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Can legume companion plants control weeds without decreasing crop yield? A meta-analysis

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ABSTRACT

Companion plant intercropping involves growing a cash crop with another plant that is not harvested, to confer a set of benefits on the crop and the environment. Weed control and herbicide use reduction are one of the principal reasons for adopting this approach. Companion plants should compete with weeds for light, nutrients and water, but they may also compete with the crop. The species grown must therefore be carefully chosen and managed so as to outcompete weeds but limit competition with the crop and yield loss. In this meta-analysis, we aimed to quantify the effects of companion plants on weed regulation and cash crop yields, and to analyze their sources of variability. We reviewed different intercropping systems involving an annual cash crop and a legume companion plant from around the world. We report data from 34 scientific articles, corresponding to 476 experimental units (i.e. combinations of site × year × cash crop × legume companion plant species × agricultural practices), and we explore whether intercropping with legume companion plants can control weeds while maintaining crop yield. Yield and weed biomass ratios were analyzed as response variables. We used the type of cash crop (straw cereals, maize or other crops), the methods used to establish the companion plants (living mulch, synchronized sowing or relay intercropping) and the overlap between the growth periods of the companion plants and the cash crop as explanatory variables.

Intercropping with a companion plant resulted in a lower weed biomass and a higher yield (win-win situation) than non-weeded or weeded control treatments, in 52% and 36%, respectively, of the experimental units considered. A higher weed biomass associated with a lower yield (lose-lose) was observed in only 13% and 26% of the experimental units, in comparisons with non-weeded and weeded control treatments, respectively. Considering all the experimental units together, the companion plants had no significant effect on cash crop yield, but significantly decreased weed biomass, by 56% relatively to a non-weeded control treatment, and 42% relative to a weeded control treatment. The greatest benefits from companion plant intercropping were reported for maize, with yields 37% higher than those for non-weeded control treatments. The other explanatory variables tested had no significant effect on yield or weed control. Thus, the use of legume companion plants generally seems to enhance weed control without reducing crop yield, but the conditions giving rise to win-win situations should be explored further, to encourage the spread of this technique among farmers.

1. Introduction

The sustainability of conventional chemical weed control is in doubt. More than 200 weeds are known to be resistant to at least one herbicide (Heap, 2014). Furthermore, the number of chemicals available is decreasing, due to a lack of innovation and because the most dangerous molecules are being withdrawn from the market (Heap, 2014). Society is also demanding a more sustainable agriculture, protecting against groundwater contamination and better respecting biodiversity and human health. Modern agriculture is therefore evolving, with lower levels of herbicide use and the promotion of ecologically based weed management approaches (Liebman et al., 2007).

Two agroecological practices with a number of beneficial effects are known to suppress weeds (Wezel et al., 2014): (i) intercropping, i.e. the growth of two or more crops in the same space for a

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significant part of their growing periods (Malézieux et al., 2009; Willey, 1979) and (ii) the use of cover crops, i.e. plants grown in the field between two crop cycles, to provide a set of ecosystem services (Hartwig and Ammon, 2002). Weed suppression by intercropping or cover cropping is based on key ecological principles, such as increasing competition between the sown plants and weeds for light, nutrients, and water, and for underground and aboveground space, interfering with weed growth and slowing down their establishment (Liebman and Dyck, 1993). It has also been suggested that intercrops are more efficient than sole crops at capturing a greater proportion of the available resources for plant growth, at the expense of weeds (Fukai and Trenbath, 1993; Liebman and Dyck, 1993; Malézieux et al., 2009).

At the interface between intercropping and cover cropping, some systems involve the intercropping of a cash crop (CC) with a cover crop, also called a companion plant (CP), that is sown not to be harvested, but to provide added economic or environmental benefits, such as decreasing the risk of crop failure, controlling weeds and pests, and improving soil fertility (Liebman and Dyck, 1993). A CP can be introduced into the cropping sequence in several ways (Fig. 1). The CC can be sown directly into the living mulch formed by a CP previously grown in the field (Hartwig and Ammon, 2002). Synchronized sowing of the CC and the CP is another option. In this case, the CC and CP are sown the same day, or a few days apart, so as to favor the establishment of one or other of the intercropping components. Finally, the CC and CP can be cultivated by relay intercropping. This method involves the sowing of the CP under a well-established CC canopy before maturity (Coolman and Hoyt, 1993). The CP emerges within the CC, and grows slowly due to its limited access to light. In this third case, the CP is kept in the field as a cover crop after the CC has been harvested. These three establishment methods may result in different levels of competition between the crop and the companion plants, due to differences in the duration of the overlap between the growth cycles of the CC and the CP (Fukai and Trenbath, 1993).

The CP competes with the weeds for resources, but it may also compete with the CC (Echtenkamp and Moonmaw, 1989; Hiltbrunner et al., 2007; Liebman and Dyck, 1993). The effects of CP on CC yields and weeds may vary between CP species (Abdin et al., 2000; Hiltbrunner et al., 2007). Legume species are good candidate CPs for use in intercropping and are frequently considered in experiments assessing the benefits of CPs, because they produce biomass and compete with weeds without competing strongly with the CC for nitrogen, due to their ability to fix nitrogen from the atmosphere. For example, peas grown in intercropping situations rely heavily on N_2 fixation, which provides 90–95% of their aboveground N content (Corre-Hellou et al., 2011; Hauggaard-Nielsen et al., 2001). There is, however, currently no consensus in the scientific literature about the concomitant effects of CPs on CC yield and weed control. Several studies have shown that the use of CPs can both increase (or at least maintain) crop yields and decrease weed biomass (win-win) (Brust et al., 2011; Caamal-Maldonado et al., 2001; Correia et al., 2014; Deguchi et al., 2015). Other studies have suggested that the use of CPs may lead to a decrease in CC yield and an increase in weed biomass (lose-lose) (Abdin et al., 2000; Echtenkamp and Moonmaw, 1989; Thorsted et al., 2006). Some studies have also indicated that CPs may both decrease weed biomass and crop yield (Ilnicki and Enache, 1992; Pouryousef et al., 2015; Pridham and Entz, 2008; Vanek et al., 2005).

Many studies have assessed the effects of CP plants in a specific context, but there has been no global quantitative analysis of all the available data to assess the overall benefits and limitations of CP intercropping. We aimed to quantify the overall effects of CPs on weed regulation and CC yields from published data, and to analyze their sources of variability. We performed a meta-analysis of studies assessing the effects of legume CPs on crop yield and weed biomass. We reviewed data for 34 scientific articles dealing with different intercropping systems including an annual CC and a legume CP from across the world. We hypothesized that the use of legume CPs would improve weed control without decreasing CC yield. We used the type of CC (small grains, maize or other crops), the method used for CP establishment (living mulch, synchronized sowing or relay intercropping) and the overlap between the growth periods of the CP and CC as explanatory variables for the performance of the intercropping systems studied.

Table 1
Literature search equations.

Topics	Boolean equation expressions
i) Intercropping	(undersow* OR underseed* OR interseed* OR intercrop* OR companion OR "living mulch*" OR interplant* OR understorey)
ii) Weed control	AND (weed*)
iii) Legume plant family	AND (legum* OR faba* OR trifolium OR clover OR melilotus OR lucerne OR alfalfa OR medic OR medicago OR vicia OR vetch OR fenugreek OR trigonella OR lathyrus OR trefoil OR lens OR lentil OR pisum OR pea)
iv) No perennial intercropping or intercropping of two cash crops	NOT (vineyard OR pastures OR grassland OR orchard OR agroforestry OR "maize-cowpea" OR "pea-wheat" OR "pea-barley" OR "barley-pea")

2. Materials and methods

2.1. Review and study selection

We performed a literature review of articles published in peer-reviewed journals, using the Institute for Scientific Information Web of Science Database (http://apps.webofknowledge.com) in June 2015. The search equation included four expressions (Table 1): (i) a list of terms referring to intercropping, (ii) the term "weed*" which targeted studies dealing with weed control, (iii) a list of terms referring to Fabaceae/legume species, and (iv) a list of terms used to exclude references dealing specifically with the intercropping of two cash crops or of perennial crops.

This search equation retrieved 404 papers, 69 of which were found to have relevant titles and abstracts, and to be eligible for the meta-analysis. The full texts of these articles were read in detail, and 34 papers were retained on the basis of the following criteria: (i) CC yields were reported, (ii) weed biomass was measured at least once during the crop cycle or during the cover crop period after harvest, (iii) yield and weed biomass data were reported for both the intercropped treatment and the sole crop control treatment, (iv) the CPs used in intercropped treatments were legume species or mixtures of legume/non-legume species, and (v) the CC was seeded at the same rate in the CC and CC + CP treatments (additive intercrop design). When only aggregated data were published (i.e. data averaged over years, sites or treatments), the authors were contacted and asked to provide data for the individual experimental units. An experimental unit is defined here as a unique combination of site × year × CC species × CP species × agricultural practices (tillage, fertilization, time and seeding rates, etc.), for the comparison of different CP species. Articles reporting data already included in another paper (e.g. series of papers based on the same experiments) were not selected. The references cited in the studies were also reviewed to identify additional papers.

On the basis of these criteria, we selected 34 articles (Table 2) published from 1984 to 2015 and reporting data for 476 experimental units from 191 experiments for the meta-analysis. Each

Table 2
Selected studies for the meta-analysis.

Ref.	Country	System	Cash crop species	Method of CP establishment	Companion plant species	Nb. of exp. units	Nb. of site-years	W CT	NW CT	Period of weed sampling			
										S1	S2	S3	S4
(Abdin et al., 2000)	Canada	Conv.	Maize	SS.	*Medicago lupulina, M. sativa, Melilotus officinalis, Trifolium alexandrinum, T. fragiferum, T. incarnatum, T. pratense, T. repens, T. resupinatum,T. subterraneum, Vicia villosa*	32	3	x	x			x	
(Akobundu and Okigbo, 1984)	Nigeria	Conv.	Maize	LM.	*Arachis repens, Desmodium triflorum, Indigofera spicata*	3	1	x			x		
(Amossé et al., 2013; Amossé et al., 2014)	France	Org.	Winter wheat	RI.	*Medicago lupulina, M. sativa, Trifolium pratense, T. repens*	32	8		x	x	x	x	x
(Bergkvist, 2003)	Sweden	Conv.	Winter wheat	LM.	*Trifolium repens* (3 cultivars)	9	2		x			x	
(Bergkvist, 2003)	Sweden	Conv.	Winter wheat	LM.	*Trifolium repens*	14	2	x				x	
(Bergkvist et al., 2011)	Sweden	Conv.	Winter wheat	RI.	*Trifolium pratense, Trifolium repens, Trifolium repens + Lolium perenne*	64	4	x	x			x	
(Blaser et al., 2011)	USA	Conv.	Winter wheat, Triticale	RI.	*Trifolium pratense* (2 cultivars), *Medicago sativa*	54	3		x				x
(Brandsæter et al., 1998)	Norway	Conv.	White cabbage	SS.	*Trifolium repens, Trifolium subterraneum*	4	1	x			x	x	
(Brust et al., 2011)	Germany	Conv.	Spelt	RI.	*Trifolium repens, Trifolium resupinatum*	4	1		x			x	
(Caamal-Maldonado et al., 2001)	Mexico	Conv.	Maize	SS.	*Canavalia ensiformis, Mucuna pruriens*	6	3	x				x	
(Campiglia et al., 2014)	Italy	Conv.	Durum wheat	SS.	*Trifolium subterraneum*	12	2		x			x	
(Carof et al., 2007a, 2007b)	France	Conv.	Winter wheat	LM.	*Lotus corniculatus, Medicago lupulina, Medicago sativa, Trifolium repens*	12	3	x			x		
(Correia et al., 2014)	East Timor	Conv.	Maize	SS.	*Mucuna pruriens*	25	5	x				x	
(Deguchi et al., 2015)	Japan	Org.	Maize	LM.	*Trifolium repens*	2	1		x			x	
(De Haan et al., 1997)	USA	Conv.	Maize	SS.	*Medicago scutellata* (2 cultivars), *Medicago polymorpha*	15	3		x		x		
(Echtenkamp and Moonmaw 1989)	USA	Conv.	Maize	LM.	*Trifolium repens, Trifolium repens + Avena sativa, Trifolium repens + Festuca rubra, Vicia villosa, Vicia villosa + Avena sativa, Vicia villosa + Festuca rubra, Vicia villosa + Secale cereale + Avena sativa*	12	2	x			x		

(Enache and Ilnicki, 1990)	USA	Conv.	Maize	LM.	*Trifolium subterraneum*	9	3	x			x	x	
(Flores-Sanchez et al., 2013)	Mexico	Conv.	Maize	SS.	*Canavalia brasiliensis, Mucuna pruriens*	14	2	x					x
(Hartl, 1989)	Austria	Org.	Winter wheat	RI.	*Medicago lupulina, Trifolium resupinatum, Trifolium repens*	3	1		x		x		
(Hauggaard-Nielsen et al., 2012)	Denmark	Org.	Faba bean, lupin, pea, oat and pea + oat	SS.	*Trifolium repens + Lolium perenne*	10	2		x			x	
(Ilnicki and Enache 1992)	USA	Conv.	Soybean	LM.	*Trifolium subterraneum*	7	2	x	x	x		x	
(Jamshidi et al., 2013)	Iran	Org.	Maize	SS.	*Vigna unguiculata*	6	2		x			x	
(Mohler, 1991)	USA	Conv.	Maize	LM.	*Trifolium repens*	8	4	x				x	
(Moynihan et al., 1996)	USA	Conv.	Spring barley	SS.	*Medicago lupulina, Medicago truncatula, Medicago polymorpha*	12	4		x				x
(Ohlander et al., 1996)	Sweden	Conv.	Spring barley	SS.	*Trifolium pratense*	40	6	x				x	
(Pouryousef et al., 2015)	Iran	Org.	Coriander	SS.	*Trigonella foenum-graecum*	20	2	x	x			x	
(Pridham and Entz 2008)	Canada	Org.	Spring wheat	SS.	*Trifolium pratense, Vicia villosa*	6	3		x	x		x	
(Romaneckas et al., 2012)	Lithuania	Conv.	Maize	SS.	*Medicago lupulina, Trifolium resupinatum, Trifolium pratense*	6	2		x	x	x	x	
(Samarajeewa et al., 2005)	Japan	Conv.	Winter wheat	SS.	*Astragalus sinicus*	6	2		x	x	x	x	
(Sánchez Vallduví and Sarandón, 2011)	Argentina	Conv.	Flax	SS.	*Trifolium pratense*	4	2		x	x		x	
(Talgre et al., 2009)	Estonia	Conv.	Spring barley	SS.	*Lotus corniculatus, Medicago sativa Medicago media, Pisum sativum, Trifolium pratense*	5	1		x				x
(Thorsted et al., 2006)	Denmark	Conv.	Winter wheat	LM.	*Trifolium repens*	8	1	x				x	
(Uchino et al., 2009)	Japan	Org.	Maize	SS.	*Vicia villosa*	3	1		x	x	x	x	
(Vanek et al., 2005)	USA	Org.	Pumpkins	SS.	*Vicia villosa, Vicia villosa + Secale cereale*	8	4	x	x		x		
					Total	475	88						

Ref. = Reference, Conv. = conventional farming system, Org. = Organic farming system, LM = Living mulch, SS = Synchronized sowing, RI = Relay intercropping. NW CT = Non-weeded control treatment, W CT = Weeded control treatment, S1 = early stage, S2, intermediate stage, S3 = maturity, S4 = after harvest.

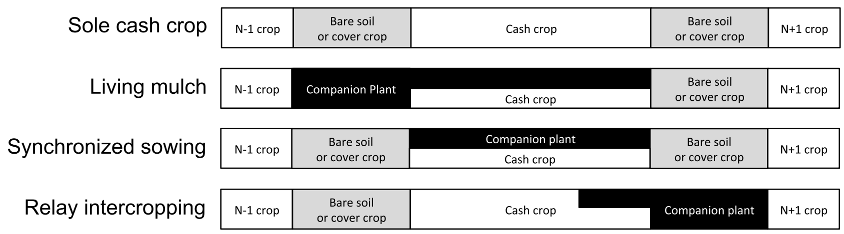

Fig. 1. Three methods for establishing companion plants (in black) in a cash crop (in white).

selected study reported data collected in one or several individual experiments.

2.2. Data extraction

Data were either extracted from published tables and figures with dedicated digitization software (Plotdigitizer, http://plotdigitizer.sourceforge.net/), or directly retrieved from the authors (about one third of the studies). Depending on the type of crop, yield data (in $\mathrm{Mg\,ha^{-1}}$) referred to dry or fresh biomass (dry matter (DM) or fresh matter (FM)), total harvested biomass or marketable biomass (e.g. for vegetables). Weed biomass data were reported in grams of DM per m^{-2}. All but one study measured total weed biomass. The remaining study reported only the biomass of *Brassica* weeds (Sánchez Vallduví and Sarandón, 2011). The weed data for this study were treated like total weed data in other studies. Weed density data were reported as the number of plants per m^2. Weed data were acquired at four different stages of the cash crop: early stage (between crop emergence and canopy closure, S1), intermediate stage (between canopy closure and seed or vegetable formation, S2), crop maturity (between seed formation and harvest, S3) and during the cover crop period after crop harvest (before soil tillage or sowing of the next crop, S4). The number of replicates was also extracted, together with the variance of mean values, when reported by the authors.

Weeding operations can influence the competition between CC and CP plants. We therefore distinguished between two categories of control treatments: (i) weeded control treatments in which the CC, grown as a sole crop, was weeded by chemical, mechanical or hand weeding methods after the sowing of the CP, and (ii) non-weeded control treatments in which the CC, grown as a sole crop, was not weeded after the sowing of the CP. In most papers, CP + CC treatments were compared with only one type of control, but two papers included one control treatment of each type. In these two studies, the experimental units were compared with both control treatments. Two of the studies with weeded control treatments compared different weeding methods (hand, mechanical or chemical weeding). In these two studies, the data for the different weeded control treatments were averaged to give a single control treatment value, to limit the redundancy arising from multiple comparisons within a single experiment. The corresponding CP + CC treatments were compared with the averaged control treatment. "Weed-free check" treatments are not representative of common agricultural practice and were not considered here.

If the weed biomass was below $2\,\mathrm{g\,DM\,m^{-2}}$ (about $15\,\mathrm{g\,FM\,m^{-2}}$) in the control treatment of a given experiment, we considered the plot to be insufficiently infested for evaluation of the weed-suppressing effects of the CP. This threshold of weed biomass was not exceeded in six experiments with non-weeded control treatments and 12 experiments with weeded control treatments. The corresponding experimental units were not considered further in analyses including weed biomass (30 and 39 experimental units, respectively). The raw data are presented in supplementary materials (Multimedia component 1). These additional figures indicate the ranges of values of yields, weed biomasses and weed densities.

2.3. Statistical analysis

Effect sizes for CPs were analyzed by calculating three types of ratios, defined as follows:

$$R_{yield} = Yiel_{CC+CP}/\mathrm{Yield}_{CC} \tag{1}$$

$$R_{BM} = Weed\ biomass_{CC+CP}/\mathrm{Weedbiomass}_{CC} \tag{2}$$

$$R_{density} = Weed\ density_{CC+CP}/\mathrm{Weeddensity}_{CC} \tag{3}$$

where the subscripts CC + CP and CC indicate the intercrop and sole crop, respectively. The ratios in Eq. (1) and Eq. (2) were calculated for all experiments and the ratio in Eq. (3) was calculated for experiments including weed density measurements. All ratios were calculated with data averaged over replicates. When data were available for both weeded and non-weeded sole CC controls, the ratios (Eq. (1)–(3)) were calculated for each CC control in turn. The dataset consisted of 515 yield ratios, 563 weed biomass ratios and 246 weed density ratios and is freely available (Multimedia component 2).

Log-transformed ratios (L) and their variances (Var_L) were calculated for each experiment, as previously described (Hedges et al., 1999):

$$Var_L = \sigma^2_{CC}/(n_{cc}\bar{X}^2_{CC}) + \sigma^2_{CC+CP}/(n_{CC+CP}\bar{X}^2_{CC+CP}) \tag{4}$$

where σ is the standard deviation of the data (replicates of yield, weed biomass or weed density), n is the number of replicates, and $\bar{X}$ the mean value of yield, weed biomass or weed density for the CC and for the CC + CP.

In one study (Correia et al., 2014), weed biomass was zero in 15 experimental units because the CP provided total weed control. In one experimental unit in one article (Uchino et al., 2009), the yield was zero because the CP developed too much, preventing harvesting of the CC. As log ratios could not be calculated in such situations, the corresponding data were removed from the analysis.

The between-experiment variability of the ratios was analyzed through four variables characterizing CP intercropping systems:

- Type of CP establishment: living mulch, synchronized sowing, or relay intercropping (Fig. 1).
- Type of cash crop: small grains, maize, or other.
- Overlap of the growth periods of the CC and the CP ($D_{CC+CPoverlap}$, expressed in days) relative to the duration of the growth period of the CC (D_{CC}): $D_{CC+CPoverlap}/D_{CC}$

This variable is equal to one when the CC and the CP are grown together during the entire growth period of the CC (full overlap), but is lower otherwise. This variable was calculated from sowing and harvest dates when available, and from technical "gray" literature when those dates were not available from the articles included in the analysis. This variable may explain the competitiveness of the CP relative to the CC or weeds.

'Relationships between yield, weed biomass and weed density log ratios were first analyzed graphically. Contingency tables were then used to report the number of "win-win" (yield gain and weed biomass/weed density decrease), "win-lose" (yield gain and weed biomass/weed density increase), "lose-win" (yield loss and weed biomass/weed density decrease) and "lose-lose" (yield loss and weed biomass/weed density increase) situations. The trade-offs between yield and weed control were assessed only with weed data acquired at crop maturity (weed sampling at S3) because this stage integrates weed-crop competition over the whole crop cycle and can therefore be compared with crop yield. The percentage of data belonging to each of the four above-mentioned categories and its associated 95% confidence interval were estimated using a bootstrap procedure (Efron and Tibshirani, 1986), using 1000 sets of resampled log-ratios. Briefly, yield and weed biomass log-ratios were resampled from Gaussian distributions defined by N[L, $\sqrt{Var_L}$] where L is a log-ratio estimated with Eqs. (1) or (2), and Var_L is the corresponding variance given by Eq. (4). Missing variances were set equal to the mean of the variances reported in the articles. The procedure was repeated 1000 times.

Three types of mixed-effect models were developed to estimate mean effect sizes, and to study the effects of several intercropping system characteristics (type of CC, type of CP establishment and overlapping periods) through comparisons with weeded control treatments and non-weeded control treatments successively. The models are described below.

- Mean effect size estimation (model M1)

$$\log\left(Y_{ij}\right) = \mu + b_i + \varepsilon_{ij} \quad (5)$$

where Y_{ij} is one of the three ratios defined above in the j^{th} experimental unit, $j = 1,. ., P_i$ (P is the number of experimental units in one site-year) of the i^{th} site-year, $i = 1,. ., n$, μ is the log ratio mean over studies, b_i is a random site-year effect assumed to be independently and identically distributed (iid) with $b_i \sim N(0, \sigma_b 2)$, $\varepsilon_{ij} \sim N(0, \sigma_{ij} 2)$ (iid) the model residual error, $\sigma_b 2$ is the between-site-year variance, and $\sigma_{ij} 2$ is the within-site-year variance.

- Effect of three factors corresponding to the type of CC, the type of CP establishment, and combinations of the two (model M2).

$$\log\left(Y_{ij}\right) = \sum_{k=1}^{K} a_k Z_{ij}^{(k)} + b_i + \varepsilon_{ij} \quad (6)$$

where a_k is the fixed effect of the k^{th} level of the factor considered, K is the number of levels of the factor (*e.g.*, number of types of CC), and $Z_{ij}^{(k)}$ is a binary variable equal to one when the j^{th} experimental unit of the i^{th} site-year corresponds to the k^{th} level of the factor considered. Model M2 was fitted with each of the three factors successively.

- Effect of overlapping growth periods (model M3)

$$\log\left(Y_{ij}\right) = \beta_0 + \beta_1 x_{ij} + b_i + \varepsilon_{ij} \quad (7)$$

where β_0 and β_1 are two fixed parameters and x_{ij} is the j^{th} experimental unit of the i^{th} site-year. In this model, only weed data collected at S3 were included for weed biomass and density, because this stage integrates weed-crop competition over the whole crop cycle. In the other models, the weed data for the different stages were analyzed together.

Statistical analyses were performed with R 3.0.1 software (R Development Core Team, 2013). The models were fitted with the *lme()* function from the *nmle* package (Pinheiro and Bates, 2000). Two approaches were considered for estimating the within-site-year variance $\sigma_{ij}2$. In the first approach, $\sigma_{ij}2$ was expressed as a power function of the number of replicates in experimental units. In the second approach, $\sigma_{ij}2$ was fixed at the variance of the log ratio Var_L given by Eq. (4), for a subset of data for which variances were reported in the articles. Both approaches yielded similar results, so we present only the results obtained with the first approach below. Those obtained with the second approach are presented in Multimedia component 3. Parameters were estimated by the restricted maximum likelihood method (REML). The distributions of the model residuals were checked graphically. Several alternative model formulations were tested. In particular, models including "experiment" and "study" random effects were fitted to data, but they led to higher values of bayesian information criterion (Burnham and Anderson, 2002) and were not considered further (Multimedia component 4).

Publication biases were investigated for each size effect by drawing funnel plots, in which the precision of the log ratio (inverse of variance defined in Eq. (4)) was plotted against the centered effects (log ratio – mean log ratio) (Multimedia component 4) (Philibert et al., 2012; Sutton, 2000). Linear regression methods were used to check whether the dataset was unbalanced toward positive or negative values.

3. Results

3.1. Diversity of companion plant intercropping systems

The selected studies covered 15 CC species, and 26 legume species used as CPs in 18 countries (Table 2) over five continents (Fig. 2). Nine of the 34 studies were conducted according to the principles of organic farming. The main cash crops were small grains (winter and spring wheat, barley, oat and triticale) and maize for grain or silage. Various other crops were also represented at much lower frequency, including aromatic plants (coriander), grain legume crops (soybean, faba bean, lupin and pea) and field vegetables (cucurbits and cabbage).

The three methods of CP establishment were equally frequently used in small grains intercropping systems: living mulch, synchronized sowing and relay intercropping. Maize and other crops were established either in living mulches or by synchronized sowing. Small grains were the only cash crops found in relay-intercropping systems.

3.2. Trade-offs between yield and weed regulation

At crop maturity (S3), intercropping with a companion plant improved weed control in 82% of the experimental units relative to non-weeded control treatments, and in 66% of experimental units relative to weeded control treatments (Fig. 3). Intercropping resulted in lower yields for 43% of the experimental units compared with non-weeded controls and 56% of the experimental units compared with weeded control treatments. Finally, intercropping improved both weed control and yield ("win-win" situations) in 52% of experimental units compared with non-weeded controls and 36% of experimental units compared with weeded control treatments. A higher weed biomass associated with a lower yield (lose-lose) was observed in only 13% and 26% of the experimental units, in comparisons with non-weeded and weeded control treatments, respectively.

3.3. Analysis of the effects of companion plants on weed biomass ratio and weed density ratio

Globally, intercropping with a companion plant had a significant effect on weed biomass, which was 56% lower than that for

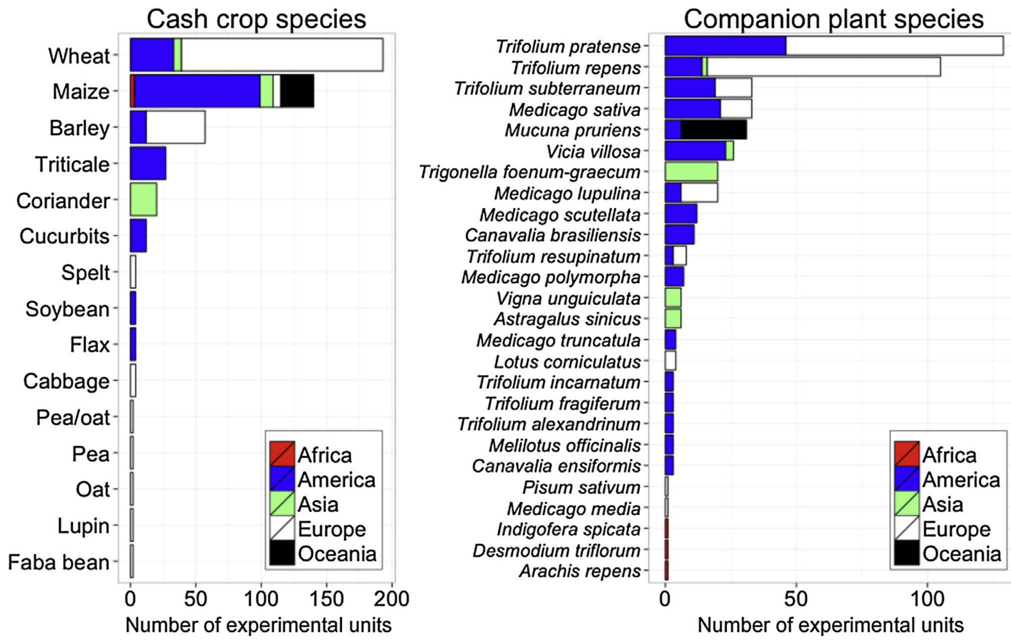

Fig. 2. Numbers of experimental units per CC species, and per CP species, relative to the continent on which the CP intercropping system was assessed. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

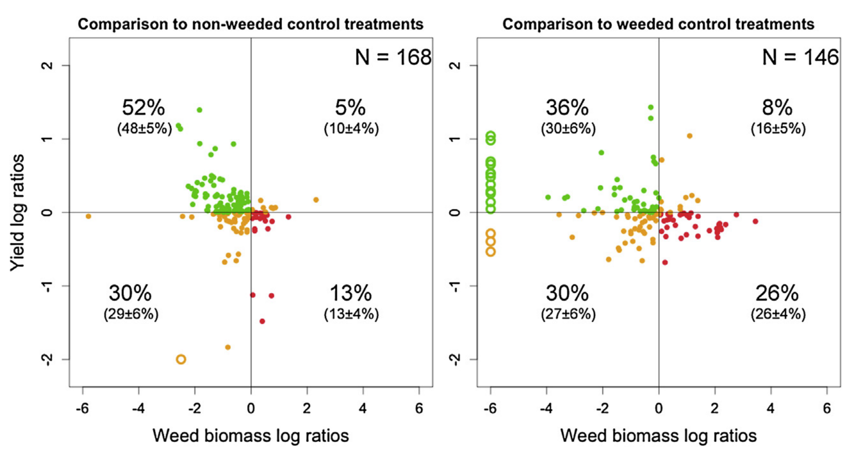

Fig. 3. Log-response ratios of yield and weed biomass at crop maturity (S3), for comparisons with non-weeded control treatments (left), and weeded control treatments (right). Open circles represent experimental units with a weed biomass or yield of zero (log ratios could not be calculated and were arbitrarily set at −6 and −2, respectively). These experimental units are included in the counts. "Win-win" and "lose-lose" situations are shown in green and red, respectively, whereas "win-lose" (upper right) and "lose-win" (bottom left) situations are both shown in orange. Percentages indicate the proportions of data in each situation. The estimation of these proportions and 95% confidence intervals, computed using a bootstrap method, are shown between brackets. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

non-weeded control treatments and 37% lower than that for weeded control treatments (Fig. 4) (See Multimedia component 5 for a table of the significances of differences between categories for each effect and each variable). This effect was consistent within each of the three CC types and within each types of CP establishment, for comparisons with non-weeded control treatments. No significant difference was found between the categories of these two factors considered independently. Nevertheless, the effects of type of CC, type of CP establishment and their combinations on weed biomass were frequently at the limits of significance for comparisons relative to weeded control treatments. In such comparisons, only "Living mulch" and "Maize – Living mulch" were found to cause a significant decrease in weed biomass. Figures shown in the Multimedia component 6 do not reveal any obvious relationship between the effect size and the weed biomass or weed density in the control treatments, unless in the case of the weed biomass in comparison to weeded control treatments where a significant negative relationship was found ($p = 0.0011$).

A significant publication bias was identified for weed biomass data for comparisons with weeded control treatments, but not for comparisons with non-weeded control treatments (Multimedia component 7).

The effects of legume CPs on weed density are not considered in detail here (see Multimedia component 8) because of the small numbers of observations and studies, limiting the generalizability of the results.

3.4. Analysis of the effects of companion plants on crop yield ratio

The intercropping of a legume companion plant with a cash crop had no overall significant effect on CC yield, whether the control treatment was weeded or non-weeded (Fig. 5). In

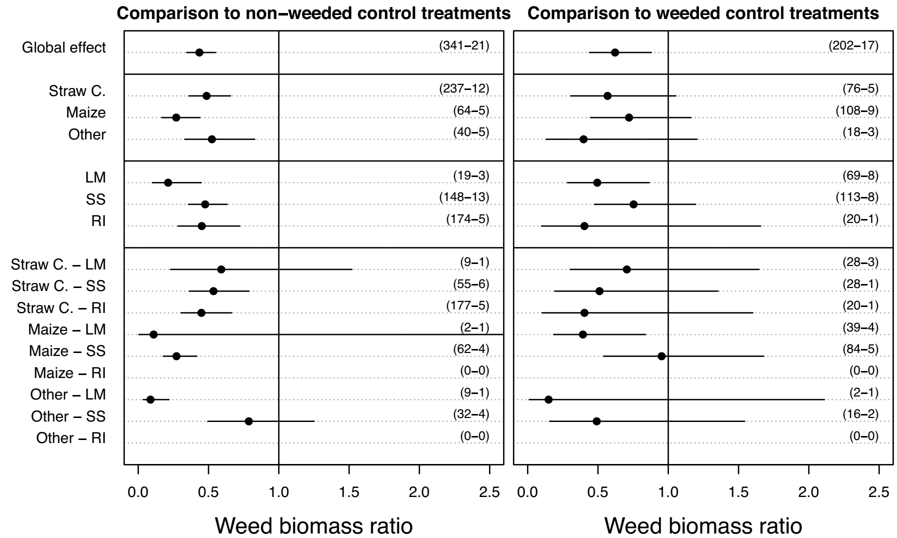

Fig. 4. Weed biomass response ratios (M1 and M2 models; mean estimates with 95% confidence intervals). The number of experimental units and the number of studies included in each category are shown in brackets, separated by a "-". Fifteen experimental units were removed from the analysis of the 'Maize – SS' category in "comparisons with weeded control treatments" because the yield was zero (log ratios could not be calculated). LM = Living mulch, SS = Synchronized sowing, RI = Relay intercropping.

analyses of the different types of CC, only maize displayed a significant increase in yield relative to non-weeded controls, with a mean effect of +37%. By comparison, for the crop type "other", intercropping significantly decreased yield (by 41%) relative to weeded control treatments.

In most situations, the method used to establish the CP could not account for yield variability. Only "living mulch" had a significant positive effect on yield (+47%) relative to non-weeded controls, but this finding was driven by the results of only three studies. In analyses of "type of CC – type of CP establishment" combinations, a significant increase in yield was also observed for maize intercropped with synchronized sowing of the CP and for "other" crops intercropped in a living mulch, relative to non-weeded control treatments (+35% and +98%, respectively). A negative effect (−37%), close to the limits of significance, was observed for small grains in which the CP was established by synchronized sowing, relative to non-weeded control treatments. In comparisons with weeded control treatments, synchronized seeding had a negative effect (−46%) on the yield of "other" crops.

The funnel plots suggested that there was no publication bias for yield data for either type of comparison (Multimedia component 7).

3.5. Analysis of the effects of overlapping growth periods

The overlap between the growth periods of the CC and the CP ranged from 0.27 (e.g. for relay intercropping) to 1 (e.g. for synchronized sowing and living mulch). It had no significant effect on any of the response effects, regardless of the type of control treatment considered (weeded or non-weeded; Multimedia component 9).

4. Discussion

4.1. Effect of legume CPs on weeds

This meta-analysis showed a systematic effect of CPs, decreasing weed biomass and density in comparisons with non-weeded control treatments, for almost all types of CC and all types of CP establishment. CPs modify environmental factors affecting weed germination, establishment and early growth (Liebman and Davis, 2000). Weed control in CP intercrops is generally associated with an acceleration of crop canopy closure, decreasing the amount of radiation available to the weeds (Jamshidi et al., 2013; Uchino et al., 2009), and thus restricting their establishment (density) and growth (dry matter) (Bilalis et al., 2010). Our results are consistent with the findings of the literature review by Liebman and Dyck, who found that weed biomass was reduced by intercropping a CC with "smothering" CPs in 87% of cases (Liebman and Dyck, 1993).

We also detected a weed-suppressing effect of CPs in comparisons with weeded control treatments, but this effect was often of borderline significance, and the CP appeared to be less efficient than in comparisons with non-weeded control treatments. This suggests that legume CPs tend to be less beneficial for weed control in situations in which weeding operations are already carried out. There are two possible reasons for this finding. First, the weeding operations are generally highly efficient, leaving little room for improvement with the introduction of intercropping with CPs. Second, a dense CP with good coverage may limit the efficiency of herbicide by an "umbrella" effect, protecting weeds. However, the experimental designs of the studies retained for the analysis were not appropriate for evaluations of the ability of CPs to replace weeding operations, and we cannot, therefore, draw any firm conclusions on this point. Given this limited efficacy, CP intercropping should instead be used in the framework of integrated weed management, together with other cropping practices, such as a long, diversified rotation and soil tillage management (Buhler, 2002).

Asymmetric funnel plots revealed a potential publication bias for weed data, for comparisons with weeded control treatments. The reasons for a publication bias concerning such comparisons but not those with non-weeded control treatments were unclear. This publication bias was probably due to unpublished studies with negative results, due to the CP overgrowing the CC and preventing its harvest, for example. This may have led to an overestimation of the effect of CPs on weed biomass in comparisons with weeded control treatments. In addition, the estimated mean effects were obtained without taking into account the 15 experimental units for which weed biomass was zero in CP treatments (total weed suppression). Taking these observations into account would increase the estimated weed-control effects of CPs.

4.2. Effect of legume CPs on crop yield

In most categories, CP intercropping had no significant effect on crop yield, suggesting that the CPs were successfully managed so

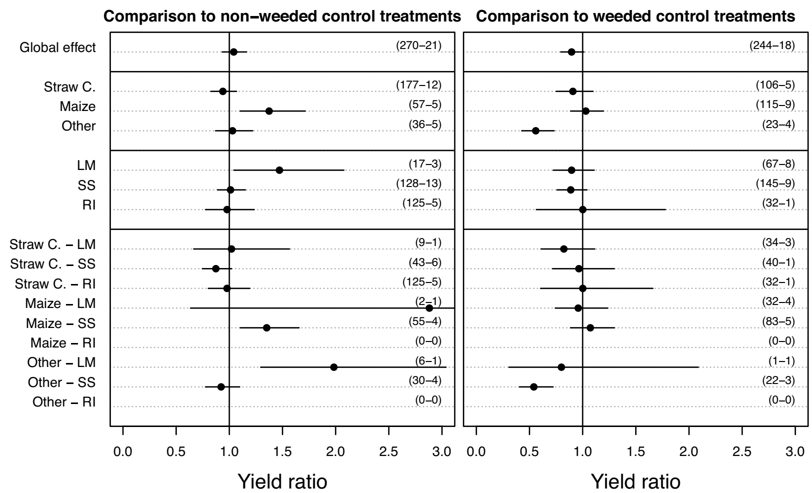

Fig. 5. Yield response ratios (M1 and M2 models; mean estimates with 95% confidence intervals). The number of experimental units and the number of studies included in each category are displayed in brackets, separated by a "-". One experimental unit was removed from the analysis of the 'Maize – SS' category in "comparisons with non-weeded control treatments" because the yield was zero (log ratios could not be calculated). LM = Living mulch, SS = Synchronized sowing, RI = Relay intercropping.

as to limit their competition with the CC. In particular, maize yields were higher in CP intercropping conditions than in non-weeded control treatments. Canopy closure in this crop, which is grown with a wide inter-row, is slow, increasing the risk of competition from weeds. It was not possible to explain such results on the basis of our meta-analysis, but the authors of the studies concerned all agreed that the yield gain was mostly due to efficient weed suppression by the CP, together with better nitrogen recycling and fixation (Abdin et al., 2000; Deguchi et al., 2015; De Haan et al., 1997; Jamshidi et al., 2013; Uchino et al., 2009). Other authors cited the same mechanisms to explain the yield gain obtained with living mulch CPs relative to non-weeded control treatments (Bergkvist, 2003; Deguchi et al., 2015; Ilnicki and Enache, 1992). In such cases, an older, established CP would be more likely than a recently established CP to supply the CC with nitrogen from its biomass and roots.

We hypothesized that a long overlapping growth period and early CP establishment would result in strong competition between the CC, CP and weeds, thus improving weed control but potentially reducing crop yield. However, we found no evidence of such an effect in our dataset. Several of the studies focusing on the synchronized sowing of CC and CP included in the meta-analysis tried to delay the establishment of the CP relative to that of the CC, to limit the competition of the CP with the CC (Brust et al., 2011; Ohlander et al., 1996; Uchino et al., 2009; Vanek et al., 2005). They showed that the CC might suffer if the CP is established too early and able to compete for nutrients in the upper layers of the soil. Yields were generally higher when the CP was established after the emergence of the CC. This effect was weakened by strip-tillage for CC sowing (Vanek et al., 2005). If CP sowing is delayed, there could be a trade-off between competition for resources to develop yield and weed suppression, because soil coverage is delayed by later sowing of the CP.

4.3. Win-win, lose-lose and other scenarios

We focused on two benefits provided to the CC by the CP: yield gain and weed control. A combined analysis of the effects of legume CPs on weeds and yield showed that, legume CPs did not generally decrease CC yield, but they did improve weed control, validating our initial hypothesis. Some types of CP intercrops, such as maize and living mulch, were found to be particularly beneficial in comparison with non-weeded control treatments. In addition to these general trends, we identified a number of "win-win", "lose-lose", "win-lose", and "lose-win" situations for the different CP intercrops, defined in terms of the impact of intercropping on CC yield and weed biomass.

A "win-win" situation was noted for 52% of the experimental units compared with non-weeded control treatments and 36% of those compared with weeded control treatments. Three mechanisms may account for these "win-win" situations. First, yield gain and weed reduction may result from the intercrop being more efficient than the sole crop at exploiting resources that might otherwise be used by weeds. By outcompeting weeds and occupying their ecological niche, the CP decreases weed-crop competition. This effect is particularly beneficial if CP-CC competition is weaker than weed-CC competition. Once the weeds are effectively suppressed, the soil N can be used for the production of crop biomass rather than weed biomass, thereby increasing yield, particularly in situations in which the CP is a legume species with low levels of soil mineral nitrogen uptake. Second, facilitation processes may partly explain these cases, particularly for nitrogen transfer from the CP to the CC, independently of any direct effect on competition between the CC and weeds. These facilitation processes may involve the mowing of the CP or its killing with an herbicide or by frost, with the biomass being returned to the soil (Carof et al., 2007a,b; Lorin et al., 2015; Thorsted et al., 2006). They may lead to improvements in phosphorus bioavailability (Hinsinger et al., 2011), mycorrhization (Gianinazzi et al., 2010), soil structure (Carof et al., 2007a, 2007b), soil sanitization, herbivore disturbance (Finch and Collier, 2000) and water availability (Brooker et al., 2016). Third, weed growth suppression may occur through allelopathy (Caamal-Maldonado et al., 2001; Jabran et al., 2015), if certain species of CP, such as buckwheat and oat, are used, but the only legumes shown to have such effects are *Medicago sativa* (Onen 2013) and a few tropical legume species such as *Crotalaria juncea* L., *Cajanus cajan* L. Millsp. and *Mucuna deeringiana* Bort. Merr. (Hepperly et al., 1992; Skinner et al., 2012; Caamal-Maldonado et al., 2001; Jabran et al., 2015; Onen, 2013).

In the "lose-lose" situations we identified (13% of experimental units compared with non-weeded controls and 26% compared with weeded controls), the CP did not improve weed control and may have competed more strongly with the crop than with weeds. It is also possible that CP sowing (in situations in which the CP was sown after the CC) triggered the emergence of additional weeds due to soil tillage for seedbed preparation. In "win-lose" situations, yield increased but with no suppression of weed biomass. Such situations were rare (only 5% in comparisons with non-weeded and 8% in comparisons with weeded controls) and may be due to facilitation processes or chance alone (experimental variability).

Finally, in "lose-win" situations, the CP competed strongly with both weeds and the CC.

Previous studies of the intercropping of two cash crop species have suggested that the yield and weed suppression advantages of intercropping are tightly coupled phenomena (Liebman and Dyck, 1993). We validated this relationship for CP intercrops, at least for situations in which the control treatments are not weeded. Weeding operations may interfere with competition interactions, so this relationship was not so pronounced for comparisons with weeded control treatments.

4.4. Perspectives for CP intercropping

This study revealed several interesting aspects of CP intercropping, the performance of which is largely dependent on experimental settings, depending on the type of CC. Many factors affect the performances of CP intercrops, and a satisfactory compromise in terms of competition between the CC and the CP may be achieved by selecting the most appropriate species or mixture of species (phenological cycle, growth habits, functional traits), temporal and spatial arrangement of the CC and CP (Campiglia et al., 2014) and specific agricultural operations to limit competition between the CC and the CP (strip-intercropping, slowing CP development by mowing or with herbicides). However, it is still important to identify the best combinations of (CC × CP × CP establishment × agricultural practices), for the particular pedoclimatic context (water, temperature) and farming system (presence of animals, available machinery, farm seed availability, etc.) concerned.

In addition to weed control, the CP may provide many other benefits, such as N supply for the following crop (Amossé et al., 2014; Bergkvist et al., 2011; Brandsæter et al., 1998), the hosting of predators, protection against erosion, and increasing soil C content. Conversely, the CP may lower the performance of the system by increasing the workload, hosting pests and decreasing net economic returns, for example. Multicriteria assessments of CP intercropping systems are therefore required to assess their benefits (Schipanski et al., 2014).

5. Conclusion

This meta-analysis showed that the use of legume CP generally enhances weed control without reducing crop yield. Weed suppression effects were higher in systems without weeding compared to systems with weeding. This result indicates that the use of CP is relevant for organic and low input systems. In particular, maize intercropped with legume CP showed yield increase, as a result of efficient weed suppression in non-weeded systems.

Legume CP intercropping could provide efficient weed control, but the conditions giving rise to win-win situations should be explored further, to encourage the spread of this technique among farmers.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fcr.2017.01.010.

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