Chapter Two - Crucifer-legume cover crop mixtures for biocontrol: Toward a new multi-service paradigm

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Crucifer – legume cover crop mixtures for biocontrol: towards a new multi-service paradigm.

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Abstract

Multi service cover crops grown during the fallow period between two main cash crops are a tool to support sustainable crop production. Crucifer - legume mixtures may provide improved multi ecosystem services compared to sole cover crops, but trade-offs between the known crucifer biocontrol potential and N cycling benefits of legumes are uncertain. We review suppressive effects of crucifers as sole crops and in mixtures with legumes for a wide range of pathogenic and beneficial organisms to compare the services and potential disservices of the strategies. We conclude that biocontrol services of crucifer sole crops could be largely maintained in crucifer-legume mixtures while improving nutrient services, and reducing potential disservices. The lack of comprehensive multi-disciplinary field studies that investigate the multi-service paradigm limit our current understanding of the trade-offs between services, but reveal fruitful research opportunities. We emphasise the need to refocus cover crop biocontrol research from a largely "pesticide" paradigm targeting maximum production of bioactive compounds by sole crucifer cover crops, to a multi-service paradigm in which selected crucifer-legume mixtures may offer promise in the quest for the sustainable intensification of agriculture.

Key words: Multi Service Cover Crops, Biofumigation, Biocontrol, Intercropping, Brassicaceae, Fabaceae, Glucosinolates, Disservices, Trade-off management, System approach.

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Introduction

Improving plant diversity in cropping systems in both space and time can enhance ecosystem services while mitigating the potential disservices generated by anthropogenic inputs (Duru et al., 2015; Gaba et al., 2015). Usually grown between two cash crops in an annual rotation, cover crops can increase diversity and provide a number of ecosystem-services. The notion of cover crops has evolved historically since the last century where it was largely developed in US agriculture (e.g. Meisinger et al., 1991) for erosion control or green manuring, but now encompasses other benefits such as biocontrol and catch crops (Justes et al., 2017). Recently the new paradigm of multi-service cover crop (MSCC) has been proposed to capture these multiple benefits using principles of agroecology (Justes and Richard, 2017). The MSCC are specifically grown in the fallow period between two main cash crops, are not harvested and their biomass remains on or in the soil. They are neither forage crops nor harvested for biogas. The potential provision of multi-services depends on the species or mix of species chosen, the management of the cover crop, the pedo-climatic conditions and the cash crop sequence involved. The potential services include i) nitrogen management, i.e. nitrate catch crop (e.g. Justes et al., 1999; Constantin et al., 2011; Thomsen & Hansen, 2014; Couëdel et al., 2018) and green manuring (e.g. Thorup-Kristensen et al. 2003; Tonito et al., 2006; Tribouillois et al., 2016), ii) nutrient cycling in general (Thorup-Kristensen et al., 2003) including for specific anions such as sulfate (Couëdel et al., 2018); iii) soil protection and improvement of soil physical properties (e.g. Blanco-Canqui et al., 2015; Justes et al., 2012), iv) organic matter and carbon storage in the soil (Justes et al., 2012; Constantin et al., 2011), v) reduced direct greenhouse gas emissions to mitigate climate change (Poeplau and Don, 2015; Tribouillois et al., 2018), and vi) suppression of weeds (e.g. Teasdale, 1996) and pathogens (e.g. Farooq et al., 2011; Reddy, 2017). In some cases, the MSCC can also contribute to ecological services such as plant pollination, maintenance of wild fauna (birds, small mammals, insects, etc.) and contribute to landscape aesthetics (Justes et al., 2017).

No cover crop or cover crop mixture will provide all of these services, and some may generate disservices such as pre-emptive competition for water and nutrients with subsequent cash crops (Thorup-Kristensen and Kirkegaard 2016). Consideration of the potential trade-offs is essential in

choosing species or species mixtures as many botanical families can be used (cruciferous, grass, legume, other families). Clearly avoiding species that may act as hosts to important diseases and pests of the main cash crop is advisable but other less obvious interactions between species in the cover crop, and between cover crop and main crop can occur. Indeed several recent studies highlight the important genotype-environment-management interactions that underpin the success of cover crop choices (Lemessa and Wakjira, 2015; Schipanski et al., 2014; Snapp et al., 2005, Farooq et al 2011). Here we focus on the potential contribution of MSCC for biocontrol in future cropping systems to reduce the use of pesticides in the sustainable intensification of agriculture.

Among cover crop species commonly used worldwide (Table 1), Brassicaceae or crucifer cover crops are especially interesting for pathogen and weed suppression due to the release of several potentially biocidal hydrolysis products such as isothiocyanates (ITCs) from the secondary metabolites known as glucosinolates (GSLs) present in their tissues (Brown and Morra, 1997; Van Dam et al., 2009). Crucifer cover-crops can generate GSL-related biocidal effects both during the growing period when hydrolysis products such as ITCs are released in the rhizosphere around the growing roots (McCully et al., 2008; Rumberger and Marschner, 2004), or when tissue disruption occurs following cover crop termination and incorporation (Matthiessen and Kirkegaard, 2006) (Figure 1). Pest, pathogen and weed suppression by ITCs via these two processes has previously been termed "biofumigation" (Kirkegaard et al., 1993), and has generated interest from both an agronomic and an ecological perspective in regulating soil biological communities (Bressan et al., 2013), including fungi (Motisi et al., 2009), bacteria (Arthy et al., 2002), nematodes (Fourie et al., 2016), and weeds (Bangarwa and Norsworthy, 2016; Jabran et al., 2015). At the end of the 20th century, biofumigation was seen as a potential option to assist in the replacement of banned chemical fumigants widely used in horticulture including methyl bromide (MeBr), and it was thought to be one of the most promising non-chemical control options at the time (Porter et al., 1999). However the levels of pathogen suppression achieved under field conditions using biofumigant cover crops alone is usually less than that achieved with fumigant chemicals, as the level of ITCs found in soil with biofumigants is much lower than that achieved with chemical fumigants such as methyl-isothiocyanate (Gimsing and Kirkegaard, 2009).

The levels achieved and their effectiveness are also influenced by the sensitivity of the pathogen of interest, but also the soil type, temperature and organic matter levels influence the activity of ITCs in soil (Gimsing and Kirkegaard, 2009). Approaches to link individual ITC release to the suppression of specific pests and pathogens have been explored in numerous controlled laboratory experiments (Brown and Morra, 1997), but less so under field conditions where many other effects of cover crops aside from ITC-related suppression are operating (Matthiessen and Kirkegaard 2006). As for the chemical fumigants such as MeBr, GSL-related biocides can also generate potentially negative effects on beneficial microbe and insect communities (Omirou et al., 2011), but these disservices and their relevance have had less focus to date within the research literature. Crucifer cover crops may also have other undesirable characteristics as cover crops such as hosting pathogens (e.g. Pythium species) or acting as non-hosts to beneficial organisms such as mycorrhizae in some systems (Ahuja et al., 2010).

[Insert Figure 1 here]. Figure 1. Hydrolysis and main degradation products of glucosinolates including the biocidal isothiocyanates.

[Insert Figure 2 here] Figure 2. Crucifer-legume mixtures used in diverse production systems. (A) Turnip rape - Egyptian clover cover crop mixture in France (© Antoine Couëdel), (B) Pea intercropped with canola in Australia (© John Kirkegaard), (C) service legumes (common vetch and lentil) intercropped with oilseed rape in France (© Terre-net Media), (D) Broccoli vegetable production intercropped with crimson clover in the US (© Mark Schonbeck).

One possible solution to improve pest and diseases suppression while avoiding potential disservices of sole-species cover crops may be to use species mixtures to provide better suppression of certain pests, diseases and weeds compared to sole crops (Trenbath, 1993; Boudreau, 2013). In particular, crucifer-legume substitutive bi-specific mixtures (i.e. 50% of each species in a mixture) have been found to outperform crucifer sole crops in terms of multiservice benefits as harvested cash crops (Fletcher et al., 2016), forage crops (Jeromela et al., 2017) or nitrate catch crops and green manures (Couëdel et al., 2018c) due to an improved biomass production (see examples of crucifer legume mixtures in Figure 2). Legumes can provide nitrogen input through N fixation (Thorup-Kristensen et al., 2003). Crucifer-legume mixtures can also achieve better resource use efficiency, due to the niche complementarity in using abiotic resources such as light, water and nutrients (Jensen, 1996) and have also been shown to

increase the amount of N mineralized for the next cash compared to crucifer sole crops (Tribouillois et al., 2016a).

Despite considerable interest in cover crop mixtures to support the concept of MSCC, few studies have investigated the impact of crucifer-legume mixtures on the suppression of pathogens and weeds. Understanding species choice to successfully combine the recognised nutrient cycling benefits of legumes with the pest suppressive potential of crucifers will be crucial to design appropriate mixtures that can achieve useful pest suppression without generating related disservices within the agroecosystem. Diversity for its own sake in agricultural systems has been called into question (Ford Denison and McGuire, 2015), but where multi-services can be demonstrated and managed in an agronomic sense, the concept can assist sustainable intensification. Our purpose was to investigate the potential to move from a largely "pesticide" paradigm that targets maximum production of bioactive compounds by sole crucifer cover crops, to a more multi-service paradigm where cover crop mixtures may assist sustainable intensification of agriculture. We firstly update the knowledge of the biocontrol potential of crucifer species used as cover crops, both in terms of the services and potential disservices. We update and build upon the previous reviews of Matthiessen and Kirkegaard (2006); Kirkegaard et al, (2009) and Motisi et al., (2010) and focus on the mechanisms behind pathogen and weed suppression by crucifer cover crops. We then consider how crucifer-legume bispecific mixtures could enhance pathogen and weed suppression and minimise disservices compared to crucifer sole crops by considering the main services and disservices reported for microbial, weed, nematode and macro-faunal suppression. We conclude by considering research approaches to fill the considerable knowledge gaps in this area, and strategies to improve cover crop species selection and breeding toward a multiservice approach.

[Insert Table 1 here] Table 1. Common names, family and species for the crops and cover crops mentioned in this review

[Insert Table 2 here] Table 2. Latin names and abbreviations used for microbes mentioned in this review

[Insert Table 3 here] Table 3. Latin names and abbreviations used for nematodes mentioned in this review

[Insert Table 4 here] Table 4. Latin names and abbreviations used for insects mentioned in this review

[Insert Table 5 here] Table 5 Most common glucosinolates found in crucifer cover crops. Examples of cover crops are not exhaustive and are derived from Couëdel et al., (2018b). *Side chain corresponds to the "R group" mentioned in Figure 2.

1. Mechanisms of pathogen and weed suppression by crucifer sole crops and mixtures

The impact of crucifer cover crops on pathogens, beneficial organisms and weeds can arise not only from allelochemical effects, but from numerous other processes such as non-hosting effects, plant cover effects, organic matter addition and soil structural effects (Figure 3). In this first section we review the conceptual interest of cover crop mixtures as tools to improve suppression of pathogens and weeds while minimising potential disservices on beneficial organisms. In each section we focus first on crucifer sole crop effects, and then consider the likely changes associated with the inclusion of a legume with the crucifer in a mixture. Figure 3 provides a schematic summary of the concepts discussed in this section. All latin names and abbreviations of crops, microbes, nematodes and insects mentioned in this review are displayed respectively in Table 2, 3 and 4.

1.1 Allelochemical production

There are about 132 different GSLs commonly found in crucifer's spp. that vary in their structure depending on the character of the organic side chain (aliphatic, aromatic or indole) (Table 5). Present in plant vacuoles, GSLs generate toxic hydrolysis products when they react with the enzyme myrosinase through tissues damage due to biofumigation or pathogen attack (Figure 2) (Andréasson and Jørgensen, 2003; Kissen et al., 2009). Biocidal molecules produced are isothiocyanates (ITCs), thiocyanates and nitriles (Figure 2) (Brown and Morra, 1997). Aliphatic GSLs produce the most volatile ITCs due to a short organic side chain while aromatic ITCs are in general less volatile but have a higher contact toxicity as they are more lipophilic to penetrate live membranes (Matthiessen and Kirkegaard, 2006). Indole GSLs do not produce ITCs and are generally considered less toxic than other GSL types (Fahey et al., 2001). GSL types and concentrations vary among crucifer species, and between root and shoot tissues of the same species (Bellostas et al., 2007; Couëdel et al., 2018b; Kirkegaard and Sarwar, 1998). Beyond GSL production, crucifers also produce other compounds that

may be biologically active such as S-containing methanethiol and dimethyl sulfide (Bending and Lincoln, 1999; Gamliel and Stapleton, 1993) or fatty acid and phenolic molecules (Brown and Morra, 1997). By reacting with GSL by-products such as H_2S, these latter's molecules could improve and prolong biocidal effects (Brown and Morra, 1997). The biofumigant potential of various crucifer cover crops has been previously reviewed (Matthiessen and Kirkegaard 2006; Motisi et al., 2010) in sole crops but not when used in mixtures.

Bispecific crucifer-legume cover crop mixtures will firstly change the diversity of allelochemicals produced (Figure 3). Indeed legumes themselves can produce a wide diversity of allelochemicals, such as phenolic acids or terpenoides, that differ among species (Mondal et al., 2015; Wink, 2013). Secondly, plant-plant interactions in mixtures can influence allelochemical concentrations and potentially decrease their biocidal effects. In mixtures, crucifers usually compete strongly with legumes for water, nutrients and light due to their rapid root and shoot growth (Kristensen and Thorup-Kristensen, 2004). Consequently on an individual plant basis, crucifers have been shown to produce higher biomass (Wortman et al., 2012), to acquire more N (Tribouillois et al., 2016; Wendling et al., 2017) and more S (Couëdel et al., 2018a; Génard et al., 2017) when grown with a legume in a mixture than in a sole crop. As N and S are both essential components of GSLs, Couëdel et al. (2018b) showed that crucifers produced more GSL per plant in mixtures compared to sole crops, but retained the same GSL types and concentration on a dry weight basis. This led to an equivalent level of protection from pests for the crucifer component of the cover crop in the mixture as for the sole crop. In contrast, for the legume component, the high competition from the crucifer could potentially reduce the allelochemical concentration and may lead to lower pest protection. These concerns are important to take into account because pests and diseases of the legume component could lead to lower biomass and hence reduce the ecosystem services associated with nitrogen and carbon cycles. It is possible that allelochemicals released by crucifers in the mixture may also protect the legume from pests or diseases to maintain the multi-services provided. On an area basis, as crucifer density is halved in the bispecific crucifer-legume mixtures, a 50% decrease in crucifer allelochemical production could be predicted (Figure 3). However Couëdel et al., (2018b) showed that for a wide range of crucifer and legume

species in mixtures, the GSL production per area was on average only reduced by 19%, thus largely retaining the pest-suppressive capacity of the crucifer within the mixture. There are no equivalent studies investigating the impact of plant-plant interaction on the allelolechemical production of legumes on an area basis. However in crucifer-legume mixtures, the effects of higher allelochemical diversity (cocktail effect) coupled with a somewhat lower production of individual and total GSL on living organisms warrants further investigation in order to assess the multiservice provision by the mixtures.

1.2 Non-host / Host / Trap effects

The fallow period between two cash crops is a key period to break the cycles of weeds and pathogens that can't survive long without a suitable host. Cover crop species are also susceptible to pathogens and must be chosen to avoid the hosting of pathogens that would otherwise decline during bare fallow periods. Crucifers are break crops, or non-hosts, of numerous pathogens (Angus et al., 2015) although despite their release of toxic compounds, they are also host or moderate host of some fungal pathogens (Lu et al., 2010), and nematodes (Ntalli and Caboni, 2017) which can reduce their effectiveness as cover crops in certain conditions. Crucifers are also non-hosts of important beneficial organisms such as mycorrhizal fungi which can be a disservice compared to other cover crops families where mycorrhizal-dependant cash crops follow in the crop sequence (Gosling et al., 2006). Crucifers have also been shown to act as trap crops where they can attract certain pest species such as nematodes (Kruger et al., 2013; Melakeberhan et al., 2006a) and insects (Ahuja et al., 2010; Badenes-Perez et al., 2004), but interfere with the feeding or reproductive cycles to reduce pest populations.

Cover crop mixtures can provide a potential solution to host plant issues of crucifers via several mechanisms (Figure 3). Firstly a dilution effect occurs as the density of crucifers are halved in bispecific mixtures, making the pest less able to locate and infest its host plants (Boudreau, 2013; Root, 1973). Secondly, a physical and visual barrier effect is enhanced by the companion crop by modifying the architecture of the stand, the pest or pathogen spread can then be disrupted as well as the energy required by insects or nematodes in the search for the host plant (Ratnadass et al., 2012; Vandermeer, 1989). Thirdly, a change in host plant morphological traits can result from plant-plant

interactions in mixtures to diminish the ability of the pest to find a host (Ratnadass et al., 2012). Finally a change in host susceptibility and attractiveness to pests can also result from plant-plant interaction by changing the host plant chemical composition, such as the production of repellent chemicals or flavour changes (Ratnadass et al., 2012).

The same mechanisms can also reduce the pathogen host effects of legumes, reducing diseases in the legume and generating improved N-related services. However special care must be taken when designing appropriate mixtures as legumes can also host numerous pests and diseases (Ahuja et al., 2010; Ntalli and Caboni, 2017) generating undesirable changes to the pathogen host status of the cover crop. The trap crop effects of crucifer cover crops on nematodes or insects could also be reduced in mixtures due to the legume component, but no studies are available on this phenomenon.

1.3 Plant cover effects via abiotic resource use

Compared to a bare soil, the presence of a growing plant cover affects light, nutrient and water fluxes as well as microclimate resulting in changes in organism communities (Vukicevich et al., 2016). Through root exudation and rhizodeposition processes, growing cover crops provide large amounts of nutrients to attract and sustain microorganisms including bacteria, non-pathogenic *Fusarium* species, *Streptomyces* and other actinomycetes (Hinsinger et al., 2009; Wichern et al., 2007). Microbial communities have been reported to suppress numerous pathogens through competition, antibiosis, and parasitism or by inducing systemic plant resistance (Audenaert et al., 2002; Rayns and Rosenfeld, 2006). As each plant family and species of cover crop specifically shape the structure of microbial communities (Buyer et al., 2010) through different exudate composition quantity and seasonality (Broeckling et al., 2008; Schweitzer et al., 2008), cover crop species mixtures could enhance soil organism diversity and activity (Berg and Smalla, 2009; Lawrence et al., 2012; Legay et al., 2014) to increase disease suppression (Bardgett and Van Der Putten, 2014; Garbeva et al., 2004). In that regard, crucifer and legumes are complementary because as sole crops they enhance different specific pathogen-suppressive microorganisms (Berg et al., 2005; Vukicevich et al., 2016). Furthermore, complementarity of resource use and root architecture between crucifers and legumes can lead to better root biomass and density in the mixture (Couëdel et al., 2018c) that may generate more

exudation and rhizodeposition (Figure 3) (Duchene et al., 2017). In mixtures, this combination of 1) higher root tissue diversity and 2) higher root biomass and density leads to increased microbial diversity and abundance in the rhizosphere (Duchene et al., 2017; Zak et al., 2003) and as a consequence improved control of pests and diseases may result (Latz et al., 2015, 2012).

Plant cover is also key to weed suppression due to competition for abiotic resources (Teasdale, 1996). Crucifer cover crops can compete strongly with weeds for nutrients, light and water due to their rapid increase in root depth and density (Thorup-Kristensen, 2001; Thorup-Kristensen et al., 2003) which allows them to capture a large amount of nitrogen and sulphur soon after sowing. Nevertheless competition for these abiotic resources could be increased in mixtures compared to pure crops thanks to a complementarity in nutrient uptake and light interception as shown previously for cereal-legume mixtures (Corre-Hellou et al., 2011; Hauggaard-Nielsen et al., 2001). Both weed biomass and diversity can be reduced by some crop mixtures compared to sole crops (Figure 3) (Poggio, 2005).

1.4 Organic matter addition

At cover crop termination, some studies report similar levels of pathogen suppression between crucifers and other cover crop species (Larkin, 2013) that could be due to the effect of organic matter addition rather than specific allelochemical effects (Zhou and Everts, 2007). Pathogen suppression by organic inputs has mostly been attributed to indirect effects of higher antagonist diversity and density rather than a decrease in pathogen inoculum (Davis et al., 1996; Ennaïfar et al., 2005). Indeed organic inputs can improve the soil biological status by increasing both the diversity and the size of beneficial species population through physico-chemical changes (Blanchart et al., 2006; Ochiai et al., 2008; Omirou et al., 2011; Sekiguchi et al., 2007). This biocontrol due to organic matter addition has been shown to last longer than the effects of specific allelochemicals such as ITCs, and is often complementary with allelochemical suppression (Cohen and Mazzola, 2006; Mazzola et al., 2007; Motisi et al., 2009).

Interestingly, high organic matter accumulation from diversified biomass also results in higher microfaunal diversity, particularly that of decomposer taxa, at the expense of herbivore/root-feeding

species (Brévault et al., 2007; Brown and Oliveira, 2004). By increasing both shoot and root total biomass production (Couëdel et al., 2018c) as well as tissue diversity, incorporated cover crop mixtures could enhance a more diverse and higher abundance of microbial communities (Figure 3) (Buyer et al., 2010; Ratnadass et al., 2012). Indeed crucifers and legumes enhance different microbes (Vukicevich et al., 2016) as the different quality of the plant litter can influence both the activity and microbial community structure (Bastian et al., 2009; Fanin et al., 2016). This can alter the suppression of soil borne diseases (Van Bruggen and Grunwal, 1996). High quality plant litter (lower C/nutrient ratio) such as that generated by legumes can attract copiotrophic microbes such as *Pseudomonas* while fungal decomposer or actidobacterias are enhanced by low quality litter decomposition (Bastian et al., 2009). We can hypothesise that a greater diversity and number of microbes in the soil would increase the likelihood of antagonism to pathogens (Altieri, 1999). Nevertheless there is a lack of specific studies on the decomposition rate of litter from cover-crop mixtures, the impact on soil microorganisms and disease suppression, and the mechanisms are likely to be complex.

1.5 Soil structural effects

Poor physical soil conditions such as inadequate drainage, poor aggregate stability and high soil compaction can exacerbate the damage from soil-borne diseases (Abawi and Widmer, 2000; Hossain et al., 2012), and weeds (Gardarin et al., 2010) and decrease mycorrhizal root colonization (Homma et al., 2012). During the period of cover crop growth, above-ground plant parts can protect soil aggregates from erosion and direct rain-drop impact while the roots can decompact the soil (Han et al., 2016), and enhance the populations of micro- and macro-faunal organisms such as earthworms (Blanco-Canqui et al., 2015). Furthermore, at cover-crop termination, cover crops can increase organic matter content to improve soil structure (Blanco-Canqui et al., 2015). Compared to other graminaceous cover crops species that have fibrous roots, the interest of crucifers is their deep taproots that can alleviate soil compaction by penetrating compact layers across different soils (Chen and Weil, 2010; White et al., 2016), and the fine surface root systems that can improve aggregation (Bodner et al., 2014; Chan and Heenan, 1996).

Crucifer - legume cover crop mixtures with complementary rooting systems (e.g. deep and shallow) have potential to improve soil structure by decreasing soil compaction more effectively than pure crops (Figure 3) (Blanco-Canqui et al., 2015; White et al., 2016). The success of mixtures nevertheless depends on soil conditions, and in some cases soil physical properties are not improved (Fernandes et al., 2011). Planting a mix of species having different shoot architecture can also provide more soil cover (Wortman et al., 2012), and thereby reduce wind and water erosion (Chen and Weil, 2010).

[Insert Figure 3 here] Figure 3. Mechanisms by which (1) crucifer cover crops can influence biocontrol of soil organisms, and (2) how these are potentially affected within a crucifer-legume mixture including services (up-arrow) and disservices (down-arrow) for pathogen suppression.

2. Ecological services and disservices of crucifer sole crops and crucifer legume mixtures

In this section, we review studies dealing with the impact of crucifers as sole cover crops and in mixtures on a wide range of living organisms. Pathogen suppression as well as impacts on beneficial organisms are discussed as they are both important processes within the system. In each subsection, we first discuss the evidence for *in vitro* toxicity of GSL-hydrolysis products on various organisms and then consider field experiments that include crucifer sole cover crops. Where possible we include studies where the inclusion of legumes in mixtures was considered, but in the absence of published literature we speculate about the possible interactions. As a guide to the discussion, Figure 4 provides a summary of the effects of crucifer sole crops and mixtures on each of the living organism classes considered.

2.1 Impact of crucifer cover crops on microbial communities

2.1.1 Pathogen suppression

In *in vitro* studies, ITCs released by crucifers have demonstrated promising biocidal effects on numerous pathogenic microbes including *Rhizoctonia solani*; *Verticilium dahliae*; *Gaeumannomyces graminis var. tritici*, *Aphanomyces euteiches and Ralstonia solanacearum* (Brown and Morra, 1997; Neubauer et al., 2014; Seassau et al., 2016; Smith and Kirkegaard, 2002). In field conditions or in soil, suppression has often been more variable between studies and depends to a significant extent on the

soil type, climate and incorporation practices used as these all influence the concentration of allelochemicals and their effectiveness in soil (Matthiessen and Kirkegaard, 2006; Motisi et al., 2010). As highlighted in Part 1, many mechanisms can be involved and can vary according to the specific pathogen considered.

For example, incidence of *R. solani* on beetroot was reduced by 45% by Indian mustard cover crops (Motisi et al., 2009) while it has been reduced by rape (-65%), and white mustard (-45%) but not by Indian mustard on potato (Larkin and Griffin, 2007; Little et al., 2004). In these studies, suppression was more effective by incorporating the cover crops rather than removing the residues, but there was evidence that suppression could occur both during growth, and after cover crop termination. Mechanisms underlying improved efficacy of crucifers compared to cereal cover crops in the suppression of *R. solani* have not only been linked to the ITCs released (Larkin, 2013), but also to the improved soil microbial biodiversity following crucifer cover crops (Ascencion et al., 2015; Cohen et al., 2005; Wiggins and Kinkel, 2005). This can explain the longer-term effects of cover crops on *R. solani* (Motisi et al., 2009) that last well beyond the period (a few days) in which ITCs remain active in the soil (Gimsing and Kirkegaard 2009). No studies are available on the effect of cover crop mixtures on *R. solani* suppression, but legumes have been reported to be less effective than crucifers in potato systems (Larkin, 2013) and cotton systems (Rothrock et al., 1995). Legumes are host to some strains of *R. solani* (You et al., 2008; You and Barbetti, 2017) so care would be needed if selecting a legume component of a mixture with crucifers for control of that pathogen.

Crucifers are considered to be good break crops for the take-all fungus *G. tritici* in cereal systems. Severity of take-all in wheat has been shown to be entirely controlled when wheat is preceded by canola compared to wheat (29 % severity) as canola does not host the pathogen (Lemerle et al., 1996). But canola was also superior to a fallow (Jadot, 1981), a faba bean (Bowerman and Banfield, 1982) and a linseed break (Kirkegaard et al., 2000) despite these also being non-hosts. This additional suppression by canola was thought to be due to ITC release from canola roots and some studies provided evidence for this in the field (Kirkegaard et al., 1994, 2000). In some cases Indian mustard showed similar or better suppression of take-all than canola (-40 % of disease incidence compared to

wheat) and this was thought to relate to the release of 2-propenyl ITC from mustard roots in addition to the 2-phenylethyl ITC released by both species (Angus et al., 1991; Kirkegaard et al., 1997). Overall the effect has been variable (Smith et al., 2004) and highly dependent upon the seasonal conditions which also influence inoculum survival. Legumes can be also considered as break-crops since they are non-host of *G. tritici* (Angus et al., 2015; Cotterill and Sivasithamparam, 1988; Lawes et al., 2013). In comparative studies, lupin showed the same impact as a break crop as canola, and clover and bean had the same efficacy as oilseed rape (Dyke and Slope, 1978). Among the legumes, Speakman et al., (1978) showed that white clover and alfalfa species had the same take-all suppression levels. Thus for a disease such as take-all, the use of crucifer-legume mixtures may provide a valuable disease suppressive capacity while maintaining other benefits of the mixture.

However for some pathogens such as *V. dahliae* it has generally been shown that it is much more difficult to achieve suppression using biofumigation. The pathogen has been found to be less sensitive to the commercial soil fumigant methyl-ITC (known as Metham sodium, Vapam) than other pathogens (Klose et al., 2008) so may be a less suitable target for biofumigant suppression. However high concentrations of dimethyl disulfide and methyl sulfide appeared to have reduced *V. dahliae* colony counts in bioassay potato stem saps in a glasshouse experiment (Wang et al., 2009). In soil, suppression of *V. dahliae* by a mixture of white and Indian mustards has been observed for potato (50 % of incidence) (Larkin et al., 2011) and for cauliflower with broccoli (-50% of severity) (Xiao et al., 1998). However these same cover crops have not been effective in suppression of *V. dahliae* in tomato (Hartz et al., 2005). ITC-related effects have not been clearly shown in *V. dahliae* suppression, but many studies evoke a different suppressive pathway related to organic matter addition (Berbegal et al., 2008; Ochiai et al., 2008; Olivier et al., 1999a; Subbarao et al., 1999). Indeed in potato fields, Davis et al. (2001) found that the level of organic matter in the soil was inversely related to *Verticillium* wilt severity. Furthermore Michel (2014) showed that mustard hay reduced the number of *V. dahliae* microsclerotia significantly in two greenhouse experiments, but this effect was presumably not caused by crucifer allelochemicals, as the aliphatic GSLs are largely lost during the hay-making process, and because the suppressive effects occurred several months after the hay application when ITCs and other

chemicals have dissipated in the soil. Increased soil microbial activity has been suggested as the cause of improved suppression following crucifer amendment (Davis et al., 2010; Larkin et al., 2011; Michel, 2014). Indeed Davis et al., (2010) and Michel (2014) found a negative relationship between *V. dahliae* population (and incidence) and soil microbial activity. The impact of crucifer-legume mixtures on microbial activity and pathogen suppression may be of interest from both an allelochemical and biomass perspective. For example legumes such pea have been shown to suppress *V. dahliae* to the same extent as rape (-40% of incidence) (Davis et al., 2010). However we are not aware of any studies that have investigated the impact of crucifer – legume mixtures on *V. dahliae* populations, nor the suitability of different legume and crucifer species for that purpose.

The effect of biofumigant crucifers on *A. euteiches,* the fungus responsible for pea root rot has been studied extensively, and significant suppression has been demonstrated for Indian and white mustard cover crops (-50% of severity) (Hossain et al., 2015). Mechanisms of suppression have been suggested to be ITC related (Chan and Close, 1987; Muehlcen et al., 1990; Papavizas and Lewis, 1970), but recent studies have also found suppression to be partly due to soil de-compaction (Hossain et al., 2015), generating a less favourable soil environment for *A. euteiches*. For this pathogen, cover crop mixtures of crucifers and legumes would presumably best be avoided. Legumes used as cover crops can host the same strains of *A. euteiches* as the subsequent cash crop legumes, leading to a disservice compared to bare soil (Levenfors and Fatehi, 2004). Green manures of soybean, snap bean and alfalfa were also ineffective to suppress the pathogen (Williams-Woodward et al., 1997).

Bacterial pathogens have often been found to be less susceptible than fungi to *in vitro* ITC (e.g. Smith and Kirkegaard 2002). Nevertheless a decrease of more than half of the bacterial wilt pathogen *R. solanacearum* abundance and incidence was observed after Indian mustard incorporation on tomato and tobacco crops (Akiew et al., 1996; Akiew and Trevorrow, 1999; Arthy et al., 2002). Olivier et al., (1999b) found a 98% reduction of *R. solanacearum* on tomato crops following turnip rape crops but this effect was not attributed to GSL production. Kirkegaard (2009) has demonstrated both short-term ITC-related and longer-term organic matter-related suppression of bacterial wilt in solanaceous crops, the former more obvious and effective on sandy soils where the ITCs are not adsorbed and inactivated

by high clay and organic matter levels in soil. Another bacterial pathogen responsible for common scab on potatoes, *S. scabies,* has also been suppressed by cabbage residues (-90% of incidence) (Gouws and Wehner, 2004). In common with fungal pathogens, few studies have investigated the impacts of crucifer-legume mixtures on pathogenic bacteria.

2.1.2 Pathogen stimulation

Despite the ability of ITCs to suppress *Fusarium spp*. and *Sclerotinia spp*. *in vitro* (Smith and Kirkegaard, 2002), crucifer cover crops host these pathogens, and are currently not considered to be effective to suppress them (Lu et al., 2010).

Incidence of *Fusarium* increased in tomato following incorporation of a mixture of white and Indian mustard (+34%) (Hartz et al., 2005) and following an Indian mustard (+11%) on watermelon (Njoroge et al., 2008). When Indian mustard and cauliflower cover crops were not incorporated in soil, the effects on disease incidence were respectively 3 and 4 times higher on strawberry compared to no cover crop (Lazzeri et al., 2003). Nevertheless incidence of *F. oxysporum* has been shown to decrease after incorporation of canola (-27%), while severity of *F. graminearum* on wheat decreased by 45% and 30 % respectively following canola and Indian mustard crops (without incorporation) (Kirkegaard and Matthiessen, 2004). Concerning *Sclerotinia spp*., Sexton et al., (2007) found a slight increase of incidence (8%) following the use of a mustard cover crop blend, while in some studies a higher microbial diversity after crucifer cover crop use was considered responsible for suppression of the fungus (Duncan et al., 2006; Hao et al., 2003; Ojaghian et al., 2012; Subbarao, 1998).

Mixtures may be an effective option when crucifers promote specific diseases, or are not effective to suppress them. For example, legumes such as hairy vetch can suppress *Fusarium* of watermelon by more than 50% through an increase in the bacterial population in soils (Zhou and Everts 2007). Though no studies exist, mixtures with legumes with this capacity could reduce the disservice of crucifers for this disease if other benefits of the crucifer are compelling.

2.1.3 Impacts on beneficial fungi and bacteria

Beyond pathogen suppressive effects, crucifer biocidal effects (positive or negative) can influence the general microbial populations including beneficial organisms that may impact soil health and fertility. In general, the impact of crucifer cover crops on beneficial organisms has received less attention than pathogens. Here we discuss the current knowledge of crucifer effects on antagonist microbes, and we then consider two specific examples; arbuscular mycorrhizal fungi (AMF) and N-cycling bacteria, with a focus on the potential for legumes in a mixture to mitigate potential disservices associated with sole crucifer cover crops.

2.1.3.1 Impacts on disease suppressive fungi and bacteria

Toxicity of the ITCs can impact non-target organisms in soil (Bending and Lincoln, 2000; Ibekwe et al., 2004; Rumberger and Marschner, 2004) and in the aquatic environment (Schultz et al., 2005). However under field conditions, the effect of crucifer growth and incorporation on the diversity of microbes has been rarely studied. Interestingly, the enhanced competition of copiotrophic soil microorganism on soil-borne pathogens can be favoured by the addition of fresh organic matter in soil (Friberg et al., 2009; Larkin and Honeycutt, 2006). For example after ITC soil disinfestation, saprophytic fungi that can have an antagonistic effect on soil parasitic organisms (e.g. *Penicillium* sp., *Trichoderma*, *Aspergillus* sp., *Gliocladium* sp.) and several others predominate (Welvaert, 1974). These fungi prolong the inhibition of the parasite by having a synergistic action with the ITC called ‘‘induced antagonism’’. Indeed, the most common example is *Trichoderma spp.* which are antagonist fungi for numerous pathogens (Kandula et al., 2015) and have been proven to be less sensitive to ITC than other fungi (Galletti et al., 2008). In soil conditions, crucifers can increase *Trichoderma* as demonstrated by Kirkegaard and Matthiessen, (2004) where both canola and mustard crops (+300%) stimulated *Trichoderma* without residue incorporation (see Kirkegaard et al., 2004). There are no studies on the impact of crucifer-legume mixtures on these soil microbial antagonists. Inclusion of legumes in mixtures may bring services by improving the functional and specific bacterial diversity as demonstrated when legumes are used at the rotation scale (Lupwayi et al., 1998). Improving spatial and temporal crop diversity at the field scale provides ecological niches for microorganisms and

encourages microbial diversity that may improve "induced antagonist" effects. Indeed general microbial population diversity were either unaffected or increased in some mixtures (Nair and Ngouajio, 2012; Reed-jones et al., 2016; Wortman et al., 2013) but the effects can be different, even for species within the same family (Maul et al., 2014; Zhou et al., 2017). Further assessment of commonly used cover crop species of legumes as sole cover crops as well as in mixtures on the populations of disease-suppressive bacteria and fungi is warranted.

2.1.3.2 Impacts on two beneficial organisms

Most crucifer cover crops are non-hosts of arbuscular mycorrhizas fungi (AMF) and may even reduce populations compared to bare soil through ITC suppressive effects. *In vitro*, 2-phenylethyl ITC has been found to be harmful to AMF (Vierhling et al, 2000). Interestingly in field conditions, rocket (*E. sativus*) a crucifer that lacks the GSL precursor Glucosturtiin (2-Phenylethyl-GSL) for 2-phenylethyl-ITC showed no AMF suppression, while Indian and white mustard were suppressive with a 70% and 56% reduction of AMF colonisation respectively on strawberry (Koron et al., 2014). In soil conditions, negative effects of Indian mustard cover crops on mycorrhizal root colonisation of the subsequent maize has been reported compared to vetch cover crops (-43%) (Njeru et al., 2014), and compared to bare soil for rape (-30%) in soybean systems (Valetti et al., 2016). However other studies have shown no negative impact of rape (Pellerin et al., 2007) or radish (White and Weil, 2010) residues on AMF colonisation on maize roots. Inclusion of legumes in cover crop mixtures could be an interesting option to convert the non-host status of the crucifer sole crop to a host status for the cover crop mixture as a whole. Legumes (with the exception of lupins) are reported to increase mycorrhizal fungi abundance and diversity more than other plant families (Duchene et al., 2017) and fungal antagonist communities differed depending on the species of the legume in the crop rotation (Taheri et al., 2016). Legume diversity at the plot level could even enhance AMF abundance as shown for clover species mixtures when soil has been amended with AMF (Zarea et al., 2009). Concerning crucifer-legume mixtures (see Table 6 for details), Wortman et al., (2013) showed that a mixture of vetch and mustard and a mixture of 8 species (including 3 crucifers) did not reduce soil AMF abundance compared to bare soil but no crucifer controls were present in the study. Lehman et al., (2012) showed that a

mixture of canola, vetch and oat had the same number of AMF propagules in soil as the oat sole crop, and had more AMF propagules than the canola sole crop. Finney et al., (2017) found no negative impact of radish on soil AMF abundance in sole cover crop and in mixtures 2 and 9 months after cover crop sowing compared to no cover crop treatments. Mechanisms of AMF-legume root interactions are still to be clarified in crucifer-legume mixtures to better understand the impacts of the inclusion of a non-host AMF crucifer in the rhizosphere on AMF soil colonisation.

In-vitro ITC applications have an impact on key soil bacterial communities involved in critical processes such as nitrogen cycling, including nitrification and nitrogen fixation (Bending and Lincoln, 2000; Rumberger and Marschner, 2004). Indeed, populations of both ammonium-oxidizing and nitrite-oxidizing bacteria and levels of nitrification were reduced by applications of ITC or other volatile sulfur compounds (Bending and Lincoln, 2000; Brown and Morra, 2009; Saad et al., 1996). Nevertheless in field conditions, these effects of crucifers have not been observed. For example nitrifying bacteria were not affected by broccoli incorporation (Omirou et al., 2011) nor by either Indian mustard or white mustard without residue incorporation (Hossain et al., 2015). Furthermore beneficial rhizobacteria (Rhizobium spp.) responsible for nitrogen fixation were not impacted by rape in soybean systems (Valetti et al., 2016) or by mustards in pea systems (Hossain et al., 2015). The same number of pea nodules were found with rapeseed residues compared to a soil left bare (Scott and Knudsen, 1999). In contrast, Muehlcen et al., (1990) found a decrease in pea nodules when rape was incorporated before sowing, as did Hossain et al., (2015) after both white and Indian mustard cultivation without residue incorporation. Nevertheless these effects were attributed more to the better N supply following crucifer green manures than bare soil (causing a lower pea root nodulation) than to a potential biofumigation effect on rhizobacteria. Theoretically, legume inclusion in mixtures should decrease any potential negative effects of the crucifers on soil microbes involved in nitrogen cycling but experiments are needed to confirm this hypothesis.

2.2 Herbicidal effects of crucifer cover crops

2.2.1 Weed suppression

It is widely known that cover crops can reduce weed germination and/or establishment (Haramoto and Gallandt, 2004; Teasdale, 1996). Cover crops mainly suppress weeds emerging while growing, but can also suppress the weeds infesting the next cash crop (Lou et al., 2016). Weed suppression from cover crops arises mainly from i) competition for abiotic resources (nutrients, light …). (McLenaghen et al., 1996; Teasdale, 1996); ii) allelopathy (Jabran et al., 2015), or iii) induced bacterial suppression (Lou et al., 2016). Levels of cover crop biomass production are often seen as a good indicator of suppressive capacity (Mirsky et al., 2013; Mohler and Teasdale, 1993) but this phenomenon is highly variable since low biomass of some cover crops can also generate high levels of suppression (Björkman et al., 2015). Among cover crops, crucifers are known to be highly effective competitors for abiotic resources thanks to their rapid growth (Brust et al., 2014), but can also generate biocidal effects via production of GSL-related suppressive compounds (Haramoto and Gallandt, 2004).

In vitro application of ITCs has been proven to inhibit or delay weed germination (Brown and Morra, 1997; Kunz et al., 2016) while weed radical growth is also reduced (Bialy et al., 1990; Wolf et al., 1984). However in soil, allelopathy and competition for resources occur simultaneously, and separating these effects can be challenging (Duke, 2015; Falquet et al., 2014; Macías et al., 2014). In addition allelopathy on weeds may occur from roots and from shoot tissues (Asaduzzaman et al., 2014). Though difficult to attribute suppression to specific mechanisms, several studies highlight that crucifer cover crops can be effective to suppress weeds. Some studies highlighted a better weed suppression by crucifers than grasses or legumes (Haramoto and Gallandt, 2005) while others did not (Smith et al., 2014). Some studies including field and controlled experiments concluded that no allelopathic effects (Lawley et al., 2012) were involved in weed suppression, while others have confirmed them (Kunz et al., 2016). Interestingly, mustards have been highlighted as effective suppressers of weeds even at relatively low levels of biomass and/or GSL concentration (Björkman et al., 2015).

The impact of crucifer cover crops on weeds has been reviewed by Haramoto and Gallandt, (2004) and more recently by Bangarwa and Norsworthy (2016). They reported weed suppression from crucifer cover crops can be up to 96% compared to bare soil. Weed (bigpod sesbania) germination after incorporation of five different crucifer species decreased by more than 95% (Vaughn and Boydston, 1997). Weed biomass and weed density can be reduced from 85% to 96% after canola compared to bare soil (Bangarwa et al., 2011). Krishnan et al., (1998) showed a 49% reduction of weed biomass after emergence of 3 different crucifer cover crops (Indian mustard, white mustard and rape) with different results for the weed and cover crop combination. This may relate to different competitive ability or to different allelochemicals released. White mustard cover crop residues reduced the weed infestation by 50 and 60%, and it delayed weed appearance by 3 and 4 weeks for the first and second years, respectively, compared to bare soil (Alcántara et al., 2011). Crucifer cover crops have a negative impact not only on weed density and dry weight but also on weed species diversity compared to fallow treatment (Mennan and Ngouajio, 2012). This study also showed a lower impact of cover crops on perennial weeds compared to annual weeds. They conclude that crucifer cover crops must be coupled with other weed suppression strategies to control both annual and perennial weeds. Some studies reported full weed control when cover crops have been coupled with half of the herbicide dose. Indeed Malik et al. (2008) reported the same weed suppression efficacy as a full herbicide dose when radish incorporation was coupled with half of the herbicide dose in maize systems.

Among the same species, cultivars can also have different suppressive effects as highlighted by Asaduzzaman et al. (2014) with 70 canola species, and by Zubair et al. (2017) with alfalfa. Thus an improvement in weed suppression could be achieved by screening cultivars and selecting those with high weed suppression potential.

Cover crops can also have a longer-term effect on weed populations through microorganism-induced suppression which extends the longevity of a cover crop's effectiveness (Inderjit, 2005; Inderjit et al., 2005; Lou et al., 2016). Indeed Mohler et al. (2012) showed that after pea cover crop incorporation, *F. oxysporum* and *F. chlamydosporum* could have biocide effects on seeds and seedlings with an impact on weed emergence. Microbes can also indirectly impact weeds by activating biocides from water-

soluble allelochemicals released soon after cover crop incorporation (Jilani et al., 2008; Williamson et al., 1992).

Mixing cover crop species is one of the strategies available to increase weed suppression compared to sole cover crops. For cash crops, it has been widely shown that improved diversity of plants in agroecosystems can increase weed suppression (Corre-Hellou et al., 2011; Hauggaard-Nielsen et al., 2001). Indeed non-legume/legume mixtures increase light interception and nutrient uptake through niche complementarity for resource use, for example through different shoot and root architecture. Another aspect less considered is the potential for additional allelopathic effects from legume species despite the lower competition for abiotic resources. Indeed many legumes can have allelopathic effects on weeds such as green manures of crimson clover (Dyck and Liebman, 1994), subterranean clover (Nagabhushana et al., 2001), red clover (Fisk et al., 2001; Ohno et al., 2000), other trifolium species (Liu et al., 2013), hairy vetch (Geddes et al., 2015; Hill et al., 2007; Kamo et al., 2003; Teasdale and Daughtry, 1993) and alfalfa (Chung and Miller, 1995).

Examples of weed suppression by cover crop mixtures often deal with cereal-legume cover crops (Creamer and Bennett, 1997; Hayden et al., 2012) but experiments including crucifer-legume mixtures are scarce (see Table 6 for details). In field conditions Kunz et al., (2016) showed the same level of weed suppression with a cover crop mixture including radish, bristle oat and Egyptian clover as with the radish sole crop. They also showed in controlled conditions that compared to sole cover crops the mixtures had similar weed germination rate, but a longer weed germination time. Furthermore a bispecific mixture including vetch and radish had better weed suppression than either of the sole cover crops (Altieri et al., 2011). In multispecies mixtures where oats had the best weed suppression of all pure cover crops, Smith et al., (2014) showed the same suppression for mixtures as the mustard sole crop while Finney et al. (2016) and Baraibar et al. (2017) showed a better suppression by mixtures than a radish sole crop. No studies deal strictly with crucifer-legume bispecific mixtures for weed suppression.

At the interface between intercropping and cover cropping, some systems involve the intercropping of a rape cash crop with a legume cover crop (also called a companion plant). In these systems, undersown legumes provide better weed suppression (from 20 to 75%) than the sole rape crop due to better soil coverage (Lorin et al., 2015). Living mulch clover sown in between cabbage rows also showed better weed suppression (up to 89%) than sole cabbage late in the season (Brandsæter et al., 1998).

In conclusion, crucifer-legume mixtures show strong potential for weed suppression through high competition and biochemical suppression of weed growth. Furthermore, resilience for weed suppression is increased in mixtures through different species growing requirements and through plant plasticity. Indeed, one species in mixtures can compensate potential deficiencies of other species during the vegetation period to maintain high weed suppression. Total weed suppression is difficult to achieve but the combination of the introduction of cover crops and the strong competition brought by mixtures would potentially make it possible to decrease herbicide use substantially. However the lack of knowledge of mechanisms of suppression makes it difficult to select the best combination of different cover crops. Selection of cover crops mixtures through traits and functional complementarity for abiotic resource use could be an efficient strategy to improve weed suppression potential of cover crops (Ranaldo et al., 2016).

2.2.2 Herbicidal effects on intercropped or companion legume

Herbicidal effects of crucifers on the companion legume in a cover crop mixture would reduce the effectiveness of the mixture. Crucifers have been shown to have herbicidal effects on legumes *in vitro* (Brown and Morra, 1997) and in field conditions for legume weeds (Bangarwa and Norsworthy, 2016). Furthermore, crucifers may compete strongly for sulfur (S) and affect legume biological N-fixation. For example Génard et al. (2016; 2017) observed that legumes in a mixture with rape had a lower S content than the sole crop, but did not observe lower N_2 fixation, while Couëdel et al., (2018a) found no strong differences in S status of various legumes when mixed with crucifers. Furthermore Jamont et al. (2013b) found that biological fixation of faba bean was increased when intercropped with rape, even if the shoot N concentration was reduced. Indeed high competition for nitrogen usually

stimulates legumes to increase biological N-fixation in mixtures (Jensen, 1996). Interestingly pea fixed more N_2 when mixed with radish than with rye (Andersen et al., 2005) while cowpea had no difference in nitrogenase activity or nodule biomass when mixed with radish or oat (Wortman and Dawson, 2015).

In a study dealing with many crucifer legumes species and cultivars (Couëdel et al., 2018c) did not find any strong incompatibilities for crop development, with the exception of radish and turnip rape which had a stronger competition than other crucifer species by reducing companion legume biomass per plant by 20% and 30% respectively. Furthermore, intercropping of rape cash crops with a legume companion crop did not show any incompatibility of development for the many legumes species tested (Lorin et al., 2015; Verret et al., 2017). Herbicidal effects of legumes can impact crucifer growth as demonstrated *in vitro* with biocidal effects of red clover on wild mustard weeds (Conklin et al., 2002; Ohno et al., 2000). Nevertheless all studies cited above showed that crucifer development improved in mixtures with legumes compared to pure crops except for rocket, that was less competitive for abiotic resources (Couëdel et al., 2018c).

2.2.3 Herbicidal effects on subsequent crops

GSL hydrolysis products such as ITCs generally have a short half-life in soil and don't persist at detectable levels beyond a few days (Gimsing and Kirkegaard, 2009; Morra and Kirkegaard, 2002). Only water soluble biocides such as thiocyanates may have a longer herbicidal effects but studies are lacking to test this hypothesis (Brown and Morra, 1996, 1995). As a result, impacts of crucifers on the subsequent crop germination and establishment would presumably be indirect through organic matter incorporation effects such as nutrient cycle impacts or changes in microorganism profiles. Krishnan et al., (1998) found similar soybean yields for many cover crops and a fallow treatment suggesting crucifer residues did not harm soybean plants. As discussed earlier, Scott and Knudsen, (1999) found that peas grown in soil with incorporated rapeseed residues had similar numbers of nodules and rhizobacteria activity to those grown in soil with no residues. Interestingly Al-Khatib et al., (1997) showed that rapeseed residue decreased subsequent pea yield and density by two compared to a rye control while it was not observed following white mustard. Similar to the impact on weeds and

companion crops, the impacts of cover crop residues could be due to nutrient availability changes more than allelochemicals as hypothesized for pea nodulation decreases following crucifer cultivation (Hossain et al., 2015; Muehlcen et al., 1990). Furthermore, maize development was reduced by mustard and turnip but not by radishes and canola cover crops (Gieske et al., 2016; Spiassi et al., 2011). Gieske et al. (2016) suggested that nutrient release by crucifer cover crops did not meet the cash crop needs, explaining the negative effects observed. Therefore, optimal cover crop termination date seems key to manage nutrient supply to match subsequent cash crop needs.

Legumes may also produce biocidal effects and may influence subsequent crop development (Mondal et al., 2015), but it is generally accepted that legumes are good preceding crops thanks to nitrogen green manure effects (Couëdel et al., 2018c; Thorup-Kristensen et al., 2003; Tribouillis et al., 2016). In this way crucifer-legume mixtures have a better nitrogen green manure effect than the pure crucifer, and may improve the growth of the subsequent main crop (Couëdel et al., 2018c). Recycling of other nutrients may also mutualize in mixtures compared to pure crops leading to better nutrition for the subsequent cash crop but studies are still needed to assess the capacity of mixtures to acquire nutrients (Couëdel et al., 2018a; Xue et al., 2016).

In conclusion, herbicidal effects of crucifers do not appear to impact legume development meaning that crucifer-legume mixtures are generally compatible. Furthermore, mixtures reduce weed growth and improve nutrient green manure effects providing improved growing conditions for the subsequent cash crop.

[Insert Table 6 here] Table 6: Summary of studies dealing with crucifer-legume cover crop mixture effects on living organisms**. "**SC" indicates sole cover crops. Living organisms appear in the same order as discussed in the text. We report a general lack of studies dealing with impacts of crucifer-legume mixtures on fungal and bacterial pathogens.

2.3 Impacts on micro- and macro-fauna

2.3.1 Nematodes

2.3.1.1 Plant parasitic nematodes

ITCs have been proven to have biocidal effects on many nematode families *in vitro* (Ntalli and Caboni, 2017). *M. incognita* (root-knot nematode) is susceptible to 2-phenylethyl, benzyl, 4-

methylthiobutyl, and 2-propenyl ITC (Luca Lazzeri et al., 2004; Zasada et al., 2009). Populations of potato cyst nematode decreased due to ITC derived from aliphatic GSL (2-propenyl GSL) and the aromatic GSL gluconasturtiin (2-phenylethyl GSL) as shown for *G. rostochiensis* and *G. pallida* when applying high 2-propenyl levels extracted from crucifer plants (Aires et al., 2009; Lord et al., 2011). A lack of gluconasturtiin in the roots of white cabbage cultivars has been shown to increase population of *Pratylenchus* spp. (root-lesion nematode) (Kabouw et al., 2010). Other field experiments demonstrated that 2-phenylethyl ITC had an impact on *P. neglectus* but clearly demonstrated that other non-GSL mechanisms were also involved (Potter et al., 1998). Furthermore, Vervoort et al. (2014) concluded that changes in nematode communities following Indian mustard soil incorporation were not due to ITC release, but to other mechanisms. Differences in nematode suppression by different crucifer species have been highlighted by some studies but the mechanisms of suppression are not well understood (Fourie et al., 2016; Kruger et al., 2013; Ntalli and Caboni, 2017).

Among mechanisms other than biocidal effects of ITCs, non-host or poor-host status of crucifers are often the key to reducing nematode populations (Kruger et al., 2013; Ratnadass et al., 2012). The selection of a non- or poor-host biofumigant cover crop is the first and most crucial step to control parasitic nematodes and it is highly dependent on the cultivar used (Pattison et al., 2006). Using a biofumigant that hosts nematodes can result in the pest population increasing during the growth stage, irrespective of the biofumigation processes following incorporation and decomposition. Under these circumstances termination of the biofumigant prior to the completion of the nematode life cycle on the biofumigant host is crucial, and is often temperature dependent (Fourie et al., 2016).

The difficult part of choosing an appropriate cover crop is that this host status depends on both the crucifer species, and on the different nematode species present. For example, canola (Mojtahedi et al., 1991) and radish were poor hosts of *M. incognita* (Curto et al., 2005) but some oil radish cultivars were among the best hosts for *M. hapla* (Edwards and Ploeg, 2014). Indian mustard and turnip were both good hosts to root-knot nematodes (Curto et al., 2005; Edwards and Ploeg, 2014). Rocket (cv. Nemat) has the potential to act as trap crop for the root-knot nematode *M. hapla* (Melakeberhan et al., 2006b), while radishes and white mustard are also trap crops for the beet cyst nematode (*H. schachtii*)

by disrupting their sexual differentiation (Müller, 1999; Schlathoelter, 2004). Turnip and rocket must be avoided for use as cover crops for suppression of root-knot nematodes (*M. arenaria, M. incognita* and *M. javanica*) as they are respectively host of 2 and 3 of these species (Liébanas and Castillo, 2004).

Suppressive effects of crucifer cover crops on plant parasitic nematodes are also explained by their impact on the wider antagonist food web through changes in soil microfauna and microflora. Indeed, free-living nematodes appeared to be less susceptible to the toxins produced by crucifer crops than plant-parasitic nematodes (Stirling and Stirling, 2003). Following cover crop incorporation, the abundance of nematode trophic groups changed, and caused an increase in bacterial feeder nematode (Valdes et al., 2012) and non-pathogenic nematode communities (Collins et al., 2006; Gruver et al., 2010; Takeda et al., 2009) which decreased parasitic nematode abundance (Piedra-Buena et al., 2015; Stirling and Eden, 2008; Treonis et al., 2010; Wang et al., 2008, 2006). Furthermore, the negative impact of Indian mustard seed meal amendments was less for beneficial nematode species *Caenorhabditis elegans* than on plant parasitic nematodes (Yu et al., 2007). Nematode suppression has also been linked to an increase in antagonistic bacterial communities following cover crop incorporation (Wang et al., 2008). Interestingly, Riga (2011) showed that it is possible to achieve full control of root-knot (*M. chitwoodi*), lesion nematodes (*P. penetrans*) and cyst root nematodes (*P. allius*) following crucifer green manure in combination with half the recommended rate of pesticide 1,3-dichloropropene (1,3-D, Telone).

Improving plant diversity is seen as a potential solution to improve nematode suppression (Ratnadass et al., 2012) but patterns are not always predictable and the driving mechanisms are poorly understood (Cortois et al., 2017). Indeed, Cortois et al. (2017) showed that for a wide range of grass and legume mixtures the abundance of all nematode feeding types, except for predatory nematodes, increased with both plant species and plant functional group diversity.

Sole legume cover crops can suppress nematodes as shown for hairy indigo and joint vetch on populations of sting nematodes (*B. longicaudatus*) and root-knot nematodes (*M. incognita*) while velvet bean lowered the populations of several root-knot nematode species (Rhoades and Forbes,

1986; Rodriguez-Kabana et al., 1992). Some tropical legumes (i.e. sunn hemp) also induced a change in nematode communities by increasing the abundance of fungal, bacterial feeding and free living nematodes while decreasing plant-feeding nematodes (Wang et al., 2006). However legumes such as hairy vetch are known to be reproductive hosts of several plant-feeding nematode species (Rich et al., 2009; Timper et al., 2006). Legume cover crops need careful screening to assess the host-non host effect of different species and varieties as demonstrated by Damour et al., (2014) on cover crop legumes in banana cropping systems. Furthermore, McLeod et al., (2001) found that clover was not more susceptible than fodder rape to *M. javanica* but that field pea was more susceptible. Bhan et al. (2010) showed that cover crops that increased nematode numbers when planted as sole crops usually gave the same result when planted in mixtures with another cover crop. For example, mixing a shrub that supressed root-lesion nematode with a susceptible host did not reduce the population of these nematodes (Desaeger and Rao, 2001). In contrast, mixing a legume host shrub of *Meloidogyne* with an antagonistic shrub reduced the populations of this nematode in soil (Desaeger and Rao, 2001). Greater clarification is needed about the host status of mixtures that are composed of host and non-host cover crops.

Interestingly, Cortois et al. (2017) showed that the abundance of nematode plant feeders increased with increasing C:N ratio of the aboveground biomass of the cover crops. In this way, crucifer-legume mixtures may decrease nematode populations compared to crucifer pure crops as their C:N ratio is generally lower (Couëdel et al., 2018c). Nevertheless, very few studies deal with crucifer-legume mixtures and their impacts on specific nematode suppression (see Table 6 for details). A mixture of vetch and radish had the same plant-feeding nematode levels as the vetch sole crop and more than the radish sole crop (Barel et al., 2017; Summers et al., 2014). However, no differences in suppression of potato cyst nematodes have been found when mixing Indian mustard, white mustard and rocket compared to sole crops. Mixtures of white and Indian mustard are in widespread use to suppress plant feeding nematodes, but their efficiency compared to sole crop is not clear (Kokalis-Burelle et al., 2013; Kruger et al., 2013). More purposeful selection of crucifer-legume mixtures combining non-

hosting species that may also enhance antagonistic soil populations could be a fruitful area of future research.

2.3.1.2 Impact on non-target beneficial nematodes

Due to different residues and resource use, plant families will not promote the same nematode feeding groups (Orwin et al., 2010; Sohlenius et al., 2011). Indeed, crucifer species have specific effects on nematode communities through the stimulation of different microflora involved in residue decomposition (Collins et al., 2006). For example, radish can enhance bacterial decomposition, while rape and rye increased the fungal decomposition processes (Bhan et al., 2010; Gruver et al., 2010). Bacterial feeding and fungal feeding nematode communities will be influenced by the quality of the residue. Some studies highlighted an increase in beneficial nematode communities (doubling of bacterivores) after crucifer incorporation (Engelbrecht, 2012; Valdes et al., 2012) even though fungivore nematodes tended to decrease (-25%) in some experiments (Valdes et al., 2012). Interestingly biocidal effects of Indian mustard seed meal amendment were on average double forplant parasitic nematodes than for beneficial nematode species *C. elegans* (Yu et al., 2007). Nevertheless, mustards have been shown to have suppressive effects against entomopathogenic nematodes regulating both insect pests or pathogenic nematodes (Henderson et al., 2009; Ramirez et al., 2009). As a result, biocontrol of insects through entomopathogenic nematodes and biofumigation processes could be challenging (Jaffuel et al., 2017).

The effect of crucifer-legume mixtures on general nematode communities have not been widely studied but Cortois et al. (2017) showed that mixing grasses and legumes increased nematode abundance and diversity compared to pure crops. Interestingly the abundance of all nematode feeding types, except for predatory nematodes, increased with both plant species and plant functional group diversity. There appears to be scope for more studies to assess the effects of crucifer-legume mixtures on beneficial nematodes.

2.3.2 Impacts on macrofauna (vertebrate and invertebrate)

Macrofaunal pest suppression is mainly an issue of concern for cover crop development and biomass production itself, as pest damage to the cover crop or the need for protection with pesticides may reduce the effectiveness or compromise the other ecosystem services of the crucifer cover crops. However, crucifer cover crops can also act as a bridge for some pests of the subsequent cash crop and the potential for these disservices must be assessed.

2.3.2.1 Impact on pathogenic insect macrofauna

Crucifers are commonly attacked by many species of insects that are either specialists or generalists (Ahuja et al., 2010). GSL production can act as feeding deterrents for polyphagous herbivores and feeding stimulant for crucifers specialists (Gols et al., 2008; Kuśnierczyk et al., 2007). *In vitro* studies showed toxic effects of ITC (especially aromatic forms) and other GSL breakdown products on many insects such as Diptera, Lepidoptera, Homopetera, Coleopetera and weevils (Björkman et al., 2011; Brown and Morra, 1997). Both levels of GSL and myrosinase concentration can increase in response to herbivore feeding (Hopkins et al., 2009). Interestingly, wild relatives of cultivated crucifers contain more GSL and both generalist and specialist pest insects are less present on them (Gols et al., 2008). High levels of total and individual GSL and myrosinase can even reduce specialist insects such as root flies, moths, aphids, beetles and weevils (Björkman et al., 2011). Indeed, high levels of GSL have been found to have an impact on development of insect's larvae, pupal weight, eggs, body weight and relative growth rate (Björkman et al., 2011). Nevertheless, some studies found no link between GSL profile and suppression of some crucifers specialists (Moyes et al., 2000). A positive relationship has been found between total GSL concentration and herbivore damage, meaning that crucifer resistance is not simply explained by total GSL levels (Giamoustaris and Mithen, 1995). Thus integrated pest management cannot simply rely on GSL-rich crucifers, but must use other methods such as plant mixtures that can generate less favorable conditions for pest reproduction and development.

Risch, (1983) and Andow, (1991) reviewed effects of various plant mixtures on different herbivore pest species and both found that more than half of the pest species were less abundant in mixtures and that around 15-20% were more abundant. More recently, a meta-analysis of Poveda et al. (2008)

showed herbivore suppression and natural enemy populations increased in 52-53% of cases while Letourneau et al. (2011) found even higher herbivore suppression (-72%) and antagonist increase (-74%) with the same dataset, but using different analysis methods.

As mentioned above, GSL concentration and types are important considerations in crucifer pest interactions, but these can change in mixtures. Couëdel et al. (2018b) highlighted that GSL concentration remained unchanged in roots but slightly increased in the shoots of crucifer cover crops when mixed with legumes compared to sole crucifer cover crops. Furthermore crucifers in mixtures showed no strong changes in GSL types and proportions. Crucifers in mixtures with legumes could therefore be less susceptible to feeding by specialists and generalist insect pests on their aerial parts. Nevertheless variability of responses in GSL concentration were observed between crucifer species and among sites, meaning that more studies are needed to understand better the effects of mixtures on GSL profiles. Furthermore these results were different to those of Björkman et al. (2008) who found decreases in aliphatic and indole GSL concentration when cabbage was mixed with clover, and Stavridou et al. (2012) who found a decrease in indolyl GSL in broccoli florets when broccoli was mixed with lettuce in a substitutive crop mixture design.

The main interest of mixtures for macrofauna pest suppression is to i) disrupt the ability of the pest to find a host due to physical barriers of the companion crop and ii) have repellent effects due the odour of the host plant (Boudreau, 2013; Finch and Collier, 2012). For crucifer crops, the effects of companion legumes on pest abundance have mainly been studied for cabbage and broccoli vegetable production (Hooks and Johnson, 2003). As a companion crop, clover species have been widely used and have reduced many pests on crucifer plants (Finch and Collier, 2000). Overall, legume companion crops have a negative effect on i) oviposition, ii) colonization and iii) tenure time (Hooks and Johnson, 2003). Effects on oviposition have been studied by Ryan et al. (1980) who reported fewer eggs laid (-11%) by *D. radicum* on cabbage when intercropped with white clover. More recent studies showed that the cabbage root fly reduced egg-laying by 36–82% when cauliflowers were intercropped with 24 other non-host plant species (Finch et al., 2003). Height of the intercrop species has been shown to impact visual stimuli leading to oviposition of *P. xylostella*, indeed fewer eggs where laid on white

cabbage when intercropped with tall compared to short red clover (Åsman et al., 2001). Finch and Kienegger (1997) found that subterranean clover must cover 50% of the vertical profile of cabbage species to reduce eight crucifer pest specialists. These studies confirm results of Weiss et al. (1994) that concluded that a lack of camouflage of canola by low growing pea explained that intercropping has no effect on abundance of *P. cruciferae*. Cadoux et al. (2015) concluded that companion legumes intercropped with rape reduced *C. picitarsis* of rape due to a dilution or visual effect. Visual stimuli can also be affected by overall cover color. Indeed crucifer aphids could be reduced by intercropping as aphids respond to visual stimuli to find host plants by contrasting the plant color with the soil color (Kennedy et al., 1961; Kring, 1972). Other studies showed that visual stimuli for cabbage flies can also decrease due to differences in shape and color of leaves when crucifers where intercropped (Altieri and Liebman, 1986; Finch and Collier, 2000; Langer et al., 2007).

Mixtures can be ineffective against some insects when there is a strong ability to find the host such as for *P. rapae* (Reddy, 2017). Interestingly, populations of *P. rapae* and *P. xylostella* were even found to be higher on broccoli mixed with a high diversity of nectar producing plants (from 34 genera) than for the broccoli sole crop (Zhao et al., 1992). In such cases, it is crucial that nectar production of the companion plant doesn't attract further pest insects of the crucifer (Zhao et al., 1992). It is also important that the companion crop doesn't attract pests of the planned subsequent cash crop. For example *A. pisum* can be increased by crimson clover and hairy vetch cover crops (Kaakeh and Dutcher, 1993).

Beyond physical effects, companion plants also combine chemical barriers for insects as their tenure time is reduced in mixed stands as the presence of a complex sensory environment may distract pests from settled feeding (Bernays, 1999). Tenure time of *P. cruciferae* was longer in pure broccoli than broccoli intercropped with faba bean and common vetch (Garcia and Altieri, 1992). These results were confirmed by Elmstrom et al., (1988) who found that *P. cruciferae* had a faster rate of immigration and spent less time on broccoli in mixtures with white clover than in pure broccoli crops.

Mixtures of different crucifer species can also decrease insect abundance. For example, flea beetles (Altieri and Gliessman, 1983; Andow et al., 1986) and aphids (Costello and Altieri, 1995; Kloen and

Altieri, 1990) had lower populations in crucifer-crucifer mixtures. Mixed crucifers can also lead to trap crop systems where one of the crucifers aimed to attract the insect to leave the other crucifer free of attacks. Indian mustard for example, is highly attractive to many insects of cabbage (Hooks and Johnson, 2003). Crucifers can even act as a dead-end as for the weed wintercress (yellow rocket) which was highly attractive for oviposition by female *P. xylostella*, but the larvae could not survive on the plant (Badenes-Perez et al., 2004). A fascinating area of work in relation to insect interactions involves the work to capture the benefits of the ancient intercropping of the GSL-containing mashua with potato in the Andes, in which suppression by the mashua companion plant provides protection from potato weevils (*C. formicarius*) and late blight (*Phytophthora infestans*) (Ortega et al., 2006). Attempts have been made to engineer the benzyl-GSL biosynthesis pathway into the potato leaves to provide *in planta* protection in contemporary potato monocultures (Geu-Flores et al., 2009).

In conclusion, despite several studies dealing with insect suppression by crucifer-legume cover crop mixtures, impacts on several specific crucifer pests have scarcely been studied including cabbage-stem flea beetle (*Psylliodes chrysocephala* and *Phyllotreta nemorum*) or even pollen beetles (*Meligethes aeneus* and *Meligethes viridescens*). Screening the suppressive effects of crucifers and legumes on insect pests along with interactive effects is required to avoid inadvertent disservices resulting from inappropriate mixtures that may exacerbate insect damage within the system.

2.3.2.2 Impact on slugs

Slugs are considered as one of the main concerns for cover crop use due to the potential to act as a bridge for slugs that infest the next cash crop. It is especially a concern for slug-sensitive cash crops such as sunflower, wheat or triticale.

Even if molluscs can be found under crucifer plants (Glen et al., 1990) it has often been found that they avoid plants with high GSL concentration (Barone and Frank, 1999; Byrnes et al., 2014). Nevertheless concentrations of GSL in agriculturally important crucifers are generally lower than wild types and can attract slugs (Stowe, 1998). Field data are lacking on other compounds that can be deterrents for slugs such as terpenes or tannins (Albrectsen et al., 2004; Fritz et al., 2001).

Interestingly grey field slug (*Deroceras reticulatum* Muller) damage has been found to be inversely proportioned to total GSL concentration in rape (Glen et al., 1990) as also confirmed by Giamoustaris and Mithen (1995) for other slugs. Interestingly, it was specifically the increase in 3-indolyl methyl-GSL (glucobrassicin) and 2-phenylethyl-GSL (gluconasturtiin) that were responsible, even when the total GSL concentration decreased.

Reduced sensitivity to slugs has been found for black mustard and *Arabidopsis* when mollusc mucus had been previously applied, due to the activation of the jasmonic pathway, and a higher production of GSL (Falk et al., 2014; Orrock, 2013). Slug damage on plants also attracts natural enemies of slugs through the emission of volatiles via the jasmonic pathway (Walling, 2000). Some studies have shown that crucifer cover crops such as mustard compared to bare soil, can either have no effect or decrease slug abundance prior to potato planting (Frost et al., 2002; Silgram et al., 2015).

Slug palatability can vary significantly between cover crops species (Briner and Frank, 1998; Charles et al., 2012; Le Gall and Tooker, 2017). Palatability of crucifers are generally high for rape, but low for some other crucifer cover crops such as Indian mustard and radish (Robin, 2011). Palatability of legumes are moderate for some cultivated species such as forage pea and crimson clover and low for cover crops such as faba bean and common vetches (Robin, 2011). Compared to other legumes tested, alfalfa had lower slug population growth (Anon, 2002). Slug damage has been found to double after red clover or vetch compared to ryegrass indicating that outside palatability, microclimate and foliage type may also play a role in slug abundance (Vernavá et al., 2004).

Surprisingly given the significant issue with slugs, we found no studies dealing with slug abundance in crucifer-legume cover-crop mixtures, although the studies discussed above suggest interactions are likely to arise between slugs and diversified cover crops. It would appear cover crop screening and mixture interactions could be a useful area of research to seek opportunities to reduce the overwintering of slugs and reduce pesticide use.

2.3.2.3 Impact on beneficial macrofauna

ITCs may attract parasitoids of crucifers pests; for example parasitoids of *D. brassicae* were attracted by traps baited with 2-phenylethyl ITC (*Platygaster subuliformis*) or 2-propenyl ITC *(Omphale clypealis)* (Murchie et al., 1997). The parasitic wasp (*Diaeretiella rapae)* of a cabbage aphid (*Brevicoryne brassicae*) is attracted by 3-butenyl ITC (Bradburne and Mithen, 2000). However, ITCs can also act as repellants to beneficial macrofauna. For example in laboratory experiments, ITCs influenced decomposer organisms such as Collembola *(Folsomia fimetari)* (Jensen et al., 2010), and the beneficial soil arthropod *Folsomia candida* had reduced survival and reproduction when pure 2-phenylethyl ITC at low concentration was applied into the soil (Van Ommen Kloeke et al., 2012).

Overall, cover crops and mulch at the soil surface generally enhance earthworm abundance (Bautista-Zúñiga et al., 2008; Ortiz-Ceballos et al., 2007). In the field, Kabouw et al. (2010) found that a high degree of intraspecific variation in root GSL profiles had no impact on earthworms and Collembola abundance. Furthermore, Fouché et al. (2016) found that broccoli, mustard and oilseed radish had no significant effect on earthworm (*Eisenia andrei*) survival or growth, even if broccoli reduced earthworm reproduction by 37%. Nevertheless, Zuluaga et al. (2015) found that high GSL cabbage cultivars could have toxic effects on springtails and earthworms, and in particular they related this to high levels in aliphatic GSLs.

As for insects pests, the use of mixtures could also impact the abundance of beneficial natural enemies through different barriers (e.g., physical, olfactory). In a general review of various intercropped plants and various beneficial species, Andow (1991) found that the population of natural enemies of pests was higher in the intercrop or species mixtures in 53% of the studies, and lower in 9%. Indeed the main hypothesis was that if parasitoids have a strong association with their insect host and/or with their host plant, this will not be affected in a mixture (Andow, 1991). However, some studies suggested that predators may be more sensitive to habitat type than to prey density (Hooks and Johnson, 2003).

It is therefore necessary to study the impact of species mixtures on both the pests and antagonists at the same time in order to identify conditions where antagonists are enhanced at the expense of pests,

and to avoid the risk of suppressing antagonists without impacts on their pests. For example cabbage intercropped with white clover reduced the number of *D. radicum* pupae per plant but also the probability that the pupal parasitoid (*Aleochara bilineata*) located in plants infested with *D. radicum*. Reductions in overwintering *D. radicum* could then be mitigated by a decrease in pupal parasitism in this system (Brown and Anderson, 1999). Similarly, compared to broccoli sole crops, Costello and Altieri (1995) found a lower incidence of the parasitoid Braconidé *Diaretiella rapae* on aphids (*Myzus persicae* and *Brevicoryne brassicae*) for a few different species of clovers and trefoil intercropped with broccoli. More antagonists of aphids (*Brevicoryne brassicae*) were found when broccoli was intercropped with mustard, and this resulted in lower aphid infestation (-40%) (Ponti et al., 2007). Interestingly, faba bean intercropped with rape was shown to attract an aphid antagonist (*Diaeretiella rapae*) due to nectar production (Jamont et al., 2014; 2013a).

Plant diversity through broader diets could also be useful to keep a level of specialist predators that may face periods of inadequate prey availability (Limburg and Rosenheim, 2001). As for microbial communities, high organic matter accumulation from diversified biomass can increase diversity of macrofauna such as decomposers (Brown and Oliveira, 2004). Communities of worms seem favoured by legumes (Ortiz-Ceballos et al., 2007). Crucifer-legume mixtures could be interesting to avoid potential negative effects of crucifers on worms as highlighted above. Cover crop legumes as sole crops are especially interesting to increase carabid activity-density (O'Rourke et al., 2008), but can also have similar effects when intercropped with wheat compared to wheat alone (Carmona and Landis, 1999). Alfalfa and kura clover intercropped either with maize and soybean can also increase carabid abundance (Prasifka et al., 2006).

A higher diversity of cover crop plants could also attract natural enemies through nectar and pollen sources for predatory insects such as shown with the use of crimson clover when grown with cotton (Tillman et al., 2004). Indeed diversified covers can enhance higher abundance and diversity of pollinators through complementarity in flowering properties such as flower nutritional value and blooming date resulting in a longer flowering period (Bretagnolle and Gaba, 2015; Potts et al., 2010; Pywell et al., 2005). Differences among the effectiveness of crucifer species to attract pollinator

insects has been previously highlighted (Eberle et al., 2015). For example, *Camelina* spp. showed higher pollinator visits than pennycress but intercrops of both species may bring higher diversity of pollinator (Groeneveld and Klein, 2014). Forage legumes have been shown to be especially interesting for bumblebees, but there is a lack of information on other non-dominant groups of pollinator (other than *Apidea*), and very few data exist for other legume cover crops (clovers, vetches, lupin etc). Nevertheless, Ellis and Barbercheck, (2015) reported that flower density was a key factor influencing the frequency of bee visitation and that this density can logically decrease in mixtures due to "dilution phenomenon". They showed that canola attracted more bees than both pea and red clover, and that canola cropped alone attracted more bees than when mixed with 3 or 5 other species including legumes, radish and rye. Potts et al. (2010) confirmed these results by showing that plant diversity *per se* did not increase bumblebee abundance, but species mixtures that increased flowering plant density did. Ellis and Barbercheck (2015) also reported that these different cover crops attracted unique bee communities through different blooming phenology and nutritional values that may increase the diversity of pollinator communities.

[Insert Figure 4 here] Figure 4. Examples of services and disservices provided by cover crops on a wide range of pathogens and beneficial organisms. Crucifer sole crops may favor (green text), suppress (red text) or have neutral/less well understood effects (blue text) on living organisms. Crucifer-legume mixtures may favor (⬆), suppress (⬇) or have unknown effects (no arrow) compared to crucifer sole crops.

2.4 Interactions and trade-offs for indirect biotic suppression

As shown on Figure 5, many links exist between different organisms that could increase the impact of cover crops on pathogens, and these interactions are considered in this section.

Beneficial macrofauna can play a key role in pest regulation as they have an impact on weeds, pathogenic fungi and pathogenic nematodes. For example, ground beetles (Coleoptera: *Carabidae*) act as antagonists of weed seeds, other insects and slugs (Bohan et al., 2011). High levels of earthworms coupled with trefoil cover crops decrease pathogenic nematodes (Boyer et al., 1999). Effects of earthworms could be mediated by i) macropore creation that could impair nematode movements and ii) direct feeding on nematodes (Blanchart et al., 1999; Boyer et al., 2013). High acarian density following mulch was also found to reduce abundance of plant parasitic nematodes (Badejo et al.,

2002; Peachey et al., 2002). Weed seed predators such as carabid are enhanced by cover crops (Gallandt et al., 2005; Ward et al., 2011) and high levels of weed predation have been reported by Heggenstaller et al. (2006) and Puricelli et al. (2005) in different cropping systems. Complementarity for weed predation has also been found between vertebrate and invertebrate macrofauna (Harrison et al., 2003). Furthermore, Ang et al. (1995) observed a competition synergy on weed suppression (Creeping thistle) between cover crops (tall fescue and crown vetch) and the weed seed predator *Cassida rubiginosa*. The suppression of weeds is important as they can act as a biological bridge to enhance plant parasitic nematodes and arthropod pests through host effects (Norris and Kogan 2005, Creech et al. 2007, Groves et al. 2001). Cover crop choice becomes complex as cover crops resistant to plant parasitic nematodes are not always the best to suppress weeds (Damour et al., 2014).

Otherwise, entomopathogenic nematodes play an interesting role to suppress pest insects. Nevertheless mustard cover crops used to suppress plant parasitic nematodes had a negative effect on beneficial entomopathogenic nematodes (*Steinernema* spp. and *Heterorhabditis* spp.) and decreased associated insect pest control (Henderson et al., 2009; Ramirez et al., 2009).

Insect pathogenic fungi such as *Hypocreales* spp. are known to kill pathogenic nematodes (Klingen et al., 2002b; Meadow et al., 2000). Those within the order of *Entomophthorales* are antagonist of *D. radicum* and *D. floralis* (Klingen, 2000; Klingen et al., 2000). Interestingly, ITC released by rocket was found to be toxic to germination and growth of insect pathogenic fungi of *Galleria mellonella in vitro,* while no inhibition on *Tolypocladium cylindrosporum* and an enhancement of *Metarhizium anisopliae* (*M. anisopliae*) insect pathogenic fungi was observed in soil in microcosms (Klingen et al. 2002a). Soluble extracts of other crucifer species can enhance germination and development of *M. anisopliae* on the mustard beetle (*Phaedon cochleariae*) (Inyang et al., 1999). Another study showed that cover crops and other practices enhancing soil biological diversity enhanced insect pathogenic fungi *M. anisopliae* and *Adelina* sp. and increased suppression of larvae population of the Coleoptera *Antitrogus parvulus* in sugar cane crops (Allsopp et al., 2003).

These interactions and biological regulations between living organisms represent an interspersing of indirect biocontrol effects of cover crops, especially when beneficial macrofauna and insect pathogenic fungi can be enhanced.

[Insert Figure 5 here] Figure 5. Specific examples of biotic interaction between living organisms providing indirect pathogen suppression from pure crucifer cover crop use. Green, red and black frames respectively represent positive, negative and neutral (or poorly understood) effects of crucifer sole cover crop on living organisms. Green and red arrows represent positive and negative effects respectively occurring between living organisms and relevant literature are provided.

2.5 Summary of research opportunities to support a new multiservice paradigm

Our review of the pest and disease suppression potential by crucifer sole crops reinforces the widely reported pest-suppression potential they exhibit, although the suppressive potential is clearly quite variable for different target organisms. Disservices generated by negative impacts on beneficial organisms were scarce and may not represent a strong concern when selecting a crucifer cover crop for biocontrol. Often there was a focus on individual crucifer species for suppression of a given pathogen, and there may be potential to consider a more diverse range of crucifer species. In that context, definitive links between pathogen suppression and GSL-derived allelochemicals, previously emphasized by Matthiessen and Kirkegaard (2006), were still missing from many studies. Such links are important to make informed selections of specific crucifers rich in biocidal GSLs where this forms a critical service for the cover crop. However, disease suppression was not always associated with higher GSL-producing crops, and was also observed with non-crucifer crops to a similar degree, indicating that other mechanisms and interactions are important. In that sense, sole crucifer cover crops may not always be the best solution to suppress pathogens. The level of added organic matter needed for pathogen suppression may be a more important driver of pest suppression, and then it becomes important to understand the relative merits of sole crops and mixtures. It can be a difficult methodological task to separate experimentally these effects, as the amount of organic matter added is also linked to allelochemical production in most cases. Experiments including appropriate control treatments without biocidal molecules are needed to separate these effects (discussed further in Section 3).

The summaries in Table 6 and Figure 4 emphasise the overall lack of experiments dealing with the suppressive effects of cover crop mixtures on soil-borne fungal and bacterial pathogens. Above-ground organisms such as insects and weeds have been the focus of several studies on cover-crop mixtures which may relate to the relative ease with which they can be monitored compared with below-ground pathogens such as fungi and bacteria. Thus the impact of mixtures on a wide range of belowground organisms, both pathogenic and beneficial, remains to be investigated. For crucifer-legume mixtures, the main concern in terms of pathogen management is to select the best species mixtures for suppressive effects that also avoid pest enhancement (through hosting). Screening both crucifer and legume species of interest for host status of the most relevant pests and pathogens is a first crucial step. Screening at the cultivar scale may also be a necessary refinement as host, non-host and allelopathic potential have all been shown to be potentially cultivar dependant (Asaduzzaman et al., 2013; Damour et al., 2014). Beyond the host status effects, below-ground interactions in species mixtures for key beneficial organisms such as AMF and rhizobia are also of interest to avoid the potential nutrient disservices of the cover crop mixtures. Recent advances in molecular techniques applied to the ecology of soil-borne organisms provide a major advance to help unravel below-ground interactions in mixtures (Canfora et al., 2016; Orgiazzi et al., 2015; Yang et al., 2014). These new tools overcome some of the difficulties in measuring and monitoring the populations and dynamics of fungal and bacterial pathogens and provide significant scope to shed light on the potential for multi-services provision of crucifer-legume mixtures.

3. Towards improved understanding of mechanisms behind pathogen suppression

This review highlights the numerous mechanisms involved in pest suppression by cover crops and the importance of careful selection of appropriate cover crop species for use in mixtures. Several aspects of experimental design and approach must be considered to generate improved understanding of such mechanisms.

3.1 Isolating GSL effects

When using crucifers, it is important to know whether GSL production has an effect on the organisms of interest or not (e.g. Vervoort et al., 2014), as the choice of crucifer (or not), and an appropriate species and cultivar depends upon it. The use of non-GSL containing plants as controls, or more ideally crucifer cultivars with high and low concentrations of specific GSLs, are useful tools in this regard (Kirkegaard 2009). Many studies used low and high GSL-containing plants to determine GSL biocidal effects, but a control with a crucifer containing no GSL is ideal as the threshold of toxicity is unknown, and low GSL production could still engender biocidal effects. For example, canola double 0 ("00") or canola quality Indian mustard cultivars producing very low seed GSL levels are often not suitable as GSLs are still produced in the shoot and root tissues in appreciable quantities (Kirkegaard et al., 2000), though some lines with close to undetectable levels of specific GSLs have been identified. Another approach used to create GSL-free crucifer effects is to transgenically remove the myrosinase cells, as shown for rape seeds by Borgen et al. (2010) and so limit the hydrolysis to ITCs. However myrosinase enzymes are also present in the soil and can transform GSL released from crucifers into biocidal compounds which can limit this approach in non-sterile soils (Gimsing and Kirkegaard, 2009). On the other hand, the biosynthetic pathways of GSL in plants are well known and knockout mutants lacking the gene responsible (CYP79) can be designed to create non-GSL containing plants used for experimental controls. Halkier and Gershenzon (2006) even report that future metabolic efforts could provide the possibility to design crucifers free of certain GSLs, permitting an even deeper analysis of the effects of individual GSL on plant pathogens. Indeed crucifers always produced more than one GSL, and it is key to isolate individual GSL effects to guide crucifer selection based on levels of individual GSLs. This approach could also unravel the confusing "cocktail" effects resulting from the interaction of different GSLs produced by a single cultivar. Understanding such GSL cocktail effects is a major challenge as it could unravel unexpected causes of pathogen suppression and lead to an even higher biocontrol potential.

In the case of crucifer - legume mixtures, allelochemical cocktail effects are especially interesting to assess as legumes also have specific and different allelochemical properties. The biofumigation potential of mixtures could be more thoroughly tested against both sole crucifer and legume cover

crops for the specific pathogens of interest. Mixtures containing GSL-free crucifers could also be compared especially on beneficial microbe populations and on legume growth, as GSLs produced by crucifers could impair the N services provided by the legumes. Concerning herbicide effects of crucifers, if no GSL-free cultivars are available, clues of GSL effects are still possible to achieve using experimental designs aimed to isolate allelochemical effects. For example biocidal effects of crucifers on companion legumes could be assessed in a similar way to that of Falquet et al., (2014) for weeds, by trying to isolate competition for aerial resources from the allelopathy brought by crucifers (Figure 6).

[Insert Figure 6 here] Figure 6. Experimental design to differentiate effects of light competition from other effects on pigweed suppression by buckwheat in Switzerland (© Judith Wirth).

3.2 Systems agronomy approach for better biofumigant management

Even when GSL-related effects are proven through well-chosen controls, it is always in a specific soil and climate context. Biofumigation efficacy is difficult to generalise as GSL conversion to ITCs and the fate of ITCs in soil for a targeted organism is highly dependent of pedoclimatic conditions and agronomic practices (Figure 7) (Gimsing and Kirkegaard, 2009). Thus a theoretical mechanistic "pesticide" approach linking GSL production per area and fate of GSL to predict overall toxicity of biofumigants seems complicated under field conditions due to a "Pandora's Box" phenomenon (see Figure 7). Moreover, the initial GSL production by cover crops is also dependant on these conditions and also highly variable even when using the same cultivars (Björkman et al., 2011).

A new multi-service paradigm based on a systems approach taking into account agronomic practices and other mechanisms responsible for biocontrol is needed to make better species choices and guide biofumigant management (Figure 7) (Kirkegaard and Matthiessesn 2004; Matthiessen and Kirkegaard 2006; Kirkegaard 2009). First it is important to understand when biocontrol effects occur as it can happen both during the growing period of the cover crop and after cover crop termination (e.g Motisi et al., 2009). If biocontrol mainly occurs before termination, less effort is required to optimize incorporation. Timing and termination techniques can also significantly influence efficiency of biocontrol through allelochemical fate, decomposition of organic matter and soil structure (Gimsing and Kirkegaard 2009), but to date, this has not been the focus of many field studies.

Correct assessment of biofumigation effects on pests and beneficial organisms is required to assess both services and potential disservices, and this can be challenging in the field. In that regard, novel soil ecology approaches based on new DNA monitoring of populations or inoculum levels of a wide range of both pest and beneficial organisms is a relatively new tool that is providing new insights into the effects on the soil biological systems (Canfora et al., 2016; Orgiazzi et al., 2015; Yang et al., 2014). However, practitioners must be careful to remain focussed on the most important interactions, as the amount of data emerging from these studies while interesting, can also distract attention from those interactions that drive the sustainable productivity of the system.

[Insert Figure 7 here] Figure 7: Representation of the pesticide based approach initially used for the biofumigation concept versus an approach designed to optimize biofumigant management for multiservice provision. (Equation from Kirkegaard and Sarwar (1998); BP = biofumigation potential for a particular target organism; Biomass total = biomass of whole cover crop; [GSL] = total GSL concentration; $Toxicity_{GSL}$ means toxicity of a specific glucosinolate.

3.3 Links between biotic and abiotic services of multi-service cover crops

Beyond the biotic services considered in this review, MSCC also bring many abiotic services such as improved soil properties, better nutrient cycling and greenhouse gas emission mitigation (Kaye and Quemada, 2017; Thorup-Kristensen et al., 2003). Multiservice approaches taking into account abiotic and biotic services are growing (Therond, 2017), and are key to correctly assess the overall effect of cover crops (Justes et al., 2012; 2017; Finney et al., 2017; Schipanski et al., 2014). Nevertheless in a meta-analysis, Seppelt et al. (2011) found that 50% of studies analyse individual services without considering interactions with other services. This multiservice approach has often been used at the landscape scale (Maes et al., 2012; Raudsepp-Hearne et al., 2010) but few studies at the agronomic plot or field scale assess interactions between biotic changes after cover crop use and abiotic services (Therond et al., 2017).

Two common examples of the interests of biotic services brought by cover crops leading to abiotic services are earthworm and nematode population enhancement. A well-known example of interactions between biotic and abiotic services is the role of earthworms to improve soil structure, decompose organic matter, stimulate microorganisms and contribute to the carbon and other nutrient cycling in soil (Jefferey et al. 2010). Indeed earthworms hasten the degradation and incorporation of restudies

(Ortiz-Ceballos et al., 2007), improve the cohesion among and between aggregates (Kinderiene, 2006; Reeleder et al., 2006) generate better vertical porosity (Shipitalo and Le Bayon, 2004) and incorporate nutrients in aggregates (Fonte et al., 2007).

Cover cropping usually increases the diversity of beneficial nematodes communities. Nematodes are in general considered as good indicators of soil physical and chemical proprieties (DuPont et al., 2009; Porazinska et al., 1999), and the structure of the community has been linked to nitrogen (Ferris et al., 2004) and phosphorus mineralization (Takeda et al., 2009) as well as plant productivity (DuPont et al., 2009). However, clearer and convincing relationships between the populations or activities of these organisms and the functioning of the cover crop in delivering beneficial services to the system must be demonstrated to encourage adoption of such strategies.

Cover crop biomass can be considered a key indicator for both biotic and abiotic services since without sufficient growth the MSCC will not provide sufficient services and secondary metabolites may not be produced in sufficient quantity (see Figure 8). Indeed for a given cover crop species, high cover crop biomass leads to better carbon sequestration, better nutrient uptake and recycling (Thorup-Kristensen et al., 2003) as well as better soil structure through root de-compaction processes and the higher levels of organic matter added. Nevertheless high cover crop biomass can also lead to abiotic disservices, such as pre-emptive competition for water and nutrient resources compared to bare soil (Figure 8) (Thorup-Kristensen et al., 2003; Thorup-Kristensen and Kirkegaard, 2016). High cover crop biomass generally improves the suppressive mechanisms involved in pest and pathogen suppression as highlighted in Figure 8. Through an overall increase in biomass production compared to sole crops (Tribouillois et al., 2016), mixtures can improve both abiotic and biotic services to enhance better cash crop yields. Indeed the biomass produced by mixtures is enhanced due to the potential to better suppress crucifer and legume pathogens, and a better resource use efficiency (nutrients, light, water …). Over years and sites, mixtures could also be seen as a way to increase the likelihood of maintaining high levels of biomass under variable seasons, where conditions may be less favourable for one component of the mixture, although we can find no experiments or meta-analyses to validate this hypothesis (Smith et al., 2014; Wortman et al., 2012). However in a meta-analysis dealing with

harvested cash crops, Raseduzzaman and Jensen (2017) found that cereal-legume intercrops increased resilience compared to sole crops through reduced yield variability. Another interesting aspect of cover crop mixtures is their capacity to mutualize services through species characteristic diversity. Interestingly, Finney et al. (2017) concluded that multi-specific cover crop mixtures did not necessarily increase the levels of individual services compared to the best of the sole cover crops but decreased the levels of disservices generated by the sole crops. This emphasises the importance of considering all of the potential impacts of changing from sole crops to mixtures rather than focussing on a specific mechanism of interest.

[Insert Figure 8 here] Figure 8. Biotic and abiotic services through enhanced cover crop biomass production in mixtures. Full lines represent enhanced effects while dotted lines represent decreased effects compared to sole crucifer cover crop. Black arrows represent increased (⬆) and decreased (⬇) effects in mixtures compared to sole crucifer cover crop.

3.4 The multi-service paradigm to guide cover crop selection

As cover crops can impact many aspects of the production system, a multiservice paradigm is a relevant approach. A single focus (e.g. biocontrol from specific natural compounds such as GSLs) ignores both the other services from the crucifer (organic matter input, trap crop, soil structural improvement) as well as those that may arise from a legume in the mixture (N services). A key practical question remains the selection and the assemblage of species, and also the choice of cultivars.

We propose a 3-step multi-criteria approach to assist better cover crop selection and to provide a framework to consider the merit of mixtures. The level of information required regarding some aspects of the approach also points to numerous ongoing research gaps. (Figure 9).

3.4.1 Step 1: Selection of objectives based on multi-services

Step 1 (Figure 9) considers the main services targeted and the level of compromise between services, to guide the selection of species or the proportion of species in mixtures. We assume there is no single cover crop species or approach that will suit every situation and objective.

Field characteristics such as chemical soil fertility may influence the choices made. For example on poorer soils, a high percentage of legumes in the mixture may be advised as catch crop services are less relevant, while nutrient green manure effects may be significant. In the case of more fertile soil,

species with high catch crop properties could reduce nutrient losses and avoid groundwater pollution. Physical soil fertility improvement through soil de-compaction would suggest use of cover crops with strong taproots or mixtures with different rooting systems. Specific pathogen suppression may also be optimized with the use of specific crucifer or legume species Antagonisms between desired services and unwanted disservices may occur (e.g. green manure effect of legumes are incompatible with *Aphanomyces* suppression). Therefore one classification of the services according to short- and long-term effects is also important when selecting a cover species, including the profitability for farmers.

Farmers may conduct their own *in situ* experiments to address issues of interest and pertinence regarding cover crops choices according to their objectives and the desired services. Many cover crop management options may be tested prior to identifying the optimum MSCC system. The "learning curve" process of farmers must also be taken into account on many components of cover crop management (e.g. sowing and termination methods and timing) to improve the chances of achieving the multiservices targeted (White et al., 2016). By increasing the research in these areas, advisors and producers will have access to additional resources and be better equipped to optimise cover crop techniques on their farm.

3.2 Step 2: Assessing and improving multi-services provided by cover crops

Selection of cover crop cultivars is significantly less advanced than for cash crops and to date has been mainly based on biomass production and nitrogen catch crop traits. Few cultivars have been specifically breed for biofumigation by maximizing GSL (or other allelochemical) production (Indian and white mustard species) (Lazzeri et al., 2004)). Significant potential exists to better use the genetic variability offered by crucifer and legume cover crop species to achieve multi-services properties, but there is a great need for robust cover crop characterization of cultivars or available germplasms.

Based on our own experiments (Couëdel et al., 2018a, 2018b, 2018c), Figure 9 shows an example of multi-services to evaluate cover crops. Even on cultivars already certified and used, we report significant knowledge gaps on the capacity of cover crops to capture and recycle nutrients other than nitrogen. Nutrients such as S, Ca, Mg, K and Mg are subject to leaching and represent a major source of economic loss and pollution when lost in ground water. Other nutrients such as P are more subject

to run-off and cover crops could play a key role in their recycling. In our experimental conditions, we found no major differences between cover crop species of the same family for a single abiotic service such as catch crop or green manure, but screening is needed in other conditions and for longer growing periods (fallow period >3 months) to confirm this. Despite some data on such abiotic services, data on the biocontrol potential of many cover crops (GSL production, weed control, impact on pathogen and beneficial organisms) is lacking. Potential disservices such as disease hosting, invasive characteristics of the cover crop species (through seed production) require special vigilance during the selection process.

Assessment of species mixture performance for nitrogen-related services are available, but data are lacking on many other services. Special selection of plant traits for better complementarity of abiotic resource use and pathogen control would provide the basis to improve multiservices in mixtures (Figure 9). The ecological theory "the more diverse, the better" of cover crop mixtures must be challenged and confirmed, as bispecific mixtures could be effective and sufficient to generate a significant improvement in multi-services provision while reducing management complexity and avoiding unwanted species competition (Smith et al., 2014).

3.3 Step 3: Agronomic considerations

Key technical opportunities and constraints influencing agronomic and economic cover crop performance occur mainly at sowing and termination as cover crops do not require intensive management during their growth in the fallow period between two cash crops. Sowing costs, emergence dynamics and sensitivity to termination methods are the main specific agronomic issues to take into account when choosing cover crop species (Figure 9).

Seed costs represent a significant cost of establishment (Bergtold et al., 2017), and seed costs, seeding rate and uncontrolled factors, such as seed availability can be highly variety dependant. Few studies have identified the optimal density for a targeted service (mainly a high level of biomass), yet it is the main way to reduce sowing costs. Special care has to be taken when advising seeding density as low recommendations could be risky in the case of inadequate crop emergence and could produce very heterogeneous covers. Seeding density should then be condition specific (weather, soil). Species

mixtures could be seen as an interesting solution to spread the risk in the case of non-optimal crop establishment, but are generally more costly than sole crops, in particular the most common crucifers (Figure 9). Sowing of mixtures may also require species with similar seed size, as successful emergence of cover crops from a given depth is dependent on it (Tribouillois et al., 2018).

Ensuring good cover crop emergence is a major challenge and one of the main sources of variability in obtaining the desired ecosystem services in regions with hot and dry summers (Teixeira et al., 2016), with high temperatures, high evaporation and low rainfall. Therefore cover crop choice should also depend on thermic and water conditions in the seedbed since species have different sensitivity to these abiotic stresses. In a laboratory study, germination of legumes was more sensitive than crucifers to high temperatures while only radish and turnip seemed to have less water stress than other crucifer or legume species (Tribouillois et al., 2016b). Even if field data are lacking to advise on the emergence of species depending on soil and climate conditions, modelling has been used to predict emergence date of cover crops in different geographic zones depending on water availability and temperature (Constantin et al., 2015a, 2015b; Tribouillois et al., 2018). Predicting germination rate and emergence date for different species could be especially interesting in mixtures, as it could influence the interactions and the levels of services provided.

The interaction of cover crop growth with soil type and climate, has an impact on the method of termination. Tillage and herbicides are relatively efficient termination methods whatever cover crop species is used, however these methods have many drawbacks such as environmental and economic costs (Lu et al., 2000). Other mechanical termination such as rolling or incorporation at low depth provides an alternative approach but success is highly variable between species. Mustard species are relatively easy to terminate while crucifers with strong tap root (radish and turnip) and legumes species are more difficult to kill. Frost killing is the best solution but is not always guaranteed in temperate and Mediterranean climates even during winter. Interestingly some species such as white mustard or Egyptian clover can be winter killed by frost in harsh winters reducing termination costs. Termination of cover crop mixtures is even more challenging as species can be at different growth

stages, have different sensitivity to herbicides or mechanical termination methods. Selecting species with similar requirements can improve termination success.

In conclusion, despite promising techniques to successfully establish and terminate multi-services cover crops, there is little published literature on the agronomy to economically optimise management of specific cover crop species, and even less for cover crop mixtures.

3.4 Using the multi-service guideline

To illustrate the use of the multi-step guideline proposed in Figure 9, we provide two contrasting situations where cover crop choice is considered in different initial cropping conditions with different objectives.

In case of northern European cropping conditions, with pedoclimates and cropping systems highly sensitive to nutrient leaching (due to high rainfall during fallow period) and poor in nutrient content, the objectives of desired services (step 1) would include a strong catch crop, green manure effects and weed control. Crucifer-legume mixtures could be advised to mutualise both services of nutrient catch crop and nutrient green manure effects (Step 2). Couëdel et al. (2018c) showed good complementarity of growth for clover and vetch species with many crucifer species. Mustard - clover spp. or mustard - vetch spp. mixtures could also be a good option when targeting multi-services from cover cropping. Legume species choice could depends on climatic conditions as Egyptian clover (i.e cv. Tabor) is highly sensitive to frost while crimson clover (e.g. cv. Cegalo) is not. We showed in this review many examples where white mustard has a strong weed suppression without generating strong disservices on beneficial organisms. Many fungal diseases can also represent a strong factor limiting cash crop production in humid climates. For example, white mustards have been showed to efficiently suppress *R. solani* in sugar beet or potato systems (Larkin and Griffin, 2007; Motisi et al., 2009) but legumes may need to be avoided as they can be host of the fungi. In that case trade-offs between disease suppression and nitrogen green manure by legumes must be considered (step 1 and 2). Step 3 shows that mustard is also easy to terminate but not clover and vetches, meaning that special care has to be taken during termination.

In case of dry fallow periods with high temperature in summer, combined with compacted soils such as in southern Europe or Australia, objectives would be to include nutrient green manure services combined with soil de-compaction. Indeed in areas with low rainfall, drainage and then nutrient leaching rarely occurs and catch crop effects of cover crops may not be important, while pre-emptive competition for water and N may be critical issues. Crucifers with strong taproots and low water use and good tolerance of stress can be advised such as radish or turnip for soil de-compaction, while a high density of legumes tolerant to temperature and water stress such as Egyptian clover could also be considered (step 2 and 3). Warmer climates can also induce higher insect pest damage on crucifer cover crops and inclusion of legume has to be considered as a repellent solution (step 1 and 2). Tall cultivars of Egyptian clovers could then be chosen as a visual and physical insect repellent to protect radishes and turnip from flies or weevils attacks for example (step 2). Despite high sensitivity of many fungal diseases to humid conditions, some are still harmful in warm and dry climates such as *G.tritici* (step 1). Canola and Indian mustard cover crops are interesting to suppress *G.tritici* and can be used in mixtures as legumes are also break crops (step 2).

In these two examples, steps 2 and 3 are interrelated and must be considered together after a first phase of objective selection. Objectives of step 1 may need to be classified by order of importance and trade-offs have to be clearly assessed, as antagonism can occur between multi-services targeted.

[Insert Figure 9 here] Figure 9. Three-step guideline to improve cover crop species choice. “0”, “+”, “++”, “+++” mean respectively almost zero, low, medium and strong knowledge for each service or agronomic characteristic. Pink, light green and dark green colours mean respectively low, medium and strong level of performance for each service or agronomic characteristic. White frames mean that not enough data are available on level of performance, and may represent research opportunities.

Conclusion

This review suggests crucifer-legume cover crop mixtures may be a promising approach to increase the multi-services in cropping systems. The biofumigant services of crucifers could be largely maintained in species mixtures while some of the disservices on beneficial organisms could be potentially decreased. However while there are a few field studies on different aspects of species mixtures, there is a dearth of comprehensive multi-disciplinary studies that adopt a multi-services

paradigm, so that many of the theoretical hypotheses for the benefits of mixtures have not been demonstrated to date. It is clear that there must be special care taken in cover crop selection of species in mixtures to avoid pathogen increase and incompatibility of crop growth between the species which can reduce the effectiveness of mixtures. Within the broad range of tools available in agro-ecological crop protection, multi-service cover crop mixtures cannot be seen as a stand-alone solution to manage pests and pathogens, but it is likely that adequate levels of control will require combinations with other pest management tactics. By taking a wider systems approach, beyond pest management, by using a multi-services paradigm, cover crops may enhance the physical, chemical and biological fertility of the soil. Understanding the trade-offs between abiotic and biotic services within a systems approach is now key to assess services and disservices provided by cover crop mixtures.

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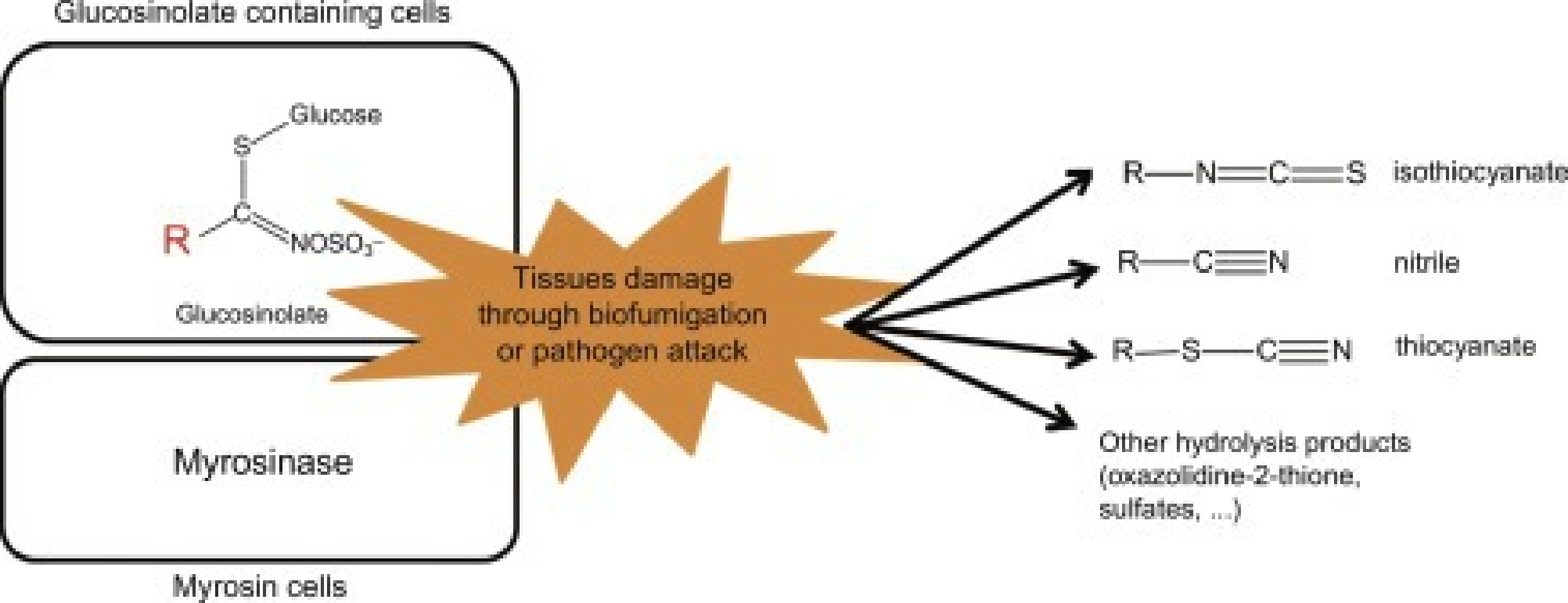
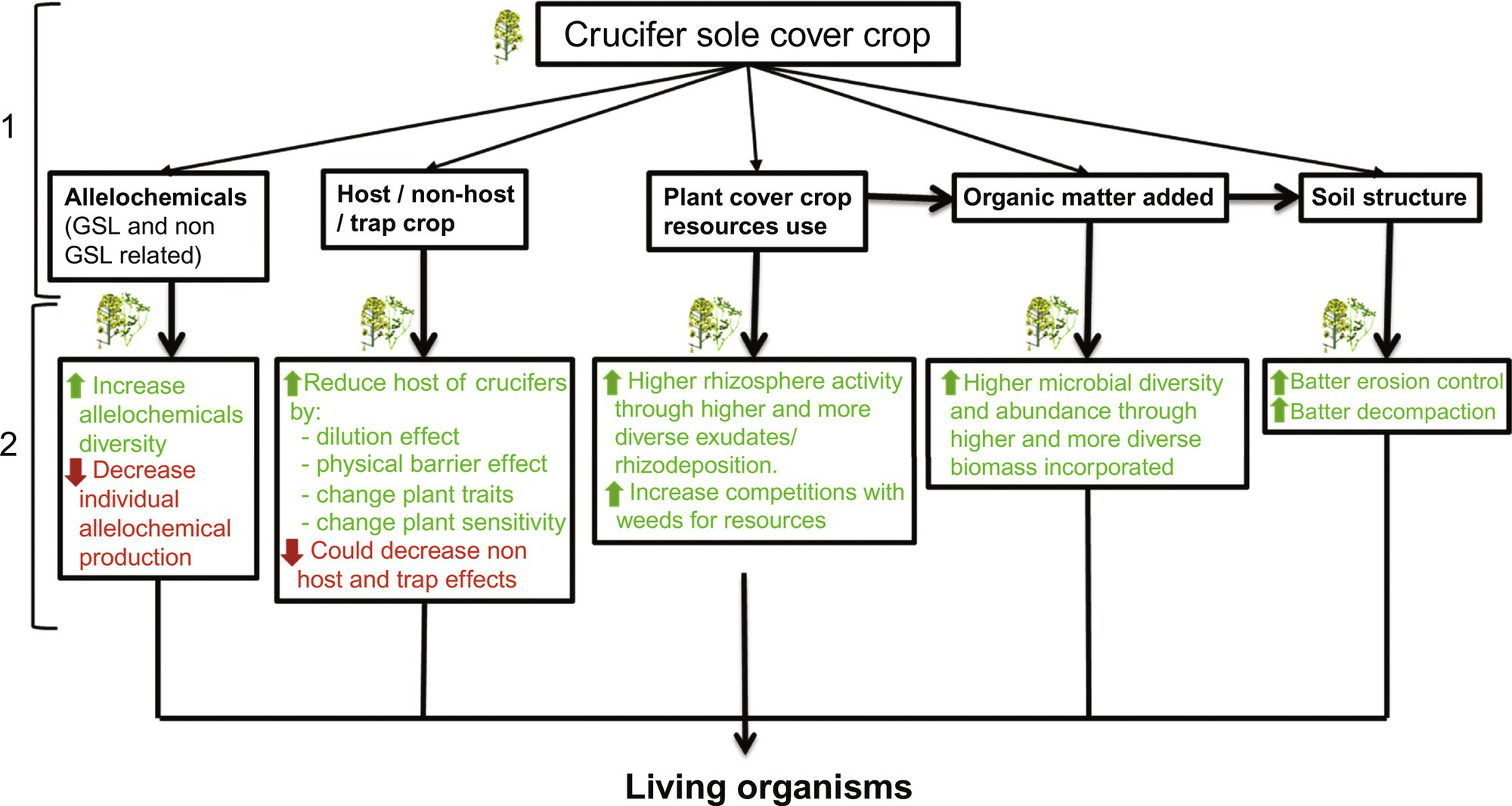

Glucosinolate containing cells
Glucose
S
C
R
NOSO3-
Glucosinolate
Myrosinase
Myrosin cells
Tissues damage
through biofumigation
or pathogen attack
R—N=C=S
isothiocyanate
R—C≡N
nitrile
R—S—C≡N
thiocyanate
Other hydrolysis products
(oxazolidine-2-thione,
sulfates, ...)

A
B
C
D


Crucifer sole cover crop
1
2
Allelochemicals (GSL and non GSL related)
Host / non-host / trap crop
Plant cover crop resources use
Organic matter added
Soil structure
Increase allelochemicals diversity
Decrease individual allelochemical production
Reduce host of crucifers by:
- dilution effect
- physical barrier effect
- change plant traits
- change plant sensitivity
Could decrease non host and trap effects
Higher rhizosphere activity through higher and more diverse exudates/ rhizodeposition.
Increase competitions with weeds for resources
Higher microbial diversity and abundance through higher and more diverse biomass incorporated
Batter erosion control
Batter decompaction
Living organisms

= impact on pathogens

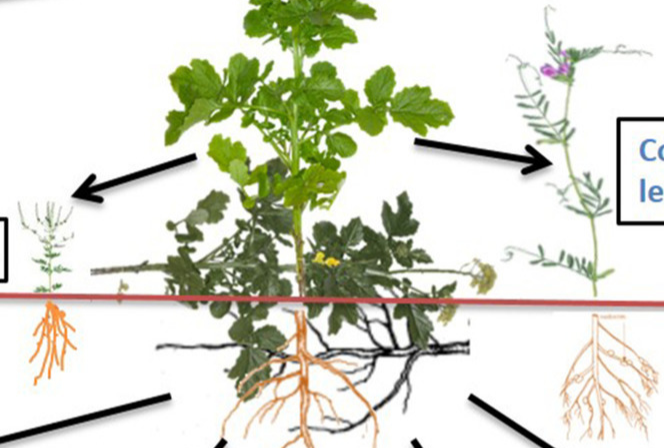
= impact on beneficials

Aerial pathogenic macrofauna
Aphids ⬇
Beetles ⬇
Flies ⬇
Slugs

weeds ⬇

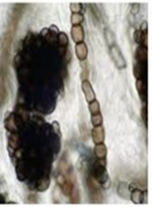
Aerial beneficial macrofauna
Bees ⬆
Arthropods ⬆

Companion legume



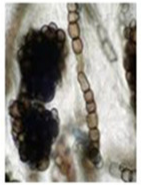
Next crop ⬆

Pathogenic fungi and bacteria
R. solani
G. tritici
V. dahliae
A. euteiches ⬆
R. solanacearum
S. scabies
Fusarium spp.
Sclerotinia spp.
Pythium spp.

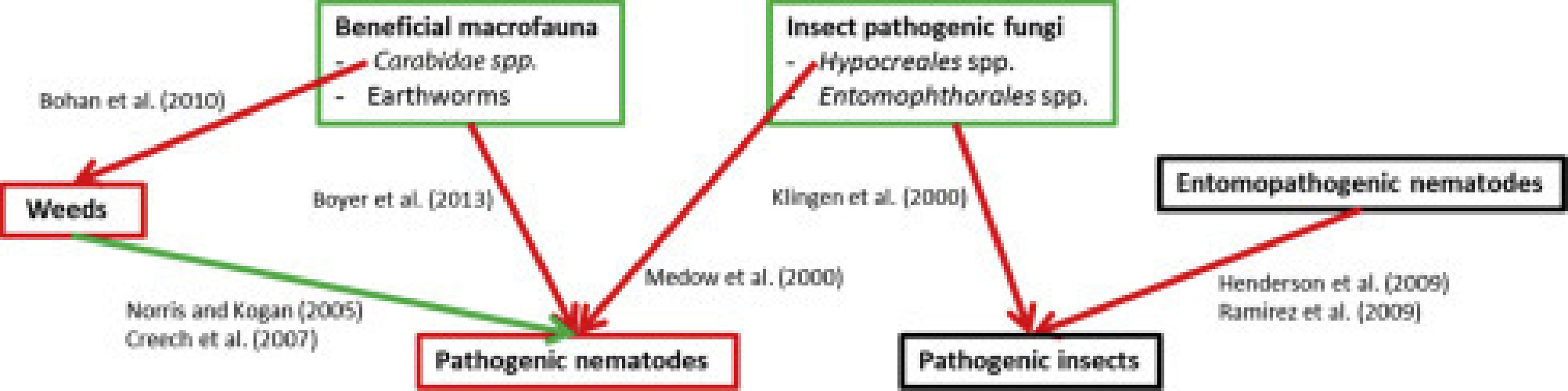


Pathogenic nematodes
M. incognita
P. neglectus
H.schachtii

Beneficial microbes
Mycorrhizae
Nitrifying bacteria ⬆
Rhizobium ⬆
Trichoderma spp.
General microbes



Underground beneficial macrofauna
Beneficial nematodes
Earthworms


Beneficial macrofauna
- Carabidae spp.
- Earthworms
Insect pathogenic fungi
- Hypocreales spp.
- Entomophthorales spp.
Entomopathogenic nematodes
Bohan et al. (2010)
Weeds
Boyer et al. (2013)
Klingen et al. (2000)
Medow et al. (2000)
Henderson et al. (2009)
Ramirez et al. (2009)
Norris and Kogan (2005)
Creech et al. (2007)
Pathogenic nematodes
Pathogenic insects

shade
light

Determination of biofumigation potential (BP)

$$BP = \sum_{i=1 \text{ à } n} Biomass_{total} \times [GSL]_i \times Toxicity_{GSLi}$$

equation from Kirkegaard and Sarwar (1998)

with i = glucosinolate i

First approach

Pesticide derived approach

1) % of conversion GSL → ITC

2) % ITC to reach targeted organism

3) Toxicity ITC on targeted organisms

Mechanistic approach to determine GSL toxicity → Pandora's Box because each step is highly dependent of soil and climate conditions and agronomic management

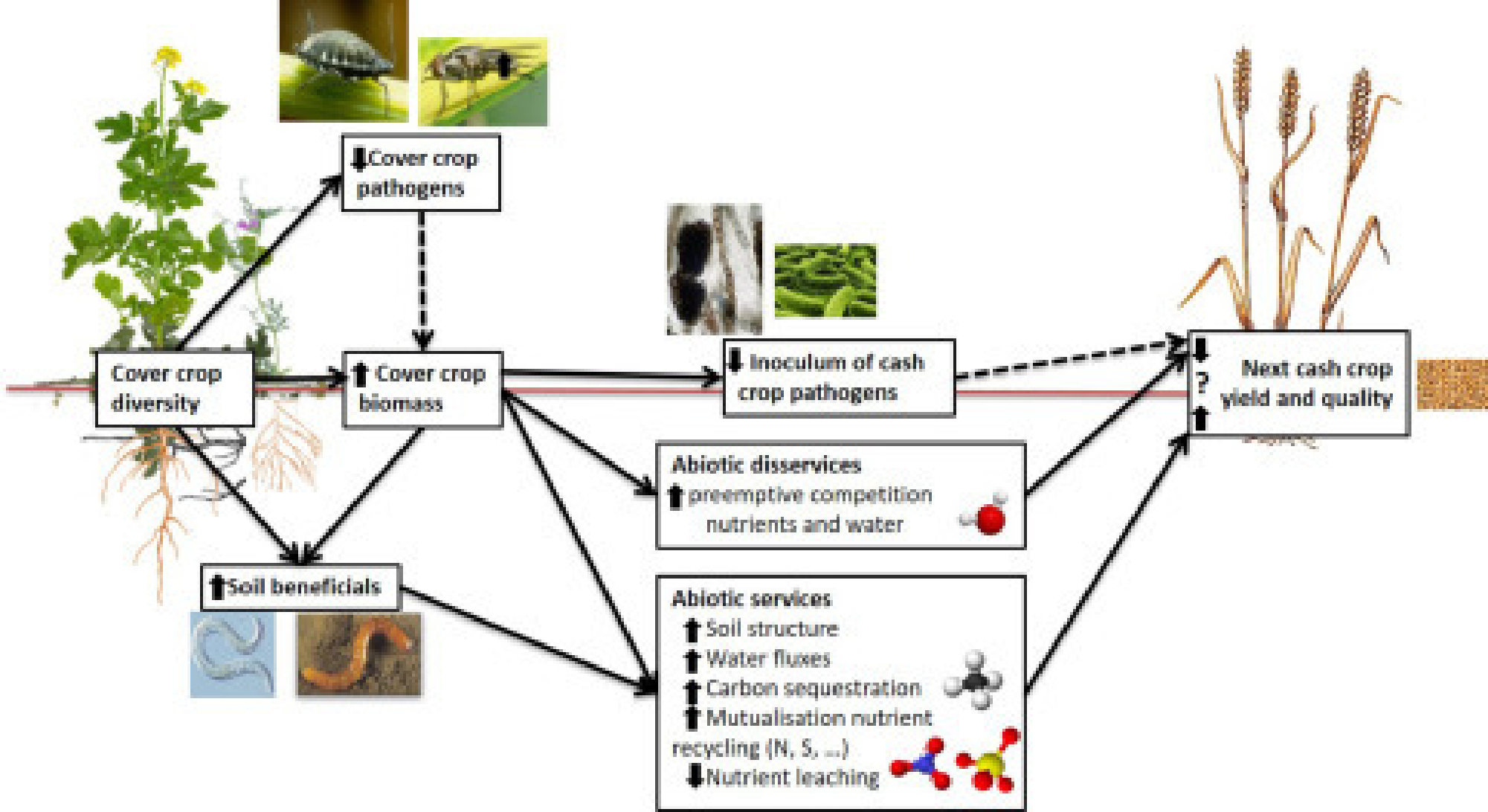
New paradigm

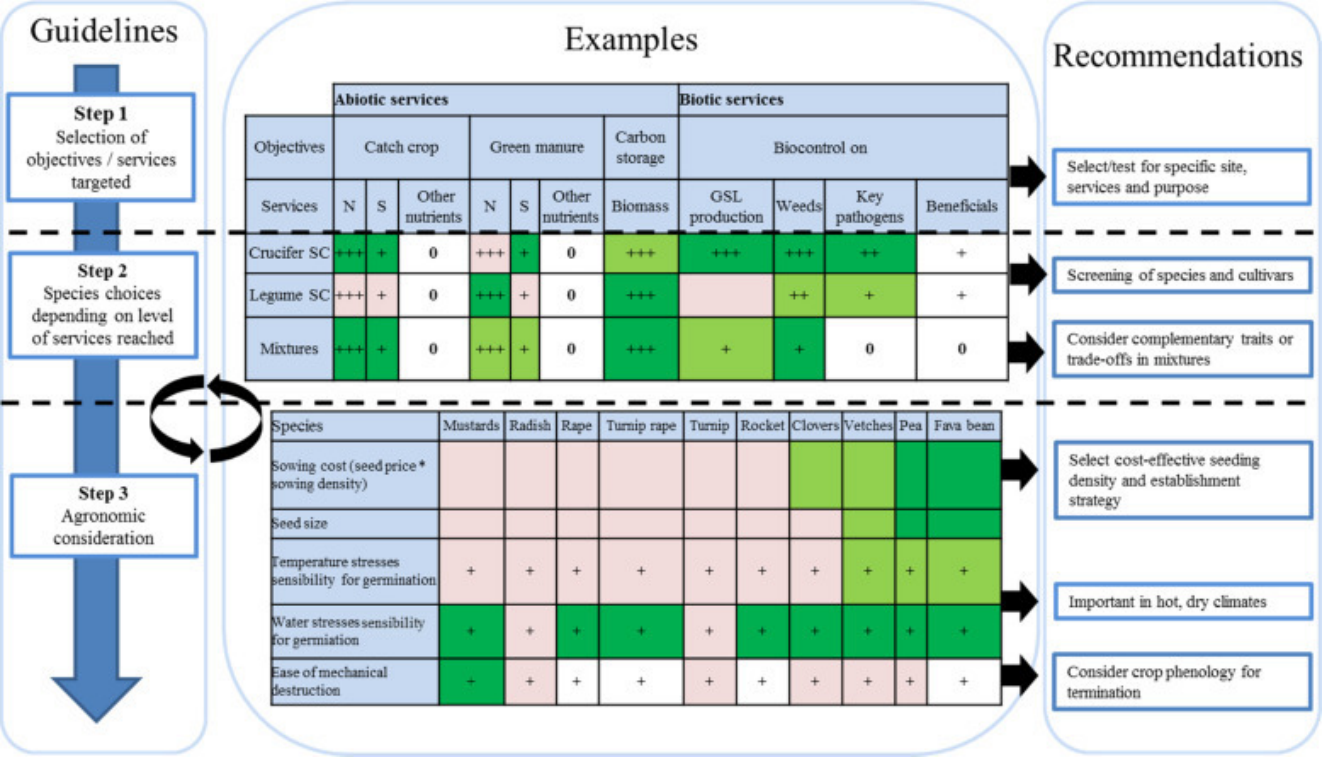
Ecological systems approach

- Timing of effects

- Termination management of cover crops

- Novel soil ecology approaches


Cover crop pathogens
Cover crop diversity
Cover crop biomass
Inoculum of cash crop pathogens
Next cash crop yield and quality
?
Abiotic disservices
preemptive competition
nutrients and water
Soil beneficials
Abiotic services
Soil structure
Water fluxes
Carbon sequestration
Mutualisation nutrient recycling (N, S, ...)
Nutrient leaching


Guidelines
Step 1
Selection of objectives / services targeted
Step 2
Species choices depending on level of services reached
Step 3
Agronomic consideration
Examples
Abiotic services
Biotic services
Objectives
Catch crop
Green manure
Carbon storage
Biocontrol on
Services
N
S
Other nutrients
N
S
Other nutrients
Biomass
GSL production
Weeds
Key pathogens
Beneficials
Crucifer SC +++ + 0 +++ + 0 +++ +++ +++ ++ +
Legume SC +++ + 0 +++ + 0 +++ ++ + +
Mixtures +++ + 0 +++ + 0 +++ + + 0 0
Species
Mustards
Radish
Rape
Turnip rape
Turnip
Rocket
Clovers
Vetches
Pea
Fava bean
Sowing cost (seed price * sowing density)
Seed size
Temperature stresses sensibility for germination + + + + + + + + + +
Water stresses sensibility for germiation + + + + + + + + + +
Ease of mechanical destruction + + + + + + + + + +
Recommendations
Select/test for specific site, services and purpose
Screening of species and cultivars
Consider complementary traits or trade-offs in mixtures
Select cost-effective seeding density and establishment strategy
Important in hot, dry climates
Consider crop phenology for termination