborne fungus of sunflower (Martin-Sanz et al., 2018; Molinero-Ruiz, 2019). In the context of climate change, Macrophomina phaseolina could be favored by ground dryness and temperatures of 28–30°C (Šárová et al., 2003). S. sclerotiorum and V. dahliae could tolerate unfavorable periods better (Wilhem, 1955; Debaeke et al., 2017a) via their long-term structures – sclerotia and microsclerotia (MS), respectively –, which remain viable in the soil for many years (Mol et al., 1995; Ćosić et al., 2012).

1.1.2 The challenge of managing soilborne fungi

Protecting crops from soilborne organisms is more challenging than protecting them from foliar pests (Matthiessen and Kirkegaard, 2006). Soilborne fungi such as V. dahliae and M. phaseolina can survive as MS up to 14 years (Wilhem, 1955) and 4 years (Watanabe, 1973), respectively. S. sclerotiorum produces sclerotia that may survive for 3 years (Ćosić et al., 2012). Soilborne pathogens can coexist in the soil (Raaijmakers et al., 2009), and their heterogeneous distribution makes monitoring them costly and usually ineffective (Matthiessen and Kirkegaard, 2006). For many oilseed diseases, genetic resistance is one of the most effective protection methods, but it breaks down frequently due to the appearance of new virulent strains, as observed for sunflower diseases (Vear, 2016; Debaeke et al., 2017b; Molinero-Ruiz, 2019). To reduce the pressure of soilborne pathogens, farmers used to fumigate vegetable and ornamental crops intensively with methyl bromide (Hoffmann and Malkomes, 1974; Duniwuy, 2002; Martin, 2003). However, methyl bromide was phased out under the Montreal Protocol in 2005 due to its depleting effects on the ozone layer (Laegdsmand et al., 2007; Gimsing and Kirkegaard, 2009). Other synthetic compounds were subsequently used to control soilborne pathogens, such as 1,3-dichloropropene (phased out in the European Union [EU] in 2007), chloropicrin (phased out in the EU in 2012) and methyl-isothiocyanate (MITC), the primary breakdown product of metam-sodium (Ibekwe, 2004). MITC has a broad biocidal activity but alters important soil functions such as nutrient cycling (Macalady et al., 1998). It is also highly volatile, with much of it transferred to the atmosphere after application (Dungan et al., 2003).

Like for genetic resistance, maintaining the efficacy of pesticides after repeated use is difficult (Matthiessen and Kirkegaard, 2006). Synthetic fumigants may become less toxic due to soilborne pathogens developing resistance (Goldman et al., 1994) and/or increased biodegradation of their chemicals (Warton et al., 2003). This latter misunderstood phenomenon comes from the ability of microorganisms, mainly bacteria, to catabolize xenobiotes in the soil after repeated exposures with a short interval between applications (Warton et al., 2003; Matthiessen and Kirkegaard, 2006). Microorganisms can accelerate the degradation, which decreases their persistence and effectiveness for soilborne pathogens (Warton et al., 2003; Di Primo et al., 2003). This phenomenon has been observed with metam sodium used for potato (Solanum tuberosum) Verticillium wilt (VV) (Di Primo et al., 2003). When a soil develops increased biodegradation, fumigation requires several years before it can recover an effective biocidal effect (Warton et al., 2003). In the meantime, the use of fumigants seems ineffective and wasteful (Matthiessen and Kirkegaard, 2006).

1.1.3 Alternatives for managing soilborne diseases

The breakdown of resistance and the current context of agroecological transition have decreased the use of broad-spectrum fumigants (Warmington and Clarkson, 2016) and increased interest in alternative methods of crop protection (Martin, 2003). Reliance on combined and natural mechanisms to protect crops has been encouraged by Integrated Pest Management (IPM), as described in the EU Framework Directive 2009/128/EC. IPM is implemented through eight principles, and the first one is based on preventing and/or suppressing harmful organisms using a variety of methods, such as crop rotations. IPM favors the use of sustainable biological methods (Barzman et al., 2015). Since isothiocyanates (ITCs) are biologically active compounds, and MITC is
widely used as a fumigant, there is interest in transposing this biocidal activity of biological sources of ITCs to suppress soilborne pathogens and diseases (Brown and Morra, 1997; Matthiessen and Kirkegaard, 2006; Gimsing and Kirkegaard, 2006). This natural alternative to fumigation, called “biofumigation” (Kirkegaard et al., 1993), involves growing, chopping and incorporating crops that produce ITCs. Brassicaceae (crucifers) are widely used for this technique (see part 2).

The utility of biofumigation has been observed for protecting vegetable crops (Michel, 2014; Morris et al., 2020) and, to a lesser extent, wheat (Triticum aestivum, Kirkegaard et al., 2000) and beetroot (Beta vulgaris ssp. vulgaris, Motisi et al., 2009). Many studies of in vitro approaches have shown promising results of biofumigation for soilborne diseases. In the field, however, the effectiveness of biofumigation has varied more (Motisi et al., 2010; Morris et al., 2020). Nonetheless, mechanisms for suppressing pathogens effectively in the field are increasingly understood (Kirkegaard and Matthiessen, 2004; Matthiessen and Kirkegaard, 2006; Morris et al., 2020), and biofumigation appears to be an environmentally friendly defense strategy (Lazzeri et al., 2004) considered as a part of IPM (Gimsing and Kirkegaard, 2009; Kruger et al., 2013). Among oilseed crops, sunflower seems to be particularly suitable for protection using biofumigation. It is sown in spring, after a long fallow period when soils are usually left bare. A Brassicaceae cover crop introduced during this period would fit into the rotation easily, thus diversifying it. It would also improve:

- soil structure and reduce erosion (Thorup-Kristensen et al., 2003; Justes et al., 2012);
- nutrient management, through catch crop and green manure effects for nitrates and sulfates (Constantin et al., 2011; Couèdel et al., 2018a; Couèdel et al., 2018b);
- soil organic matter (Kirkegaard and Matthiessen, 2004).

To follow the fundamental agroecological principle of diversifying crop rotations (Altieri, 1999), this review does not discuss rapeseed protection using Brassicaceae cover crops and biofumigation. However, it does present studies that used Brassicaceae as a biofumigant crop. Biotic stresses are not still a major issue for soybean in France (Lamichhane et al., 2020) or in Europe. This is in part because soybean is currently grown on small areas and in diversified rotations (Lamichhane et al., 2020). The interest in biofumigation to protect soybean remains low and studies rare. Thus, this review excludes soybean protection using biofumigation, although some studies showed promising results. Fayzalla et al. (2009) showed that soybean root rot and soybean wilt, caused by Fusarium oxysporum, Rhizoctonia solani, M. phaseolina and Sclerotium rolfsii, could be reduced with mustard in field conditions.

With a focus on sunflower, the objectives of this review are to:

- highlight the main factors that determine effective biofumigation;
- review studies on laboratory or field experiments performed to evaluate suppressive effects of synthetic GSLs/ITCs or Brassicaceae incorporation on V. dahliae, S. sclerotiorum and M. phaseolina.

Since studies of sunflower protection using biofumigation are rare (to our knowledge), most studies concerned other plant hosts. Thus, after describing the biofumigation concept and process briefly, factors that drive ITC production are detailed to provide a set of mechanisms that results in effective biofumigation. Suppressive effects of glucosinolate (GSL) products on sunflower soilborne diseases are reviewed based on studies of a variety of host crops. Finally, non-GSL-related suppressive effects of biofumigation and the utility of including Fabaceae with Brassicaceae to protect sunflower against soilborne disease are also discussed.

2 The biofumigation process

2.1 Biofumigation concept and the use of Brassicaceae

Biofumigation is defined as the suppressive effect of GSL-containing species on soilborne pathogens through the liberation of volatile compounds, mainly ITCs, released after hydrolysis of GSLs by the enzyme myrosinase during tissue disruption and incorporation into the soil (Kirkegaard et al., 1993; Kirkegaard and Matthiessen, 2004). GSLs occur naturally in families of the order Capparales: Tovariaceae, Resedaceae, Capparaceae, Moringaceae and mainly Brassicaceae (Fenwick et al., 1983; Brown and Morra, 1997; Van Dam et al., 2009). They are widely cultivated as vegetables (cabbage [B. oleracea var. capitata], radish [Raphanus raphanistrum subsp. sativus], and rocket [Eruca vesicaria ssp. sativa]), condiments (mustard [Brassica juncea]), forage (fodder radish [Raphanus sativus var. longipinnatus] and turnip rape [Brassica rapa subsp. rapa]), oilseed crops and cover crops during fallow periods. However, plants that contain GSLs can be used to control soilborne pathogens through biofumigation (Kirkegaard et al., 1993; Brown and Morra, 1997; Matthiessen and Kirkegaard, 2006) and are considered to be a biological alternative to conventional soil fumigation (Brown and Morra, 1997; Matthiessen and Kirkegaard, 2006; Laegsgaard et al., 2007; Clarkson et al., 2015). Bactericidal activity of ITCs has been reported (Brown and Morra, 1997; Smith and Kirkegaard, 2002; Bending and Lincoln, 2000), as have fungicidal (Angus et al., 1994; Manici et al., 2000; Smith and Kirkegaard, 2002), nematicidal (Lazzeri et al., 1993; Riga, 2011; Ntalli and Caboni, 2017), insecticidal (Borek et al., 1995a; Borek et al., 1998) and herbicidal activities (Haramoto and Gallandt, 2004). Biofumigation can reduce pest abundance and disease incidence (Morris et al., 2020), but its degree of pest suppression can vary significantly. Some studies concluded that biofumigation did not suppress soilborne pathogens (reviewed by Kirkegaard and Matthiessen, 2004; Motisi et al., 2010). After rape incorporation, Davis et al. (1996) observed no significant differences in V. dahliae population in the soil compared to that without residue incorporation, while the incidence of VW on potato was reduced significantly compared to that on potato grown after a fallow period. VW can be caused by an interaction between V. dahliae and nematodes like Pratylenchus penetrans (Martin et al., 1982; Rowe and Powelson 2002) or Pratylenchus neglectus (Scholte and s’Jacob, 1990) which may facilitate the penetration of V. dahliae in roots, but no information is available about the direct effect of residue
incorporation on *P. neglectus* in this study. However, no significant correlation has been found between VW symptoms or yield and the nematode. Hartz et al. (2005) also reported that biofumigation (with mustard) did not significantly reduce *V. dahliae* population in the soil or VW on tomato (*Solanium lycopersicum*). A review of Motisi et al. (2010) noted an increase in disease intensity after biofumigation for some pathogens. Moreover, some studies may not be published because they unexpectedly observe no significant effects of biofumigation (Morris et al., 2020). This variability is due to the many biological and physical factors that influence the effectiveness of biofumigation (Motisi et al., 2010). Thus, knowledge about GSL and ITC production, and a systematic approach to field research through analytical studies are needed (Kirkegaard and Matthiessen, 2004).

### 2.2 The GSL-myrosinase system

GSLs are organic anions characterized by a common *b*-thioglucose, a sulfonated oxime moiety and a side-chain group (Fenwick et al., 1983). This side chain determines the type of GSL: aromatic, aliphatic or indolyl (Fenwick et al., 1983; Brown and Morra, 1997; Mithen, 2001). To date, 132 GSLs have been identified in Brassicaceae tissues (Couëdel et al., 2019). Native GSLs have little or no biocidal activity or toxicity (Manici et al., 1997). Species that contain GSL produce myrosinase, a group of similar-acting enzymes (Brown and Morra, 1997) that are also produced by some microorganisms in soils (Gimsing and Kirkegaard, 2009). In intact plant tissues, GSLs and myrosinase are physically separated (Gimsing and Kirkegaard, 2009). The isolation seems to be intercellular (Brown and Morra, 1997), with GSLs in the vacuoles and myrosinase in specialized myrosin cells (Höglund et al., 1992). Both compounds are distributed throughout Brassicaceae tissues (Wittstock and Gershenzon, 2002), and cells must be disrupted physically for them to contact each other (Brown and Morra, 1997). The result is rapid hydrolysis into biologically active products such as ITCs and other products of GSL degradation, such as nitriles, organic cyanides, oxazolidinethiones and ionic thiocyanates (Brown and Morra, 1997; Gardiner et al., 1999). Mature tissues have less myrosinase activity (Iversen and Baggerud, 1980).

### 2.3 GSL-hydrolysis products and non-GSL products

The biocidal effect of the products of GSL hydrolysis is function of the chemical composition of the GSL side chain, their concentration, environmental conditions and the exposure time of the target organism (Fenwick et al., 1983; Lazzeri et al., 1993; Laedsgmand et al., 2007; Gimsing and Kirkegaard, 2009). Each compound differs in its persistence in the soil, stability and toxicity (Borek et al., 1995b; Manici et al., 2000).

ITCs are produced rapidly after Brassicaceae tissues are disrupted (Morra and Kirkegaard, 2002). Their concentration in the soil peaks 30 min after incorporation and can be detected for up to 12 days (Gimsing and Kirkegaard, 2006). ITCs are highly volatile, and the shorter their side chain is, the more volatile they are (Brown and Morra, 1997). Due to their high volatility, their toxicity is assumed to spread around the point of chopping (Angus et al., 1994). Only aliphatic and aromatic GSLs produce ITCs (Matthiessen and Kirkegaard, 2006), and they are recognized as the most biologically active products of GSL hydrolysis, with broad-spectrum activity (Fenwick et al., 1983; Brown and Morra, 1997; Matthiessen and Kirkegaard, 2006). ITCs are toxic because of their irreversible interaction with proteins, mainly nucleophilic reagents (Brown and Morra, 1997; Borek et al., 1995a). The reaction damages the protein structure and functions of pest cells (Dufour et al., 2015).

Despite the lower toxicity of the other products of GSL hydrolysis, they may also help control soilborne organisms and work synergistically with ITCs (Brown and Morra, 1997). Other non-GSL secondary metabolites, such as sulfur-containing organic compounds (e.g. sulfoxides, amino acids such as methionine and cysteine, sulfonium compounds) may also have toxic effects on soil organisms (Bending and Lincoln, 1999).

### 3 Increasing biofumigation effectiveness for sunflower production

With more than 350 genera (Beilstein et al., 2006; Abideen et al., 2013) and 3200 species (Abideen et al., 2013), Brassicaceae present a wide scope for farmers to choose the most promising crops for effective biofumigation, based on their GSL concentrations and profiles, and biomass production (Sarwar et al., 2004). Farmers can act at multiple levels to improve the biofumigation potential (Borek et al., 1995b; Brown and Morra, 1997; Matthiessen and Kirkegaard, 2006; Gimsing and Kirkegaard, 2009):

- choice of Brassicaceae species;
- amount and profile of GSLs produced by the crop;
- rate of GSL conversion into ITCs;
- persistence of biocidal compounds in the soil.

#### 3.1 The choice of the biofumigant Brassicaceae species

Morris et al. (2020) emphasized that species in the genus *Eruca* and *Raphanus* had the highest biofumigation effectiveness. However, most studies about biofumigation concern brown, white or Ethiopian mustard and rape (rapeseed and forage rape) (Sarwar et al., 1998; Kirkegaard and Matthiessen, 2004; Reau et al., 2005; Clarkson et al., 2015). Brown mustard has high concentrations of sinigrin GSL, which hydrolyzes into 2-propenyl-ITCs. Considered as a highly toxic ITC (Motisi, 2009), it may explain brown mustard’s promising results for crop protection (see part 4). The utility of choosing forage rape cultivars as a biofumigant crop was demonstrated by Gardiner et al. (1999), who studied products of hydrolysis after incorporation of cv. Dwarf Essex. Plants were incorporated using a rototiller at the bud-to-early-flowering stage. The most abundant product of hydrolysis measured in the soil was the 2-phenylethyl-ITC (2-PE-ITC), obtained from the aromatic 2-phenylethyl-GSL (2-PE-GSL), the main GSL in the roots of both cultivars. Smith and Kirkegaard (2002) demonstrated the toxicity of this ITC to pests. Moreover, Larkin et al. (2010)
measured a lower VW incidence on potato after forage rape (cv. Dwarf Essex) incorporation as green manure compared to a continuous potato (non-rotation) control. However, farmers harvest rapeseed crops to produce oil, so destroying them at the flowering stage and/or incorporating them as a green manure seems unrealistic in the context of oilseed crop production. The advantage of rapeseed would rely more on an allelopathic effect during development, with continuous production of ITCs by its living roots (Rumberger and Marschner, 2003) or after harvest, during roots decomposition (Reau et al., 2005), both of which would provide a source of biocidal compounds (mainly ITCs) against soilborne fungi. Rumberger and Marschner (2003) demonstrated this phenomenon, observing that live roots of canola cv. Monty (low root GSL) and cv. Rainbow (high root GSL) released 2-PE-ITC continuously into the rhizosphere, which affected soil microbial communities (bacteria and eukaryotes) without accumulating in the soil. Despite the interest in rape for its allelopathic and, to a lesser extent, biofumigant effects, the trend since the 1960s has been to select and breed varieties with lower GSL concentrations. Thus, “double-low” varieties (i.e. low in erucic acid and GSLs) have been introduced (Boag et al., 1990). GSLs may be undesirable or even toxic to mammals (rats and roe deer) when GSL concentrations increase in rape tissues (Fenwick et al., 1983; Boag et al., 1990). It is possible, however, to breed canola with higher 2-PE-ITC concentration without affecting shoot or seed GSL concentrations (Potter et al., 2000). Since the GSL concentration necessary to have a toxic effect on soilborne pathogens remains unknown, low-GSL cultivars may still have biocidal effects (Couédel et al., 2019). For example, Kirkegaard et al. (2000) found no significant difference in the decrease in inoculum survival of the fungus G. graminis var. tritici between canola with high (cv. Tamara and cv. Karoo) and low (cv. Oscar and cv. Monty) root GSL concentrations, even though the pairs of varieties produced different 2-PE-ITC concentrations. In a pot experiment, Michel et al. (2008) showed that the number of live MS of V. dahliae in soils after the low GSL canola (cv. Talent) were approximately 60 MS/g of soil, compared to that in an unamended control (approximatively 90 MS/g of soil), but the differences were not significant. To our knowledge, no study has examined the potential of rapeseed to control soilborne diseases of sunflower in field (through biofumigation and/or allelopathic effects). Seassau et al. (2016) observed, in vitro, a significant reduction in the germination or the development of V. dahliae (strains from sunflower) exposed to rapeseed (cv. Mosa), selected for its low GSL concentration compared to the unamended control.

Although most studies have focused on Brassicaceae green manures for biofumigation, seed meals could be used as an alternative strategy (Mazzola et al., 2001) since they have more biological activity than green manures. GSLs are concentrated in the seeds and retained in the meal after crushing (Borek and Morra 2005). Thus, seed meals can be a source of GSLs (Brown and Morra, 1997; Morra and Borek, 2010) that stimulate soil microbial communities and suppress soilborne pathogens (Mazzola et al., 2017). This alternative, however, would be better suited for small areas of crops with high commercial value than large areas of sunflower because of the high cost of seed meals.

### 3.2 Increasing GSL concentrations and profiles

A positive relation exists between GSL concentrations in Brassicaceae tissues and their ability to suppress pests and diseases during biofumigation (Morris et al., 2020). The concentration and the profiles of GSLs (aliphatic, aromatic and indolyl) vary among Brassicaceae species (Kirkegaard and Sarwar, 1998; Bellostas et al., 2004; Bhandari et al., 2015) and between their shoots and roots (Kirkegaard and Sarwar, 1998; Van Dam et al., 2009; Bhandari et al., 2015). Roots usually have higher GSL concentrations than shoots, even though roots have lower biomass than shoots (Gimsing and Kirkegaard, 2006; Van Dam et al., 2009; Bhandari et al., 2015). This difference may be explained by a higher pathogen pressure belowground than aboveground (Van Dam et al., 2009; Bhandari et al., 2015). Biotic stress, such as herbivore damage and pathogen infection, increases GSL concentrations in Brassicaceae tissues (Van Dam et al., 2009). It is important that biotic stress does not decrease biomass production too much, however, because a positive relation exists between Brassicaceae biomass and its GSL concentrations (Kirkegaard and Sarwar, 1998). A large amount of biomass is thus required for effective biofumigation (Clarkson et al., 2015). Morris et al. (2020) predicted that less than 0.53 t dry matter of biomass/ha would result in ineffective biofumigation. Thus, it is important that cover crops be established well to maximize their biomass. While application of fertilizers (nitrogen and sulfur) increases GSL concentrations (Booth et al., 1991; Li et al., 2007), applying them to cover crops is neither recommended nor profitable.

The effectiveness of biofumigation also depends on the growth stage of the plant. During development of Brassicaceae, GSLs turn over or redistribute within its organs (Booth et al., 1991). GSL concentration peaks at the early flowering stage in the whole plant, then it starts to decrease in shoots and roots and increase in the seeds, whose GSL concentration peaks at maturity (Booth et al., 1991; Sarwar and Kirkegaard, 1998; Michel, 2008). Because seeds have much less biomass than shoots and roots, which decreases the amount of biomass available for biofumigation (Morris et al., 2020), the optimal timing for biofumigation is at the maximum value of biomass × GSL concentration (Matthiessen and Kirkegaard, 2006). The recommended stage at which to destroy crops is thus flowering (Michel, 2008), which also has the advantage of avoiding seed-set.

### 3.3 Improving the conversion of GSLs into ITCs

For effective biofumigation, maximizing the hydrolysis reaction that converts GSLs into ITCs is crucial to generate high ITC concentration in the soil (Borek et al., 1995b; Brown and Morra, 1997; Gimsing and Kirkegaard, 2009). Under laboratory conditions, Brassicaceae sometimes released only 19% of the total potential ITCs produced (Brown et al., 1991). This conversion efficiency reached 62.5–100% for Brassicaceae seed meals in sterile sand (Neubauer et al., 2015). In the field, the efficiency was estimated at 60% (Gimsing and Kirkegaard, 2006). The efficiency depends mainly on agronomic practices and soil and climate conditions. The stage of development of the Brassicaceae for biofumigation
must be considered, due to the decrease in myrosinase activity in mature tissues (Iversen and Baggerud, 1980). Brassicaceae tissues must be chopped finely to maximize contact between myrosinase and GSLs (Matthiessen and Kirkegaard, 2006). Thus, chopping at high speed and using hammers instead of blades is recommended (Matthiessen et al., 2004; Michel, 2008). Dilution with large amounts of water is then crucial to ensure tissue maceration and soil moisture to hydrolyze GSLs into ITCs and other products (Matthiessen et al., 2004; Michel, 2008; Gimsing and Kirkegaard, 2009). ITC concentration increased by up to 7–10-fold when 42 mm of water was added to a soil after biofumigation (Matthiessen et al., 2004). However, Gimsing and Kirkegaard (2006) observed no difference after irrigating with 18 mm over 3 hours after biofumigation. Warmer temperatures also increase hydrolysis (Matthiessen and Kirkegaard, 2006; Michel, 2008; Gimsing and Kirkegaard, 2009). Matthiessen and Shackleton (2005) observed that the biological activity of 2-PE-ITC was significantly lower at 5°C than at 10–20°C. Consequently, farmers should carefully choose the day on which to perform biofumigation. Days with temperatures above 10°C and with rain forecast to fall within a few days could improve the conversion of GSLs into ITCs, which would favor effective biofumigation. In the soil, a pH around neutral results in ITC production, while acid pH favors nitrile production (Brown and Morra, 1997).

3.4 Maximize persistence of ITCs in the soil

Un-hydrolyzed GSLs and the ITCs produced persist in soils from a few days to a few weeks (Brown and Morra, 1997), with the concentrations of GSL and ITC peaking 30 min after Brassicaceae incorporation (Gimsing and Kirkegaard, 2006) to 30 hours (Gardiner et al., 1999). Maximizing the persistence of ITCs is crucial to increase the duration of exposure of soilborne pathogens, which increases biofumigation effectiveness (Borek et al., 1995b; Brown and Morra, 1997).

The main pathway of ITC losses is volatility (Brown and Morra, 1997). To decrease these losses, solarization is used with vegetable crops to trap volatile ITCs (Morris et al., 2020). This technique consists of covering the soil with transparent polyethylene sheets (Katan, 1981), but it is impractical over larger areas, such as those of oilseed crops. Thus, rapid incorporation of the chopped Brassicaceae is highly recommended (Gimsing and Kirkegaard, 2006; Michel, 2008). Sorption on soil components is another pathway of ITC loss. For example, ITCs had lower toxicity in soils with high organic matter content (>1%) (Gimsing and Kirkegaard, 2009; Neubauer et al., 2014), which suggests that ITCs reacted with organic matter’s nucleophilic reagents. Soil pH and texture had little influence on ITC persistence in the soil (Brown and Morra, 1997), unlike heavy rainfall (70–90 mm), which could cause ITCs to leach, thus reducing their persistence (Laegdsmand et al., 2007).

Microbial degradation is a key factor that influences ITC losses in the soils (Brown and Morra, 1997). Using an autoclaved soil in biofumigation experiments increased the stability of ITCs (Rumberger and Marschner, 2003). Farmers have little influence on this factor, but soils that have never been fumigated may not experience increased biodegradation (Warton et al., 2003). Because fumigation is used less often with oilseed crops than with vegetable crops, mainly because of the high cost of protecting large areas, soils of oilseed crops may not experience this increased biodegradation.

4 Suppressive effects of GSL products on the soilborne diseases of sunflower targeted

Under optimal conditions that maximize GSL concentrations, their conversion into ITCs and persistence in the soil, the effectiveness of biofumigation will depend greatly on the target species, since pathogens vary greatly in their sensitivity to ITCs (Brown and Morra, 1997; Smith and Kirkegaard, 2002). To assess the sensitivity of sunflower pathogens to biofumigation, this review focuses on laboratory or field experiments performed to evaluate suppressive effects of synthetic GSLs/ITCs or Brassicaceae incorporation on V. dahliae, S. sclerotiorum and M. phaseolina (Tab. 1). Since studies of sunflower protection using biofumigation are rare (to our knowledge), most studies concerned other plant hosts of these pathogens, mainly vegetable.

4.1 Experiment using synthetic ITCs/GSLs

In vitro studies of synthetic ITCs or synthetic GSL + myrosinase tested the sensitivity of pathogens and screened the most effective GSL profiles (Tab. 1, part a). Neubauer et al. (2014) tested five ITCs, all of which were lethal to V. dahliae MS. Aromatic ITCs (benzyl-ITC and phenylethyl-ITC obtained by Glucotropaeolin and Gluconasturtitin hydrolysis) were much more toxic than aliphatic ITCs. Among the same profiles of ITCs (aromatic or aliphatic), ITCs with lower molecular weight tended to be more effective than ITCs with higher molecular weight. To suppress S. sclerotiorum, aromatic ITCs were also more effective than aliphatic ITCs. Overall, benzyl-ITC was the most effective ITC against S. sclerotiorum mycelial development and sclerotia (Kurt et al., 2011), while methyl-ITC and allyl-ITC were among the most effective ITCs at reducing mycelial growth (Kurt et al., 2011; Ojaghian et al., 2012). For M. phaseolina, mycelial development was also reduced by allyl-ITC (Mazzola et al., 2017).

4.2 Experiments using Brassicaceae (in vitro or in pots)

To screen the potentially most effective varieties and/or species of Brassicaceae, and to assess effects of hydrolysis products of GSLs to manage soilborne fungi, experiments were performed using Brassicaceae biomass (e.g. crushed, ground, macerated) instead of synthetic compounds (Tab. 1, part b). To control V. dahliae, S. sclerotiorum and M. phaseolina, mustard varieties, especially Brassica juncea (brown/Indian mustard), were used mainly as a source of GSLs and ITCs in biofumigation studies. Mustard species often showed significant suppression of V. dahliae (Olivier et al., 1999; Neubauer et al., 2015; Seassau et al., 2016), S. sclerotiorum (Ojaghian et al., 2012; Rahimi et al., 2014; Warmington and Clarkson, 2016) and M. phaseolina (Mazzola et al., 2017). Some cultivars of turnip rape (Brassica rapa), forage radish
Table 1. Summary of the suppressive effects of GSLs/ITCs or Brassicaceae against three soilborne fungi of sunflower: Verticillium dahliae, Sclerotinia sclerotiorum and Macrophomina phaseolina using synthetic GSLs-/-ITCs in vitro or in pot (a), Brassicaceae in vitro or in pot (b), Brassicaceae in greenhouse and in the field (c), and at the rotation scale (d).

Target pathogen/plant: fungus studied and plant from which it was isolated (when mentioned); methods: GSLs/ITCs used or destruction/incorporation mechanisms of the Brassicaceae; Brassica species (cv./var.): the Brassicaceae and the cultivar or variety (when mentioned) used for biofumigation; crop to protect: the host plant; GSL/ITC measured: compounds in the Macrophomina phaseolina; MS: microsclerotia; NA: not available; NS: not significant; S.s: Sclerotinia sclerotiorum; UC: unamended/untreated control; V.d: Verticillium dahlia; VW: Verticillium wilt.

(a) In vitro or in pot experiments using synthetic ITCs/GSLs

| Target pathogen/plant | Methods | Main results | Reference |
|-----------------------|---------|--------------|-----------|
| V.dahliae/strawberry  | Soil infested with MS exposed to 3 aliphatic (methyl ITC, 2-propenyl ITC, 4-methylsulfinyl-3-butenyl-ITC) and 2 aromatics (benzyl-ITC, 2-PE ITC) versus UC | All ITCs suppressed MS | Neubauer et al. (2014) |
|                       |         | Aromatic ITC were more toxic than aliphatic ITC |          |
| V.dahliae/strawberry  | 22 natural soil and sterile quartz sand infested with MS exposed to 150 nmol/g of 2-propenyl-ITC versus UC | In sterilized soil: 100% of MS suppressed | Neubauer et al. (2014) |
| S. sclerotiorum       | S.s and other pathogens exposed to different concentrations of pure-ITC (methyl, allyl and butyl-ITC) versus UC | S.s had among the lowest tolerance to 2-PE-ITC than other pathogens | Smith and Kirkegaard (2002) |
| S. sclerotiorum       | Mycelium exposed to different concentrations of pure ITC (methyl, allyl and butyl-ITC) versus UC | Reduction of the mycelial growth | Ojaghian et al. (2012) |
|                       |         | 100% of inhibition at the highest concentration of methyl and allyl ITCs |          |
| S. sclerotiorum       | S.s exposed to different concentrations of pure aliphatic ITC (methyl, allyl, butyl and ethyl) and aromatic (ethyl, phenyl, benzyl and 2-PE) versus UC | Methyl and benzyl-ITC reduced mycelial growth | Kurt et al. (2011) |
|                       |         | Benzyl-ITC reduced sclerotia viability |          |
|                       |         | All ITCs (except low concentration of phenyl and 2-PE) reduced the production of apothecial |          |
| S. sclerotiorum       | Infested soils transplanted with pepper seedlings exposed to synthetic ITCs (Kurt et al., 2011*) | Aliphyl and 2-PE ITCs reduced the incidence of S.s on pepper by 76.7% and 70% at low concentration, respectively | Kurt et al. (2011) |
| S. sclerotiorum       | Sclerotia of S.c or other pathogens exposed to different concentrations of synthetic GSLs (2-propenyl, 2-hydro-3-butanyl, benzyl, and methylsulfinylalkyl) | GSLs inhibited S.s growth | Manici et al. (1997) |
|                       |         | Methylsulfinylalkyl was the most effective |          |

(b) In vitro and pot experiment studies using Brassicaceae

| Target pathogen | Methods | Main results | Reference |
|-----------------|---------|--------------|-----------|
| V.dahliae/sunflower | Mycelium or MS exposed to shoots and roots of Br sampled at mid-flowering and grinded separately versus UC | Br reduced mycelial growth (B. juncea, the most effective) and MS germination (B. rapa, the most effective) | Seassau et al. (2016) |
| V.dahliae/eggplant and cotton | Mycelium exposed to powdered tissues of Br | NA | Fan et al. (2008) |
| V.dahliae/NA | Mycelium exposed to macerated leaf and stem of Br sampled at flowering versus UC | 1 g of B. oleracea reduced mycelial growth by 68.7% | Olivier et al. (1999) |
| V.dahliae/strawberry | 19 cv. of B. juncea, R. sativus and S. alba | Main GSLs measured in shoots of B. juncea: | Neubauer et al. (2014) |
Sterile quartz sand infested with MS amended with freeze-dried ground Br sampled at mid-flowering or non-Br species versus UC

### V. dahliae/strawberry
- MS exposed to seed meals of Br or autoclaved seed meals versus UC
  - 16 cv. of S. alba, B. carinata, B. rapa.
  - Main ITC measured in seeds: S. alba: 4-hydroxybenzyl, B. rapa: 3-butenyl, 4-pentenyl, 2-PE

| Target pathogen | Methods | Crop to protect (cv./var.) | GSL/ITC measured | Main results | Reference |
|-----------------|---------|--------------------------|-----------------|-------------|-----------|
| V. dahliae | 1 field/2 years: Br chopped at early flowering, incorporated and the soil was compacted versus bare soil (UC) | B. juncea (Etamine), R. sativus | Measured in shoots and roots: overall during the 2 years: B. juncea: 2-propenyl, 4-methylthio-3-butenyl, R. sativus: 4-hydroxybenzyl, 1-methoxy-3-indolymethyl, 2-hydroxy-3-butenyl and 1-methoxy-3-indolymethyl | Br reduced VW severity both years | Galaup et al. (pers. comm.) |
| V. dahliae | 1 greenhouse/1 year: soils infested with MS sampled from fields exposed to biofumigation (Pinkerton et al., 2000*) versus sterile soils (UC) | B. napus (Dwarf Essex), Eggplants (Imperial Black Beauty) | NA | Br reduced eggplants biomass compared to UC | Pinkerton et al. (2000) |

*ISCI-99, ISCI-20 = high GSL; – NA Living MS were reduced by 66% with ISCI-99, Michel et al. (2008) 55% with ISCI-20. NS effect of Talent

(c) Field and greenhouse studies

| Reference |
|-----------|
| Sharma et al., 1995 |
| Michel et al. (2008) |
| Rahimi (2014) |
| Ojaghian et al. (2012) |
| Clarkson (2016) |
| Ojaghian et al. (2012) |
| Clarkson (2016) |
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| Sharma et al., 1995 |
| Michel et al. (2008) |
| Rahimi (2014) |
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| Sharma et al., 1995 |
| Michel et al. (2008) |
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| Sharma et al., 1995 |
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| Clarkson (2016) |
| Ojaghian et al. (2012) |
| Sharma et al., 1995 |
| Michel et al. (2008) |
| Rahimi (2014) |
| Ojaghian et al. (2012) |
| Clarkson (2016) |
| Ojaghian et al. (2012) |
| Clarkson (2016) |
| Ojaghian et al. (2012) |
| V. dahliae | 1 field/2 years: Br cut at ground level, chopped, spread and rotovated below 25 cm depth, irrigated (field capacity) compared to non-Br species and bare soil, all treatments were solarized or non-solarized (a.o.t) | B. napus (Dwarf Essex) | Norway Maple trees | NA | Br combined with solarization reduce VW severity compared to Br sole crop |
| V. dahliae | 1 field/2 years: broccoli residue chopped, incorporated, and disked versus UC (a.o.t) | B. oleracea (italica) | Cauliflower (White Rock) | NA | MS densities decreased after Br compared to initial densities (50 to 75% reduction) VW severity was lower after Br compared to UC The plant height, the number of harvestable heads and the weight of total harvest increased compared to UC Hartz et al. (2005) |
| V. dahliae | 6 field trials/2 years: Br flail-mowed, incorporated both years and rolled; sprinkler-irrigated the second year compared to non-Br species and bare soil (UC) (a.o.t) | B. napus (Humus), B. juncea (Pacifi Gold), S. alba (Ida Gold, ISCI 20), Caliente Tomato (Halley) | For above ground biomass during one year: B. juncea: 2-propenyl, S. alba: benzyl 4-hydroxybenzyl | NA | NS suppressive effect on V.d in the soil Overall, no effect on tomato fruit productivity in the six field trials compared to bare soil Garibaldi et al. (2009) |
| V. dahliae | 2 fields/1 year: fresh cauliflower residues disk/incorporated twice below 25–30 cm depth and irrigated versus UC (a.o.t) | B. oleracea (Marine) | Artichoke (Blanca de Tudela) | NA | Partial results of biofumigation Biofumigation combined with grafting was more efficient MS densities remained low compared to UC (NS) Inconsistent effects of Br residue on disease incidence, severity, and yield Ochiai et al. (2007) |
| V. dahliae | 2 fields/2 years: Br compared to non-Br species and UC | B. oleracea (Excelsior) | Potato (Russet Burbank) | NA | NS effect on root infection and yield compared with UC Michel et al. (2008) |
| V. dahliae | 1 field/1 year: Br incorporated at flowering with a rototiller (twice) compared to non-Br species and UC | B. juncea (ISCI-20) | Strawberry (Elanta) | NA | Reduction of MS by 19% compared with UC Michel et al. (2008) |
| V. dahliae | 2 farms/1 year: Br finely mulched at flowering and incorporated with a rototiller versus UC (a.o.t) | B. juncea (ISCI-20) | Sweet pepper (Red beetthorn, Somborka) | NA | Overall, reduction of MS in both farms (48% to 74%) Michel et al. (2008) |
| V. dahliae | 1 Greenhouse/1 year: dried Br sampled at full flowering, incorporated below 20 cm depth, irrigated (35 mm), compared to non-Br and UC (a.o.t) | B. juncea (ISCI-99 and Etamine) | Tomato (Admiro) Methylsulfinylalkyl, benzyl, 2-propenyl, and 2-hydro-3-butenyl | NA | Short-term: NS effect on MS reduction Long-term: MS reduced by 80% Michel (2014) |
| V. dahliae | 1 greenhouse/1 year: biofence expanded on soil surface (250 g/m²), incorporated below 20 cm depth, irrigation (20 mm water + biofence flowable) 6 times, compared to non-Br and UC (a.o.t) | Biofence | Tomato (Admiro) | NA | NS effect of biofence and biofence FL Michel (2014) |
| Target pathogen | Methods | Brassica species (cv./var.) | Crop to protect | GSL/ITC measured | Main results | Reference |
|-----------------|---------|-----------------------------|-----------------|------------------|-------------|----------|
| *V. dahliae*  | 10 years of 2-year rotation with potato–Br (1 × Br–1 × P) Br was either incorporated as green manure (Dwarf Essex) or harvested without incorporation (canola) compared to non-Br Crops and continuous potato (1 × P–1 × P) | *B. napus* (canola), *B. napus* (Dwarf Essex) | Potato (Russet Burbank) | NA | Overall, rapeseed reduced VW and canola had inconsistent effects Higher tuber yields after Canola (+6.8%) compared to continuous potato, and inconsistent effects of rapeseed | *Larkin* et al. (2010) |
|                 | 7 years with potato–Br rotation (3 × Br–2 × P–1 × Br–1 × P) Br was incorporated into the soil by disking or rotovating compared to non-Br species and bare soil | *B. napus* (Dwarf Essex and Bridger) | Potato (Russet Burbank) | NA | Inconsistent effects of Br on V. d. population in the soil Reduction in VW NS differences of the yield compared to bare soil (see *Davis* et al., 1996) | *Davis* et al. (2010) |
| *V. dahliae*  | 5 years with potato–Br rotation (3 × Br–2 × P) Br was incorporated into the soil by disking or rotovating compared to non-Br species and bare soil (UC) | *B. napus* (Dwarf Essex and Bridger) | Potato (Russet Burbank) | NA | Overall, NS effects on V. d. and yield Reduction in VW | *Davis* et al. (1996) |
| *V. dahliae*  | 2 fields with strawberry–Br rotation compared to non-Br rotation (a.o.t) Br was harvested and residues flaked shredded, air dried on the soil surface for 48 h and incorporated into the soil below 15-20 cm depth with a rototiller | *B. oleracea* (Marathon), *B. oleracea* (Oliver) | Strawberry (Selva) | NA | Reduction of MS density (up to 83%), and VW severity in the rotation with Br Increase of strawberry growth | *Subbarao* et al. (2007) |
(Raphanus sativus), Kohlrabi (Brassica oleracea cv. caulorapa) and B. napus were among the most effective species, but were more variable than B. juncea. In these studies, anti-fungal effects of ITCs and other products of GSL hydrolysis were assessed on mycelial growth and/or the long-term survival structures of the pathogens. Effectiveness of Brassicaceae varied among the forms of the pathogens. Seassau et al. (2016) showed that mycelial growth of V. dahliae isolated from sunflower was suppressed mainly by B. juncea, while MS germination was suppressed mainly by B. rapa. Since biofumigation occurs a few months before sunflower sowing, its suppressive effects would affect long-term survival structures of pathogens because of the low persistence of GSLs and ITCs.

4.3 Field approaches to biofumigation

In vitro and pot studies have shown promising biocidal effects on V. dahliae, S. sclerotiorum and M. phaseolina. In field conditions, however, results varied more among studies (Tab. 1, part c), due to the many factors that influence the effectiveness of biofumigation. The only study of sunflower crop protection reported a significant reduction in VW incidence and severity following three Brassicaceae cover crops and biofumigation compared to that with a bare soil (Galaup et al., pers. comm.). In both years of its field experiment, R. sativus was the Brassicaceae that reduced VW incidence the most, followed by B. rapa and B. juncea. The ability of biofumigation with a given species to reduce VW varied between years due to differences in the biomass incorporated into the soil each year. The largest reduction in VW was associated with the largest biomass produced. In strawberry (Fragaria × ananassa) field experiments, Michel et al. (2008) observed a significant reduction of MS in soils after biofumigation with B. juncea. Conversely, Hartz et al. (2005) considered B. juncea an ineffective biofumigant: it did not decrease the density of V. dahliae in the soil and had no effect on tomato productivity compared to a fallow control. Michel (2014) observed no significant effects of B. juncea on V. dahliae density in the soil, in the short-term, but a reduction of 80% was observed a few months after biofumigation. Because of the low persistence of ITCs, they could not have caused this suppressive effect. Instead, the reduction in MS may have been caused by stimulation of specific groups of microbial communities during mustard decomposition and organic matter addition, as supported by other studies (Mazzola et al., 2007; Ochiai et al., 2008; Mazzola et al., 2017). Thus, organic inputs could improve soil biological status by increasing both the diversity and size of populations of beneficial species through physico-chemical changes (Ochiai et al., 2008; Davis et al., 2010; Omirou et al., 2011).

5 Non-GSL-related suppressive effects on pathogens, and the multifunctionality of Brassicaceae

Pathogen suppression by green manure addition has been attributed to indirect effects of higher microbial competition rather than a direct effect on pathogen inoculum (Davis et al., 1996; Davis et al., 2010). This involvement of microbial communities was supported by long-term studies at the rotation scale when Brassicaceae and non-Brassicaceae species were incorporated (Tab. 1, part d). Davis et al. (2010) observed that cover crops reduced VW on potatoes more than fallow did. Sudangrass (Sorghum vulgare var. sudanense cv. Monarch) was a more effective cover crop than B. napus cv. Dwarf Essex and cv. Bridger. The authors also suggested that another beneficial effect of sudangrass was the potential control of root knot nematodes. Larkin et al. (2010) also observed a significant reduction in VW on potato after a canola cover crop and to a lesser extent after a rapeseed cover crop. Davis et al. (2010) and Larkin et al. (2010) concluded that, beside the direct toxic effects of products of GSL hydrolysis, VW may have been suppressed due to a change in microbial communities that increased microbial competition after cover crop incorporation. The reduction in VW may be explained by the increase in Fusarium equiseti in the soil observed by Davis et al. (2010), which suggests a potential antagonism between the two fungi.

Increasingly, biofumigation benefits are considered along with other green manure benefits, such as addition of organic matter to soils (Kirkegaard and Matthiessen, 2004). This non-GSL-related pathway of suppression may be involved in reducing pathogens and disease severity in the studies that used low-GSL cultivars observed by Kirkegaard et al. (2000) and Michel et al. (2008). The potential key role of microbial communities in suppressing pathogens emphasizes the need to assess potential disservices of products of GSL hydrolysis on these beneficial communities. To date, these disservices and their influence have been rarely studied, and the review of Couëdel et al. (2019) reported inconsistent impacts of Brassicaceae on non-target species. No effect of Brassicaceae incorporation was observed on nitrifying bacteria in field studies (Omirou et al., 2011). Conversely, Bending and Lincoln (2000) observed that application of ITCs disrupted microbial communities, reducing the growth of nitrifying bacteria in clay-loam soils. One mechanism to avoid these potential disservices could be cover crop mixtures (Couëdel et al., 2019), which would provide more nutrients, and thus increase microbial diversity and activity, while preserving GSL production. Couëdel et al. (2018c) showed that, compared to Brassicaceae sole crops, 50/50 bi-species mixtures of Brassicaceae and Fabaceae reduced GSL production/ha by an average of only 19%. Mixtures would maintain most of the potential of Brassicaceae to suppress pathogens and could mutualize other benefits provided by either Brassicaceae or Fabaceae. Couëdel et al. (2018a) showed that this mixture captured the same amount of nitrate as Brassicaceae alone and had a larger nitrogen-green manure effect. This mixture also provided the same sulphate-catch crop and sulfur-green manure effects as Brassicaceae sole crops (Couëdel et al., 2018b). This result could be due to increased biomass production and abiotic-resource-use efficiency (Jensen, 1996). Besides protecting against pathogens and nutrient enrichment, mixtures provide a bundle of ecosystem services. They reduce soil disturbance and erosion, maximize water-use efficiency, increase long-term carbon sequestration and support pollinators and other beneficial insects (Therond et al., 2017; Justes and Richard, 2017; Chapagain et al., 2020). Thus, mixtures of Brassicaceae and
Nevertheless, biofumigation could still help farmers reach the microscopic and heterogeneous pathogens such as implement for soilborne fungi of sunflowers. The potential increase in some antagonist fungi (e.g., Fusarium spp., as reported by Davis et al. (2010)) after incorporating cover crops represents another ecological mechanism to suppress soilborne pathogens (Médiène et al., 2011), which could be enhanced by including Fabaceae in mixtures, because it could diversify the tissues incorporated (Couëdel et al., 2019).

Some principles of IPM, however, could be difficult to implement for soilborne fungi of sunflower. Monitoring microscopic and heterogeneous pathogens such as V. dahliae, as recommended by P2, would be too expensive. Thus, it is challenging to determine thresholds for intervention (P3). Nevertheless, biofumigation could still help farmers reach the underlying objectives of IPM: minimize use of broad-spectrum biocides, environmental contamination, disruption of beneficial communities and development of resistance (Matthiessen and Kirkegaard, 2006; Barzman et al., 2015).

6 Conclusion

Soilborne diseases threaten sunflower productivity. VW, sclerotinia head and stalk rots, and charcoal rot have been expanding worldwide in the past several years or could be in the future. They are challenging to manage because of their ability to survive in the soil and the lack of sustainable effective control methods. Thus, biofumigation could be an interesting agroecological alternative for protecting sunflower, especially as a part of IPM. This review showed that multiple factors must be considered for effective biofumigation. For sunflower production, a biofumigant crop can be grown during the fallow period just before sunflower. Ideally, the Brassicaceae should be chopped at early flowering, temperatures of ca. 10°C minimum and just before a rainy period, since high temperatures and soil water content increase the hydrolysis of GSLs into ITCs. Brassicaceae should be incorporated quickly into the soil after pulverization to reduce volatile losses.

For effective suppression by biofumigation, Brassicaceae with high GSL concentration are recommended. The types of GSLs/ITCs produced by Brassicaceae are also important to consider, since the biocidal effect of GSLs depend on the target pathogen. According to the ITCs tested and the Brassicaceae incorporated, long-term survival structures and mycelia of V. dahliae, S. sclerotiorum and M. phaseolina were susceptible most of the time.

While aromatic ITCs and mustards seem to be the most effective, an increasing number of studies emphasize non-GSL-related effects of Brassicaceae and non-Brassicaceae cover crops. Nutrient enrichment after incorporating cover crops has strong effects on microbial communities that may stimulate antagonist species of pathogens in the soil. These effects are supported by studies that show negative correlations between microbial activity/diversity and the incidence of symptoms. The potential key role of microbial communities in the suppressive effect of Brassicaceae incorporation could explain the positive results obtained with Brassicaceae with low GSL concentration, such as canola. This highlights the need to assess effects of Brassicaceae incorporation on beneficial communities precisely, since the results to date are scarce and inconsistent. Nonetheless, cover crop mixtures that include Fabaceae could be an interesting mechanism to avoid potential disservices to beneficial communities, while maintaining suppressive effects on target pathogens. Further research, including field experiments, are needed to confirm the benefits of these mixtures.

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