Review

Wheat (*Triticum aestivum* L.)-based intercropping systems for biological pest control

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Abstract

BACKGROUND: Wheat (*Triticum aestivum* L.) is one of the most cultivated crops in temperate climates. As its pests are mainly controlled with insecticides which are harmful to the environment and human health, alternative practices such as intercropping have been studied for their potential to promote biological control. Based on the published literature, this study aimed to review the effect of wheat-based intercropping systems on insect pests and their natural enemies.

RESULTS: Fifty original research papers were obtained from a systematic search of the peer-reviewed literature. Results from a vote-counting analysis indicated that, in the majority of studies, pest abundance was significantly reduced in intercropping systems compared with pure stands. However, the occurrence of their natural enemies as well as predation and parasitism rates were not significantly increased. The country where the studies took place, the type of intercropping, and the crop that was studied in the association had significant effects on these results.

CONCLUSION: These findings show that intercropping is a viable practice to decrease insecticide use in wheat production systems. Nevertheless, other practices could be combined with intercropping to favour natural enemies and enhance pest control.

Key words: sustainable agriculture, crop diversity, conservation biological control, predators, parasitoids, yield

1 INTRODUCTION

Wheat (*Triticum aestivum* L.) is one of the most important crops worldwide (ranked fifth in terms of production according to FAOSTAT (http://faostat3.fao.org/browse/Q/QC/E)). Therefore, finding alternative methods to improve its sustainable production is a major challenge for today's agriculture. Conventional farming practices contributed to increase yields during the 20th century, but are today contested for their negative impact on the environment[1,2] and human health.[3] Industrialized monoculture systems, which are highly dependent on the use of external inputs such as agrochemicals (i.e. synthetized fertilizers, chemical pesticides, growth regulators), favoured the simplification of agroecosystems.[4,5]

In contrast, promoting functional biodiversity, which supports ecological processes, may allow agricultural systems to benefit from various ecosystem services, including nutrient cycling, soil structuration and pest control.[6,7] One of the 'agrobiodiversity strategies' to improve the sustainability of wheat production (reviewed by Costanzo and Bàrberi[8]) is to increase plant species diversity at the field scale though intercropping designs.[9–11] Intercropping is defined as the cultivation of at least two plant species simultaneously in the same field,[12–14] but which are not necessarily sown and/or harvested at the same time.[15]

Andrews and Kassam[13] categorised intercropping into four principle types based on the spatial and temporal overlap of plant species: (1) mixed intercropping - two or more crops mixed with no distinct row arrangement; (2) row intercropping - two or more crops grown in separate alternate rows (when plant species are alternated within the same row it is considered as within-row intercropping); (3) strip intercropping - several rows of a crop (strip) alternated with several rows of one or more other crops; (4) relay intercropping - two or more crops grown in relay, but with the growth cycles overlapping to some degree. Choosing a type of intercropping may depend on the associated crops and their valuation after harvest, in addition to the knowledge of the famer and the level of mechanisation used.

Intercropping systems tend to produce higher yields compared to monocultures and reduce the impact of agriculture on the environment. Specifically, intercropping may improve soil conservation, fertility and crop quality, while possibly reducing the incidence of weeds, disease and insect pests.[15–17] Focusing on pests, as stated in the ‘resource concentration hypothesis’ from Root,[18] specialist herbivores are more likely to find their host plants when they are concentrated in dense or pure stands. Moreover, according to the ‘enemy hypothesis’ from Root,[18] the suppression of herbivores by their natural enemies (i.e. predators and parasitoids) is expected to be more efficient in diversified crop habitats compared to simplified ones, as they may be more abundant in environments offering a greater diversity of prey/host species and microhabitats to exploit.

Although the effect of intercropping on pests and natural enemies have been largely covered in the literature,[19–24] most comprehensive reviews are very generalists. As wheat is one of the most important crops worldwide, understanding the potential of wheat-based intercropping systems for biological control may be of crucial importance. More specifically, this study aimed at answering the following questions: (i) Are pests reduced and natural enemies favoured in wheat-based intercropping systems compared to pure stands? (ii) Is there a correlation between biological control and yield in wheat-based intercropping systems? (iii) Where and when were these systems studied? (iv) What are the technical characteristics of wheat-based intercropping systems (i.e. types of intercropping and plant species associated with wheat)? Overall, this study is expected to give valuable information about the potential of intercropping as a tool to reduce insecticide use in wheat production.

2 EXPERIMENTAL METHODS

2.1 A systematic research of the literature

To locate scientific literature related to the effect of wheat-based intercropping on pests and/or natural enemies, all terms potentially related to intercropping, wheat, pests and natural enemies were listed. These terms were then included in a single query, as follows: (intercrop* OR "crop association" OR "crop combination" OR "combined crop" OR "associated crop" OR "crop mix" OR "mixed crop" OR "mixed cropping" OR “row cropping” OR “relay cropping” OR “strip cropping”) AND (wheat OR "triticum aestivum") AND (pest* OR herbivor* OR "natural enemy" OR predator* OR parasit*). The composed terms were put between quotation marks so that the entire term was considered. For some of them, an asterisk was used to include all words that have a common core. The first step of this research was completed on 26 June 2015 by introducing the query in the search engine from the University of Liège (ULg - Belgium) e-bouquet. The search engine includes several e-journals and databases such as Scopus (Elsevier), AGRIS, CAB Abstracts and ProQuest (for the list of all databases included, see Annex 1). Thereafter, the search query was adapted to each database, as some of them use a specific query language.

The obtained references were then selected based on the abstracts of the published papers. The abstracts had to meet four criteria to be retained for further analysis. First, they had to be research papers from peer-reviewed journals. Review and meta-analysis papers were not considered, as they are based on other studies. Second, the abstracts had to focus on intercropping. As stated in the Introduction, intercropping was defined as the cultivation of at least two plant species simultaneously in the same field, without necessarily being sown and/or harvested at the same time. Wheat had to be included in the intercropping and associated plant species had to be harvestable and consumable (human consumption, animal feeding, energy production and fibres). Ornamental, grassy or woody species were excluded.

Third, insect pests and/or natural enemies (i.e. predators and parasitoids) had to be assessed by the studies and the effect of biological control had to be specified through direct (e.g. predation or parasitism rate) or indirect (e.g. abundance) indicators. Finally, the intercropping had to be compared to a pure stand control treatment. When the abstract was not available, the paper was excluded from the review. When the information contained in the abstract was not sufficiently precise to respond to criteria, the full paper was analysed. The paper was excluded from analyses if it was not obtainable.

Selected papers were then analysed in greater depth to determine the country where the study took place, the plant species associated with wheat, the type of intercropping and the effect of intercropping on yield, insect pests and/or natural enemies. Concerning insects, the effect was considered to be negative, positive or neutral when their populations declined, increased or no significant difference was detected, respectively between treatments. Furthermore, an increase in the predation or parasitism rate was considered to be a positive effect on natural enemies. In fact, both indicators allow determining the top-down impact of predators or parasitoids on their herbivorous prey or hosts. Therefore, we considered that higher predation or parasitism rates mean higher pressure on pests, which is positive for biological control. In the event that a single paper showed positive, negative and neutral effects on different insect populations, crops and intercropping designs (i.e. strip, relay, mixed), all instances were considered, hereafter termed ‘responses’.

2.2 Vote-counting method

The analysis of the selected papers was performed following the vote-counting method, which considers the number of tests supporting a theoretical relationship (i.e. in our case, if pests are reduced and natural enemies favoured in intercropping systems, compared with pure stands).

Despite a wide use of this method for analysing results of numerous different studies[25–29], vote-counting has been criticized and meta-analysis promoted.[21,23] Indeed, vote-counting presents some limits that were reviewed by Combs *et al.*[30] However, vote-counting allows the analysis of a large amount of papers for which the precise data are not always available. It is the case for several papers retrieved from the literature search, which still provide valuable findings that are worth to be considered.

2.3 Statistical analyses

In order to perform statistical analyses, a score was given to each response. The score ‘1’ was given when a positive effect on biological control was recorded (i.e. lower abundance of pests, higher abundance of predators or parasitoids, higher parasitism or predation rates, higher yield). The score ‘0’ was given when no effect or a negative effect was recorded. The Exact Bernouilli test ($P < 0.05$) was used to assess whether the frequency of responses where intercropping had a positive effect on biological control compared to pure stands differed from that expected by chance. Generalized linear models (GLMs) with binomial error (logit-link function) were fitted to assess whether (i) the country where the study took place, (ii) the type of intercropping, and (iii) the crop species that was studied had effects on the responses. These variables as well as every possible interaction were tested using a likelihood-ratio test ($P < 0.05$). Finally, the Pearson correlation between the effect of intercropping on pests, natural enemies and yield was tested ($P < 0.05$). The analyses were performed using R software.[31]

3 RESULTS

3.1 Countries and evolution through time

Out of 445 papers that were examined, 50 papers met the stated criteria. Thirty-nine of these papers were found using the search engine of the ULg. Eleven additional papers meeting the criteria were found by adapting the query to each database.

Four regions of the world are represented by the 50 studies. Twenty three were carried in China, 12 in Central and Southern Asia (i.e. India, Pakistan, Bangladesh and Iran), and 11 in North America (i.e. United States of America, Canada). Four papers refer to experiments carried in Western Europe (i.e. France, Denmark, Belgium and Germany) (Fig. 1). The oldest paper found was published in 1987 in China (Fig. 2). Since this year, one to two papers were published every year on average throughout the world. However, the number of publications increased from 2009 with 40 % of them published since this date. The first paper published in Europe was in Germany in 2006.

3.2 Plants associated with wheat and types of intercropping

Thirteen plant species were recorded in association with wheat (Table 1). The main species included cotton (*Gossypium* sp.), oilseed rape (*Brassica napus* L.) and pea (*Pisum sativum* L.). Different kinds of intercropping with wheat were implemented depending on the species used (Table 1). Strip cropping is the most common type, representing almost half of the studies, followed by relay cropping. Relay cropping was used when cotton, field bean (*Phaseolus vulgaris* L.), sorghum (*Sorghum bicolor* L.) or soybean (*Glycine max* L. Merr.) were associated with wheat. Mixed cropping was the least reported type. Pea, oilseed rape and faba bean (*Vicia faba* L.) were found mixed with wheat in this system.

3.3 Pests and their natural enemies

Forty-nine (98 %), twenty-four (48 %) and fourteen (28 %) papers assessed the effect of intercropping systems, compared to pure stands, on pests, predators and parasitoids respectively. Among them, twelve (24 %) considered both predators and parasitoids. Wheat-based intercropping systems significantly decreased pest populations compared to pure stands ($P < 0.001$), while no significant effects were observed for predators ($P = 0.480$) and parasitoids ($P = 0.359$) (Fig. 3).

Responses from pests and natural enemies varied significantly between countries where studies took place (Table 2). All responses obtained for pests in Bangladesh, Belgium, Denmark, France and Iran reported a decrease of their populations, while the opposite was observed in the only study that was carried in Germany. Variable responses were obtained in other countries, especially in the three Canadian studies (Fig. 1). As for natural enemies, the study that was carried in Iran was the only that reported an increase of predator populations or predation rate, while the opposite was observed in Belgium. As for pests, variable responses were observed in other countries. Similar results were obtained for parasitoids. The study from Pakistan was the only one reporting an increase of parasitoids abundance or parasitism rate, while a decrease was obtained in the single study from Canada.

Both pests and natural enemy responses were significantly affected by the type of intercropping (Table 2). Pest populations were always reduced in strip cropping, which also favoured predators and parasitoids more often than relay and mixed cropping. The latter reduced pests in half of the cases and never induced an increase of natural enemy populations, as well as predation and parasitism rates (Fig. 4).

Finally, such variability of responses was also observed for pests and parasitoids, but not for predators, when considering the crop species that was studied in the wheat-based intercropping system (Table 2; see Table 3 for details and associated references). Pests were reduced on the majority of crops, but rarely on oilseed rape (Fig. 5). Variable responses were obtained for other crops, especially sorghum, sugarcane (*Saccharum officinarum* L.) and mustard (*Sinapis albla* L.). Predators were not favoured on alfalfa (*Medicago sativa* L.), pea and sorghum, and a beneficial effect was recorded on cotton and wheat in only half of the cases (Fig. 5). The only study where oilseed rape was considered reported two opposite effects. As for parasitoids, all responses obtained with oilseed rape corresponded to a decrease of populations or parasitism rates, while more than a half of them were beneficial for biological control on cotton and wheat (Fig. 5).

3.4 Crop yield

The effect of intercropping on yield was assessed in only 10 of the 50 papers. Six papers reported significant higher yield in intercropping systems compared to pure stands, while a single one showed the opposite. Two of them reported no significant differences. Additionally, one paper reported significant higher yield in intercropping compared to pure stand in the first year and no significant differences in the following one. No significant correlation was found between pest reduction and yield increase ($\varphi = 0.45$, $P = 0.145$). However, higher yield was positively correlated with an increase of predator populations and predation rate ($\varphi = 0.77$, $P = 0.024$). This positive correlation was even stronger when predator and parasitoid data were analysed together ($\varphi = 0.81$, $P = 0.002$). However, not enough data were available to test such a correlation for parasitoids alone.

4 DISCUSSION

4.1 Effect on pest biological control and implication for yield

4.1.1 Insect pests and natural enemies

Wheat-based intercropping systems almost systematically have a positive effect on pest control. In fact, the number of responses reporting a decrease of their populations was significantly higher than those showing the opposite. This finding is consistent with most studies addressing the effect of plant diversity on herbivores.[20,23] Most of the mechanisms explaining how plant diversity promotes pest regulation, called associational resistance,[32] were compiled by Poveda *et al.*[33] and *Barbosa et al.*[34]. For example, pest ability to locate host plant odours may be disrupted when they are masked by volatiles from non-host plants.[32] Moreover, host plant odours may be altered when exposed to volatiles from neighbouring insect-infested[35] and non-infested[36] plants, but also after absorbing certain root exudates from adjacent non-host plants.[37] In some cases, competition between associated plants may alter the quality of host plants, which become less attractive for pests.[38] Pests may also be more attracted to associated non-host plant species and remain on these plants without infesting the main crop.[39] Alternatively, certain plants have repellent odours.[40] Other mechanisms may also affect the visual location of host plants, such as greener and/or taller non-host plants, which may camouflage the host plant[37] or even lead to its physical obstruction.[41]

Furthermore, natural enemies may exercise a top-down control on pests. However, the number of responses reporting a beneficial effect of intercropping on predators and parasitoids was not significantly higher than the one reporting the opposite. This result is not consistent with the ‘enemy hypothesis’ of Root. Several explanations have been put forward by the authors of the analysed papers to explain that. For instance, according to Hummel *et al.*[42] who found that canola-wheat intercropping did not increase ground beetle (Coleoptera:

Carabidae) populations compared to pure stands, intercropping may have altered microhabitat conditions (i.e. soil moisture, temperature and light penetration through the canopy), making the environment less suitable for some species. The same authors also found that the parasitism rates of the root maggot *Delia radicum* (L.) puparia decreased with increasing proportions of wheat in a canola-wheat intercropping system. Since *Delia* spp. caused less damage in intercropping systems compared to pure stands, it was hypothesised that the amount of volatiles emitted by infested canola plants, which attract the adult parasitoid *Aleochara bilineata* Gyll., were limited by intercropping. A similar hypothesis was proposed by Lopes *et al.*[43] to explain why adult ladybeetles and hoverflies were significantly more attracted by pure stands of pea and wheat, respectively, which were significantly more infested by aphids compared to mixed and strip cropping systems. Moreover, some practical aspects may explain that natural enemies were rarely favoured in intercropping systems. In relay-intercropping for instance, whereas this system may allow natural enemies to maintain though time, a lack of temporal overlap between the several crops may cause a dissipation of the natural enemies[44]. Also, the use of insecticides in experiments could have negatively affected natural enemies resulting in no differences between treatments[45]. Landis *et al.*[46] reported that plant diversity should benefit natural enemies partly because it may provide pollen and nectar that are alternative non-host food sources. However, a particular attention must be paid on the crop phenological and physiological characteristics that may affect natural enemies. Despite several flowering crops may produce such food sources (e.g. oilseed rape, alfalfa or faba bean with extra floral nectar), the flower architecture must be adapted to insect mouth parts[47] and the resources must be available when they are needed.[48] These aspects may explain why simply associating crops do not necessarily favour natural enemies.

4.1.2 Crop yield

There was no significant correlation between pest reduction and yield increase. This result is consistent with Letourneau *et al.*[23] who also found that beneficial effects of plant diversity on pest reduction are not systematically translated in higher yield. One reason is that the type of intercropping also influences other agronomic aspects, such as plant density and competition for resources. Yield may particularly be affected in substitutive designs like mixed intercropping, as they imply lower crop densities when compared to pure stands, but also higher competition for water, light and nutriments between associated plants.[23] However, according to Bedoussac *et al.*,[17] yield of all associated crops considered together is almost systematically higher compared to the one of each crop grown in pure stands. In our study, not enough data were obtained to fully address this question. However, we might hypothesize that minimizing the competition between intercropped plants can be achieved in relay and strip intercropping, which are also the most efficient for controlling pests and favouring natural enemies. The positive correlation between the beneficial effect of intercropping on natural enemies and higher yield may encourage following this direction. Furthermore, as noted by Letourneau *et al.*,[23] it would be interesting to determine whether eventual yield losses due to intercropping are compensated by environmental benefits and input cost reduction (in our case insecticides) in future studies.

4.2 Adopting intercropping for pest control: constraints and opportunities

4.2.1 A well-established practice in Asia that is beginning to take hold in Europe

Most studies addressing the effect of wheat-based intercropping on pests and/or natural enemies were carried out in China. Despite the fact that intercropping has been practiced in

Chinese agriculture for over 1000 years,[49] there has been a strong decline in the use of this method on the North China Plain over the last 20 years.[50] In fact, with the decrease of rural labourers and increase in farmer's income, farmers have invested in mechanisation, adopting intensive production methods. As noted by Feike *et al.*[50], one of the ways to overcome this issue is to replace the traditional labour-intensive row intercropping system by strip intercropping, which can be more easily adapted to mechanisation. Therefore, it is not surprising that many studies carried out in China have focused on this type of intercropping.

In contrast, studies remain rare on intercropping as a tool to biologically control pests in Europe. This may be because this practice needs technical adaptations (see section 4.2.2) to be implemented, which are not compatible with the conventional agriculture model that has been practiced in Europe for the last 30 years.[5] In fact, for farmers, developing intercropping systems requires new skills and tools.[11] In addition, these systems must satisfy the ecological, economic and social constraints on their farms.[5] However, the growing focus on low-input farming practices in academic environments[5,51,52] and at the political level[53,54] may explain the recent development of research on intercropping in Europe.

4.2.2 Adopting intercropping needs technical adaptations

Management and technical issues are central for developing intercropping systems. Indeed, phenological and spatial constraints of crop species must be taken into account to select viable combinations. Competition for resources (i.e. light, water, nutrient),[55] as well as allelopathic effects,[56] may limit whether associations work. Appropriate machines are also needed to sow, harvest and separate grains in mixed cropping.[15] However, the management of strip and relay intercropping systems may be facilitated, as two or more crops may be separately managed. Also, the size of the strips and the ratio between the associated crops can be adapted depending on farmer production objectives and agronomic constraints (i.e. in the selected studies, the width of the strips went from few crop rows to at least 5 m. and the ratio between crops was from 1 to 4). This may explain why the majority of studies focus on these two systems. Among the crops associated in relay, the combination of wheat with cotton is widely practiced in China[57]. As well described by Zhang *et al.*[58], “the cotton is sown in April, approximately seven weeks before the harvest date of wheat. Strips are left open in the wheat crop at sowing (October/November) to provide space for the cotton plants during their seedling stage (April, May and June). After the wheat harvest in June, cotton plants can exploit the full space, above-ground as well as below-ground.” As for mixed intercropping, wheat was only found associated with pea and oilseed rape. Wheat-pea mixtures are known to provide many benefits. For instance, wheat benefits from the symbiotic nitrogen fixation of peas, allowing to reduce fertilizer inputs.[59,60] Some experiments have been published on the effects of wheat-pea mixtures, but not necessarily on the aspect of pest control.[59–61] In comparison, studies on the effects of mixing wheat and oilseed rape seemed to be a rarer combination, at least based on the publication record.

4.2.3 Combining crops of primary importance to favour the adoption of intercropping

Intercropping systems involve cultivating two or more crops in the same place at the same time. However, one crop is often seen as more important than the other crops for economic reasons.[15] This issue may explain why intercropping was studied to mitigate pests and favour natural enemies for just one of the associated crops in most studies. Cotton, sugarcane and soybean are well-known important cash crops that are exported worldwide (FAOSTAT (http://faostat.fao.org/site/342/default.aspx)). A particular crop may also be of special economic and cultural importance in some regions, such as chili pepper (*Capsicum frutescens* L.) in China[62] or the oilseed rape variety Canola in Canada.[63]

Wheat is an essential food crop in northern China and central Asia,[64,65] as it is in Europe and North America (FAOSTAT (http://faostat3.fao.org/browse/Q/*/E)). However, wheat is rarely considered as the main crop in intercropping systems in Europe and North America. Because conventional farming practices applied to wheat production already tend to achieve high yields, producing wheat under intercropping systems may not be seen as needed for economic and food security reasons. However, it is necessary for agriculture to shift toward more ecological food production in Western countries. Developing intercropping systems that are beneficial for crops of primary importance may favour such a transition.

4.3 Needs for further research

This study shows that wheat-based intercropping systems allow reducing pest occurrence on crops, while natural enemies are not favoured in such systems when compared to pure stands. However these results varied significantly depending on the countries where the study took place, the type of intercropping and the crops studied. In Europe, more research is needed to better assess the potential of wheat-based intercropping for pest control. Despite some limiting factors, mixed intercropping deserves to be further studied, as it may also provide some benefits.

Because predators and parasitoids are not significantly favoured in intercropping systems, these latter could be combined with other practices known to efficiently support natural enemies within fields. For instance, some volatiles known to attract natural enemies can be released in fields. Wang *et al.*[66] showed that the abundance of ladybeetles and parasitism rate were higher when methyl salicylate was released in wheat-oilseed rape intercropping fields, compared to each treatment applied separately. Moreover, infrastructures such as woodlots, hedgerows and wildflower strips could be settled in farming areas as they are known to provide habitats sustaining natural enemies that prey on and parasitize pests in adjacent fields.[29,67,68] Among other factors, the regulation of pests by natural enemies depends on their presence in the surrounding landscape.[69] The conservation of natural enemies and their attraction in intercropping fields could be a way to improve the biological control of pests.

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Table 1 Plant species associated to wheat based on the type of intercropping

Type of intercropping	Crops associated with wheat	No. of papers	References
Strip cropping	Alfalfa (*Medicago sativa* L.)	4	70–73
	Garlic (*Allium sativum* L.)	2	74,75
	Mung bean (*Vigna radiata* (L.) Wilczek)	2	76,77
	Oilseed rape (*Brassica napus* L.)	7	42,66,74,78–81
	Pea (*Pisum sativum* L.)	4	82–85
	Chili pepper (*Capsicum frutescens* L.)	1	86
Relay cropping	Cotton (*Gossypium* sp.)	10	44,45,87–94
	Field bean (*Phaseolus vulgaris* L.)	1	95
	Sorghum (*Sorghum bicolor* L.)	1	96
	Soybean (*Glycine max* (L.) Merr.)	2	97,98
Mixed cropping	Oilseed rape (*Brassica napus* L.)	4	99–102
	Bean (*Vicia faba* L.)	1	103
Strip and mixed cropping	Pea (*Pisum sativum* L.)	2	43,104
Non specified	Chickpea (*Cicer arietinum* L.)	3	105–107
	Cotton (*Gossypium* sp.)	2	108,109
	Bean (*Vicia faba* L.)	1	110
	Mustard (*Sinapis alba* L.)	3	111–113
	Sugarcane (*Saccharum officinarum* L.)	1	114

Table 2 Effect of wheat-based intercropping on pests and natural enemies according to the countries where the studies took place, the type of intercropping and the crop of primary interest. Likelihood-ratio tests on GLMs; *P < 0.05; **P < 0.01; ***P < 0.001. '-' indicates that it was not possible to perform the analysis.

	Pests			**Predators**			**Parasitoids**		
Predictor variables	**df**	**χ^2**	**Pr(>Chi)**	**df**	**χ^2**	**Pr(>Chi)**	**df**	**χ^2**	**Pr(>Chi)**
Country	10	19.47	0.035 *	5	21.47	< 0.001 ***	2	7.61	0.0223 *
Type of intercropping[a]	2	18.39	< 0.001 ***	2	6.20	0.045 *	2	7.85	0.020 *
Crop	11	27.63	0.004 **	5	8.46	0.133	2	7.85	0.020 *
Crop*Type of intercropping[a]	–	–	–	–	–	–	–	–	–
Crop*Country	–	–	–	1	1.29	0.255	–	–	–
Country*Type of intercropping[a]	–	–	–	1	2.15	0.142	–	–	–

[a] papers where the intercropping design was not defined were not considered in the analysis

Table 3 Effect on pests, predators and parasitoids according to the plant species that was studied in the intercropping

Crop	**Effect**			**No. of papers**	**References**
	(-)	**(O)**	**(+)**		
Pest abundance					
Bean	♦			1	103
	♦		♦	1	95
Chickpea	♦			3	105–107
Chili pepper	♦			1	86
Cotton	♦			10	44,45,87,88,90–94,108
	♦		♦	2	89,109
Mustard	♦			2	112,113
		♦		1	111
Oilseed rape		♦		3	99–101
	♦			2	79,102
Pea	♦			1	104
Sorghum	♦	♦		1	96
Soybean	♦			2	97,98
Sugarcane	♦	♦		1	114
Wheat	♦			15	66,71–78,80–85
Wheat and alfalfa	♦			1	70
Wheat and bean	♦			1	110
Wheat and pea	♦			1	43
Predator abundance and predation rate					
Cotton			♦	5	89,91,93,108,109
		♦		2	44,45
		♦	♦	2	92,94
Oilseed rape	♦		♦	1	42
Sorghum		♦		1	96
Wheat			♦	8	66,72,75,76,78,80,83,85
		♦	♦	2	74,81
		♦		1	73
Wheat and alfalfa	♦			1	70
Wheat and pea	♦			1	43
Parasitoid abundance and parasitism rate					
Cotton		♦		1	45
			♦	2	92,93
Oilseed rape	♦	♦		1	102
Wheat		♦		1	80
		♦	♦	1	74
			♦	8	66,71,75,76,78,82,83,85

Figure 1 Mean (± SE) number of responses reporting a positive effect of wheat-based intercropping on biological control (i.e. decrease of pest and increase of natural enemy populations) on the total number of responses according to the countries where the studies took place. The ratio given in brackets corresponds to the number of responses/number of papers. Likelihood-ratio tests on GLMs; *P < 0.05; ***P < 0.001.

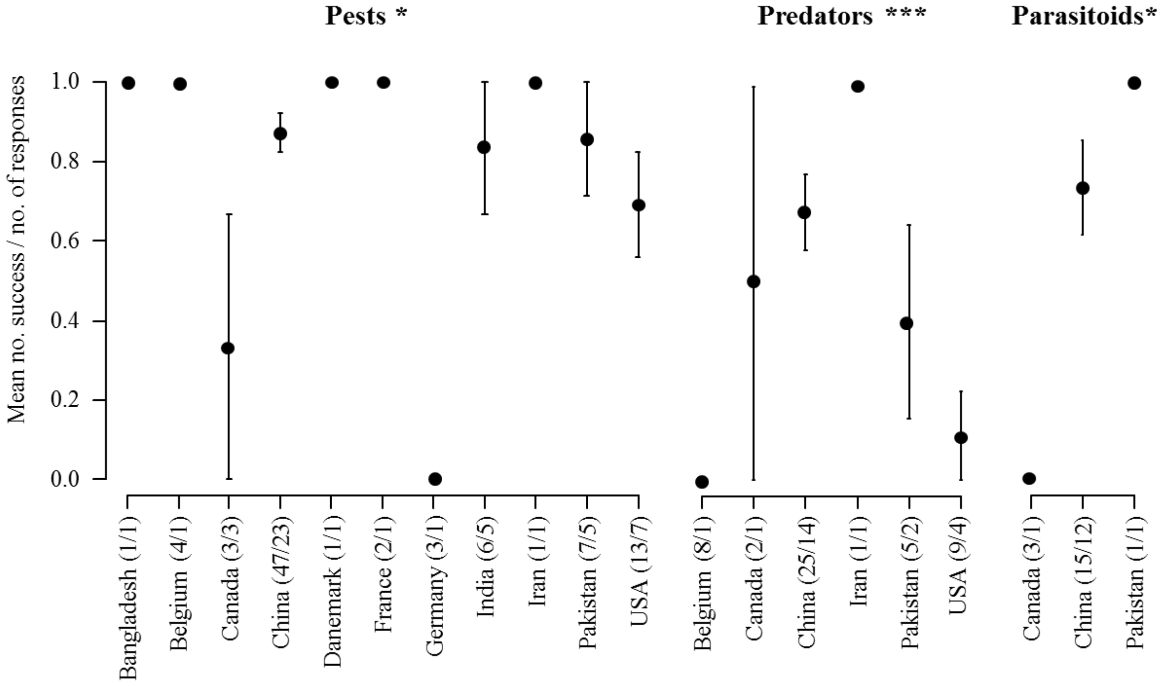

Figure 2 Evolution through time of the number of papers published on the effect of wheat-based intercropping on pests and their natural enemies.

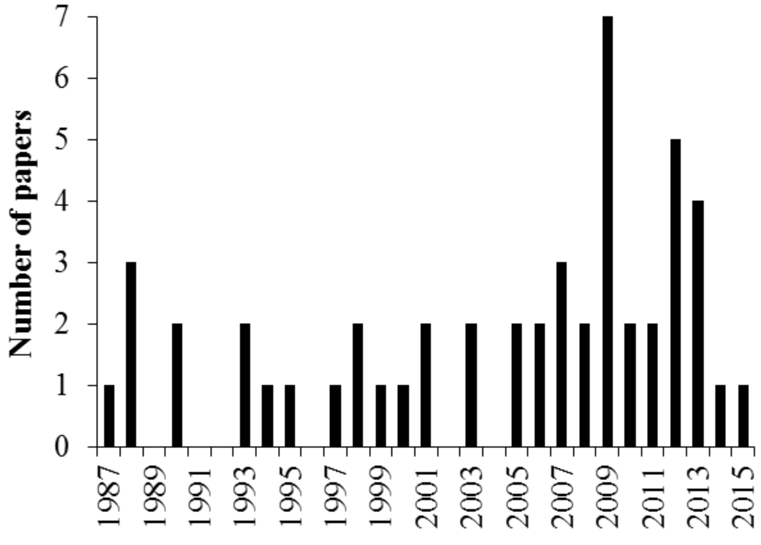

Figure 3 Ratio of the number of responses reporting a positive effect of wheat-based intercropping on biological control (i.e. decrease of pest and increase of natural enemy populations) on the total number of responses. The ratio given in brackets corresponds to the number of responses/number of papers. Exact Bernouilli test; ***P < 0.001.

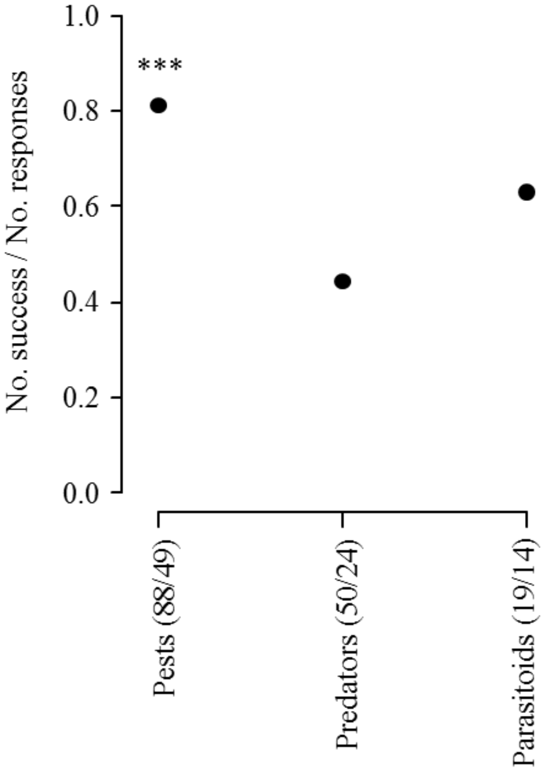

Figure 4 Mean (± SE) number of responses reporting a positive effect of wheat-based intercropping on biological control (i.e. decrease of pest and increase of natural enemy populations) on the total number of responses according to the type of wheat-based intercropping. The ratio given in brackets corresponds to the number of responses/number of papers. Likelihood-ratio tests on GLMs; *P < 0.05; ***P < 0.001.

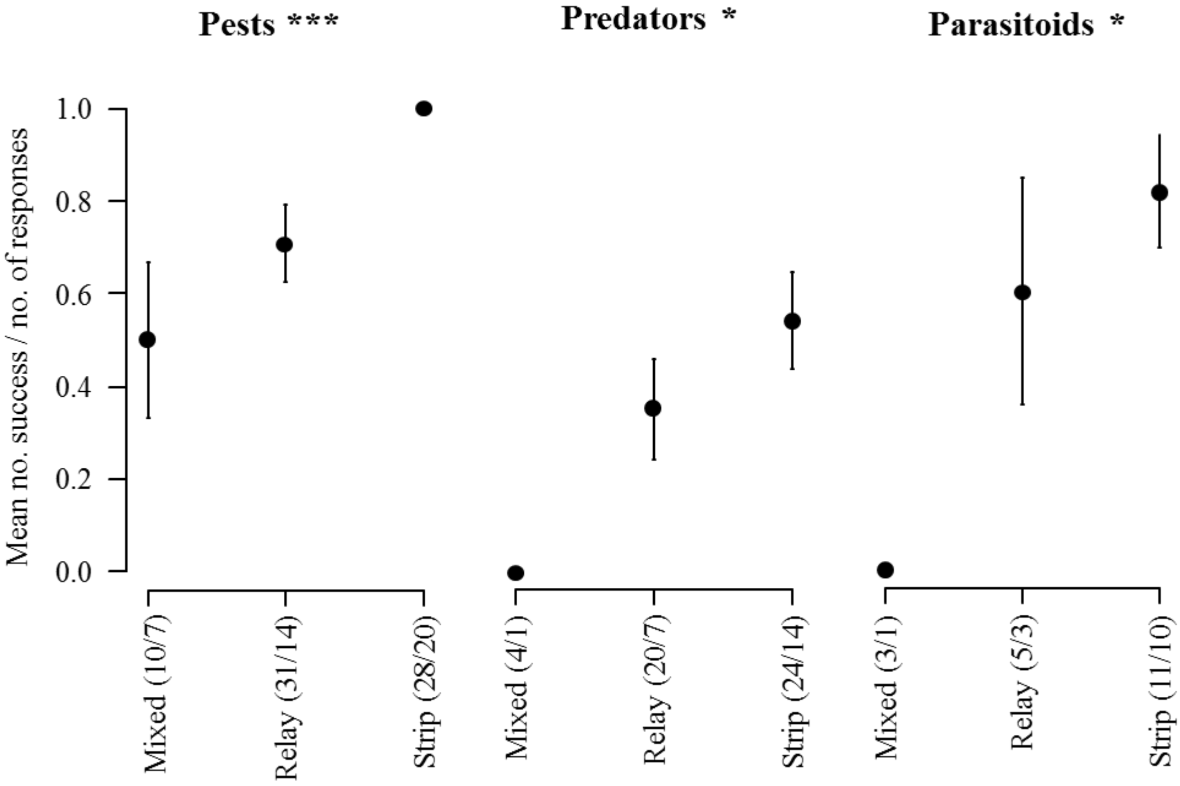

Figure 5 Mean (± SE) number of responses reporting a positive effect of wheat-based intercropping on biological control (i.e. decrease of pest and increase of natural enemy populations) on the total number of responses according to the crop species that was studied. The ratio given in brackets corresponds to the number of responses/number of papers. Likelihood-ratio tests on GLMs; *P < 0.05; **P < 0.01.