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Highlights

• Frost-sensitive companion plants can improve rapeseed cropping.
• Companion plants differ in competitiveness and facilitation effects.
• Legume CPs improve weed control and compensate for fertilizer dose reduction.
• Faba bean and faba bean + lentil mixtures have the best overall performances
• Soil and pedoclimatic conditions affect the performance of rapeseed intercropping.

Abstract

The intercropping of rapeseed with frost-sensitive companion plants (CP) has recently been proposed as a way to mitigate the negative environmental impact of rapeseed crops. Using mixed-effect linear models, we compared the yield and weed amounts of rapeseed intercropped with different CP species with that of rapeseed as a sole crop in an unique dataset of 79 field experiments covering a wide range of climate, soil and practices conditions in the northwestern part of France, from 2009 to 2015. Bayesian model averaging procedure was used to determine the relative contributions of sites characteristics to the effects of intercropping.

Before winter, field pea and faba bean had accumulated the largest amounts of dry mass, with more than 100 g m^{-2}. Rapeseed biomass was reduced by 56% by non-legume CPs and by only 18% by legume CPs, the largest decrease being caused by pea. Non-legumes decreased the nitrogen nutrition index of rapeseed by 7%, whereas pea and faba bean increased this index by 6% and 3%, respectively. Intercropping with non-legume and legume CPs reduced weed amounts by 52% and 38% respectively, with no difference between CP species. Non-legume CPs decreased rapeseed yield at harvest by 0.58 t ha^{-1}, whereas faba bean and faba bean + lentil increased yield by 0.16 and 0.12 t ha^{-1} respectively, when fertilized at the recommended rate. Intercropping with faba bean, lentil or a mixture of both made it possible to reduce nitrogen applications by 30–40 kg ha^{-1} with no significant decrease in rapeseed yield. Faba bean and faba bean + lentil mixtures had the best overall performance. This work suggests that intercropping rapeseed is promising, particularly in soils with low nitrogen content with an early sowing date in the late summer.

Keywords

Rapeseed; Oilseed rape; Intercropping; Companion plants; Weeds; Yield

1. Introduction

Almost nine million hectares are planted with winter rapeseed in Europe (the 5th most cultivated species) and 1.5 million hectares of the area under this crop are found in France (FAOSTAT, *faostat.fao.org*). Rapeseed is considered a good crop for preceding wheat, in particular, within the rotation, for several reasons: its deep rooting system structures the soil; its residues have a high nitrogen content, which is of benefit to the next crop; in cereal-dominated rotations, it breaks the cycle of diseases and weeds associated with cereal crops; and it provides high economic returns, thanks to the biofuel market (Hebinger, 2013). However, rapeseed also has negative effects on the environment. Pesticides against many pests, weeds and diseases are applied in both fall and spring, with a treatment frequency index of 5.6 in France in 2014 (Agreste, 2016), second only to that for field-cropped potatoes. In France, the mean mineral nitrogen fertilizer application in spring in 2011 was 169 kg ha^{-1}, and rapeseed is the field crop with the third highest requirement for nitrogen fertilizer (Agreste, 2014). This high nitrogen requirement, which is mostly met through the use of synthetic fertilizers, decreases the energy balance of rapeseed biofuel (van Duren et al., 2015). All these aspects call into question the overall sustainability of rapeseed cropping and suggest that alternative crop management techniques should be developed, to reduce the reliance on pesticides and fertilizer use.

Planting mixtures of plants is one way to reduce the environmental impact of agriculture, by improving crop productivity and pest regulation (Gaba et al., 2015, Malézieux et al., 2009). Companion plant (CP) 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 (Hartwig and Ammon, 2002, Liebman and Dyck, 1993). The cropping of rapeseed with simultaneously sown frost-sensitive CPs has been proposed as a means of reducing pesticide and fertilizer use (Cadoux et al., 2015, Lorin et al., 2016, Lorin et al., 2015). The rapeseed and the CP grow together until the CP is killed by frost or herbicide during the winter. The following spring, the rapeseed grows alone, like a conventional sole crop, until harvest. In the fall, the CP provides greater soil coverage and controls weeds (Cadoux et al., 2015, Liebman and Dyck, 1993, Lorin et al., 2015, Verret et al., 2017). The presence of a large amount of CP biomass can reduce damage due to insect pests in the fall, probably through visual and/or olfactory confusion (Cadoux et al., 2015, Finch and Collier, 2000). In spring, mineralization of the killed CP residues contributes to the nitrogen nutrition of the rapeseed crop (Cadoux et al., 2015, Lorin et al., 2016).

Several CP species, including members of the legume family in particular, including faba bean, lentil, vetches and berseem clover, have already been tested for intercropping with rapeseed (Cadoux et al., 2015, Lorin et al., 2016, Lorin et al., 2015). Legume species are considered good candidate CPs because they produce biomass and compete with weeds without competing strongly with the main crop for nitrogen, thanks to their ability to fix nitrogen from the atmosphere (Corre-Hellou et al., 2011, Hauggaard-Nielsen et al., 2001). However, Lorin et al. (2015) showed that CP performance, in terms of biomass production, weed control and nitrogen release, differs considerably between species. However, studies on rapeseed intercropping have not yet provided sufficient information about the variability of performance over a broad range of contexts.

The performance of the intercropping system may also be subject to interactions between the components of the system (the crop, companion plants, and weeds), agricultural practices and the environment (Gaba et al., 2015, Lithourgidis et al., 2011, Wilke and Snapp, 2008). Soil fertility is a key factor determining CP performance, as it affects competitive interactions between plants. For example, Lorin et al. (2015) showed that 11 species and mixtures of species had very different abilities to control weeds, depending on soil mineral nitrogen content at sowing (Lorin et al., 2015). In another study, seven clover species were found to control weeds more effectively in nitrogen-poor than in nitrogen-rich soils (Ross et al., 2001). Climate conditions also determine CP performance, but this effect is often nested in a "study year" effect. For instance, 12 CP species were found to compete with maize to different extents depending on the year (Abdin et al., 2000). Drought affects the performance of a maize living mulch system including kura clover (*Trifolium ambiguum*), a species that behaves well in dry environments (Ziyomo et al., 2013). An understanding of the effects of agropedoclimatic conditions on the performance of intercropping systems is crucial for selection of the best CP species in a given context.

The primary objective of this study was to quantify the effects of CPs on weed control, rapeseed competition, nitrogen nutrition and grain yield, in rapeseed crops, over a broad range of contexts. We hypothesized that the amount of CP biomass accumulated before winter would be a key intermediate variable strongly related to various aspects of CP performance, such as competition with rapeseed, weed regulation and N supply to the crop (Cadoux et al., 2015, Lorin et al., 2016, Lorin et al., 2015). Our secondary objective was to analyze the variability of the effects of these intercropping systems between trials and to rank the respective roles of CP species, climate and soil conditions, agricultural techniques, and the interactions between these variables, with the aim of facilitating the selection of CP species well-adapted to the local context.

2. Materials and methods

2.1. Field experiments

From 2009–2015, 79 trials (1 trial = 1 site × 1 year × 1 experimental design) were conducted at several sites located to the north of a diagonal line running between Bordeaux and Strasbourg, in France (Fig. 1). Local agents managed the trials, with an experimental design best suited to the available workforce resources. The studies were designed as replicated randomized blocks or on-farm non-replicated side-by-side strips. Seventeen different species of CP and 42 mixtures of two to five species were assessed in trials exploring a wide range of plant characteristics in a diversity of soil and climate conditions (see Appendix A in the Supplementary material for the list of the different companion plant species and mixtures of species tested in the trials). The main CP species and mixtures were: spring faba bean (*Vicia faba*), lentil (*Lens culinaris*), spring field pea (*Pisum sativum*), and three mixtures of legume species consisting of faba bean + lentil, grass pea (*Lathyrus sativus*) + fenugreek (*Trigonella foenum-graecum*) + lentil (GFL), and spring common vetch (*Vicia sativa*) + purple vetch (*Vicia benghalensis*) + berseem clover (*Trifolium alexandrinum*, VVC). Non-legume species were gradually abandoned over time, because they competed too strongly with the rapeseed crop, and legume species were preferred for the trials. Companion plants were sown at 75% the rate generally used for monocultures of the species concerned. For legume mixtures, the sowing density of each species was reduced proportionally, according to the number of species. The control treatment was a rapeseed sole crop. Rapeseed cultivar, sowing density, tillage, weed management practices, pest and disease control with chemical pesticides and other agricultural practices were adapted to local conditions. In early spring, the nitrogen fertilizer requirements of the rapeseed crop were determined by the nitrogen balance sheet method (Reau and Wagner, 1998). Two modes of fertilization were assessed: (i) the recommended dose, and (ii) a reduced dose, 30–40 kg ha^{-1} less than the recommended dose. As control treatment(s), each trial had either (i) a rapeseed sole crop treated with the recommended dose, (ii) a rapeseed sole crop treated with the reduced dose, or (iii) both these control treatments.

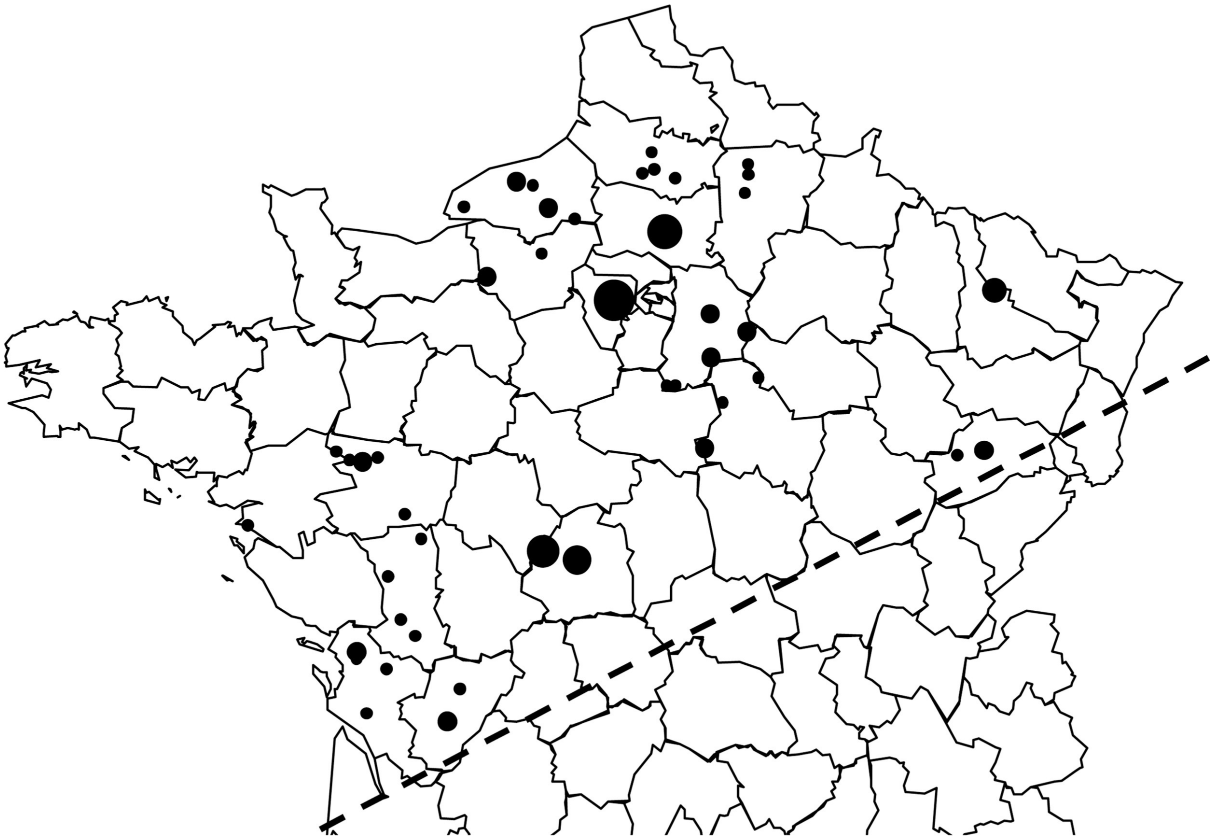

Fig. 1. Map of the trials, located in the northwestern part of France, above a diagonal line running between Bordeaux and Strasbourg (dashed line). The size of the dots is proportional to the number of trials per site, which ranged from 1 to 9.

2.2. Measurements

Before winter, whole plants of rapeseed, the CP and weeds were sampled with a single 0.5–1 m^2 quadrat for each treatment in each block. In trials without replicates, measurements were made with three to four quadrats per treatment strip. The aerial dry mass of each component was determined after drying at 80 °C for 48 h, and N content was determined by the Dumas method. The nitrogen nutrition index (NNI) of the rapeseed was determined from its aerial dry mass and N content, according to the formula proposed by Colnenne et al. (1998):

$$NNI = \frac{Rapeseed\ \ N\ \ content}{4.48 \times (rapeseed\ \ dry\ \ mass)^{-0.25}} \qquad (1)$$

At maturity, each treatment was harvested separately with a combine harvester, and yields were recorded. Not all measurements were performed systematically in all trials, depending on the resources of the institutions concerned.

2.3. Trial characteristics

For each field trial, local agents recorded a set of characteristics, including soil characteristics and agricultural practices (Table 1) (see Appendix B in the Supplementary material for a complete description of the trials, including the types of measurement performed). Daily climatic data from the nearest meteorological station to each trial, including temperature, rainfall, radiation and evapotranspiration, were acquired from Météo-France. They were summed over the period of CP growth, extending from sowing date to winter sampling date.

Table 1. List of the variables used to describe pedoclimatic conditions, agricultural practices and companion plants.

Category	Description	Unit or factor levels
Fall climate descriptors	Rainfall	mm
	Temperature	degree-days
	Radiation	J cm^{-2}
	Potential evapotranspiration	mm
Soil characteristics	Soil texture (main component)	Clay Silt Sand
	Soil depth	1 = Superficial (0–50 cm) 2 = Intermediate (50–90 cm) 3 = Deep (>90 cm)
	Soil N richness at sowing	1 = Poor (0–45 kgN ha^{-1}) 2 = Intermediate (45–90 kgN ha^{-1}) 3 = Rich (>90 kgN ha^{-1})
Agricultural practices	Tillage type	Plowing (P) Reduced tillage (RT) Direct seeding (DS)
	Type of rapeseed cultivar	Hybrid Inbred line
	Fertilizer reduction, i.e. the difference between the recommended and the applied rates of N fertilizer	kgN ha^{-1}
Companion plant characteristics	CP family	Legume Non-legume
	CP species	Faba bean Field pea Lentil Lentil + aba bean Grass pea + fenugreek + lentil (GFL) Common and purple vetches + Berseem clover (VVC)
	Dry mass (DM) of the CP before winter	g m^{-2}

2.4. Indices measuring the effects of companion plant intercropping

Intercrop performance was estimated with four indices. The competition experienced by rapeseed in intercrops before winter was analyzed by measuring the effect of the CP on rapeseed dry mass and NNI before winter, as follows:

$$R_{Rapeseed\_DM} = Rapeseed\ dry\ mass_{\ Intercroppedrapeseed}/Rapeseed\ dry\ mass_{\ Solerapeseed} \quad (2)$$

$$R_{Rapeseed\_NNI} = Rapeseed\ NNI_{\ Intercroppedrapeseed}/Rapeseed\ NNI_{\ Solerapeseed} \quad (3)$$

The effect of the CP on weeds before winter was analyzed as follows:

$$R_{Weed} = Amount\ of\ weeds_{\ Intercroppedrapeseed}/Amount\ of\ weeds_{\ Solerapeseed} \quad (4)$$

where the amount of weeds was generally assessed as weed dry mass, but sometimes as a visual estimate of weed percentage cover if weed biomass could not be measured (for only three trials). When weed biomass was below 5 g m^{-2} dry mass (about 30 g m^{-2} fresh matter) in the control treatment of a given experiment before winter, we considered the plot to be insufficiently infested for evaluation of the weed-suppressing effects of CPs. Seven trials fell below this threshold and were thus discarded from the analysis.

The effects of CPs on rapeseed yield (in t ha^{-1}) were analyzed as follows:

$$\Delta yield = Yield_{Intercroppedrapeseed} - Yield_{Solerapeseed} \quad (5)$$

This index was calculated twice: for intercropped rapeseed and sole rapeseed crops receiving the same amount of fertilizer, and for intercropped rapeseed crops receiving 30–40 kg ha^{-1} less fertilizer than sole rapeseed fertilized at the recommended dose. We decided to analyze the difference rather than a ratio, because a yield gain or loss in t ha^{-1} can easily be converted into an economic margin.
We also analyzed the CP dry mass accumulated before winter to assess both the potential of the CP species to provide benefits and their competitiveness. CP dry mass was therefore successively considered as a descriptor and a performance indicator.

2.5. Statistical analyses

2.5.1. Estimation of the mean effects of the companion plants

We evaluated the effects of the CPs on intercrop performance through two types of analyses. First, we assessed the effect of CP family: legume (or a mixture of legumes) or a non-legume species. We then focused on the six most frequently tested CP species or mixtures of species. Sixty-seven trials compared at least three of these treatments at the same time, and 12 trials tested less than three of these treatments at the same time (Appendix B, Figure B1 in the Supplementary material). Faba bean + lentil and field pea were the most and the least tested treatments, assessed in 69 and 41 trials, respectively (Appendix B, Figure B2 in the Supplementary material). We checked and confirmed that the unbalanced experimental design did not create confounding effects, such as one treatment being much more frequently tested in trials with a given set of soil conditions (texture, depth, N richness at sowing) or agricultural practices (tillage, type of rapeseed cultivar) than in trials with other conditions (Appendix B, Tables B2 to B7 in the Supplementary material).
The various performance indicators were analyzed with mixed-effect models, to determine the causes of between-trial variability and to estimate the effects of CP family and CP species for the six most frequently studied legume CP species and mixtures. We used the following model:

$$\text{M1: } Y_{ij} or \log(Y_{ij}) = \sum_{k=1}^{K} \alpha_k Z_{ij}^{(k)} + b_i + \varepsilon_{ij} \quad (6)$$

where:
• Y_{ij}, or $\log(Y_{ij})$ in the case of ratios, is the performance indicator of the j^{th} species/family in the i^{th} trial,
• K is the number of levels of the factor (*i.e.* $K = 2$ for testing family effect, $K = 6$ for testing species effect),
• α_k is the fixed effect of the k^{th} level of the considered factor,
• $Z_{ij}^{(k)}$ is a binary variable equal to one when the j^{th} species/family ofthe i^{th} trial corresponds to the k^{th} level of the considered factor,
• b_i is a random trial effect assumed to be independently and identically distributed as $b_i \sim N(0, \sigma_b^2)$ with σ_b^2 the between-trial variance,
• ε_{ij} is the residual error assumed to be independently and identically distributed $\varepsilon_{ij} \sim N(0, \sigma_{ij}^2)$ with σ_{ij}^2 the within-trial variance, expressed as a power function of the number of replicates in experimental units.

The models were fitted successively, using the two factors “CP family” and “CP species”. We used the *lme* function from the *nlme* package (Pinheiro and Bates, 2000) of R 3.0.1 software. For parameter estimation, models were fitted with the restricted maximum likelihood method.
In tests of species effects, the M1 model compares the values obtained with a given CP species to those obtained for rapeseed alone, used as the reference for the ratio and difference calculation. This approach does not strictly allow comparison between the different CP species, because not all the species were systematically assessed in each trial. For direct comparison of the effects of two CP species, we fitted the models using one species as a reference, and including in the analysis only those trials in which this species was assessed. These analyses confirmed our results and are available in the appendix (Appendix C in the Supplementary material).
We summarized the estimated effects of CP species on rapeseed crops, by representing the different effects on a radar chart after normalization with the following formula:

$$\overline{R}_{kY} = \frac{R_{kY} - R_{*Y}}{R_Y^{*} - R_{*Y}} \quad (7)$$

where is the normalized value attained with the k^{th} treatment, evaluated with the indicator Y,
is the maximum or best value attained with the various treatments, and R_{*Y} is the minimum or worst value attained, if the indicator is of the “more is better” type (i.e. CP dry mass, *Δyield*), and *vice versa* for indicators of the “less is better” type (weed ratio, rapeseed dry mass ratio) (Ramírez-García et al., 2015).

2.5.2. Exploration of the interactions between CP species and trials

We checked for differences in the behavior of the species between trials by analyzing the interactions between CP species and trials in a second mixed model (M2), as follows:

$$\text{M2:} \quad Y_{ij}\, or \log(Y_{ij}) = \sum_{k=1}^{K} \alpha_k Z_{ij}^{(k)} + \sum_{k=1}^{K} \alpha_{ki} Z_{ij}^{(k)} + b_i + \varepsilon_{ij} \quad (8)$$

where αki is the random variable effect describing the interaction between the k^{th} CP species and the trial, αki ~N(0, σ_k^2), with σ_k^2 the variance of the effect of the k^{th} species across trials.
We identified the CP species displaying the strongest interaction with each trial effect by exploring the correlations between the deviation due to CP species and the deviation due to the trial. For each performance indicator (variable Y), we calculated the difference between the effect of the i^{th} species in the j^{th} trial (
) and the mean effect of the six CP species in the j^{th} trial () (*Dev_CP*, Eq. (9)). The value obtained represents the deviation of the variable Y for each species in a specific trial from the mean value across all species within this trial. Similarly, we calculated the difference between the variable Y for the i^{th} species in the j^{th} trial () and the mean effect of this species over all trials () (*Dev_T*, Eq. (10)). The value obtained represents the deviation of the variable Y for a species in one trial from the mean value of this species across all trials.

$$DevCP_{ij}^{Y} = X_{ij}^{Y} - \overline{X_{j}^{Y}} \quad (9)$$

$$DevT_{ij}^{Y} = X_{ij}^{Y} - \overline{X_{i}^{Y}} \quad (10)$$

We investigated possible interactions between CP species and trial, by calculating Pearson’s correlation coefficient for the relationship between *Dev_CP* and *Dev_T*. A positive correlation indicates that the performance of the CP species considered in one trial (relative to the other species tested in this trial) increases with the relative performance of the trial. In other words, the species performance is affected by trial (site × year) performance. Conversely, the absence of a correlation indicates that the mean performance of one species across all trials does not explain the performance of that species in each individual trial. This analysis made it possible to identify the species for which performance was most dependent on trial conditions.

2.5.3. Relative importance of trial characteristics accounting for between-trial variability

A Bayesian model averaging (BMA) approach was used to rank the relative importance of trial characteristics relating to soil, climate and agronomic practices, to explain the between-trial variability of the six indicators of intercrop performance (Burnham and Anderson, 2002, Casagrande et al., 2009, Prost et al., 2008, Raftery et al., 1997).

Several sets of explanatory variables (Table 1) were added to the M1 model as fixed effects (Eq. (6)). Intercrop performances before winter were related to cumulative rainfall, temperature, radiation and evapotranspiration between sowing and before-winter sampling, soil characteristics including the soil type (the main textural element), soil depth and soil mineral nitrogen content at sowing, tillage type, type of rapeseed cultivar, CP species and CP biomass at winter (unless used to explain CP biomass itself). Intercrop performances at rapeseed harvest were related to soil characteristics, tillage type, type of rapeseed cultivar, CP species, decrease in fertilizer application relative to recommendations, and CP biomass at winter.

For each of the six performance indicators, all possible linear combinations of the different explanatory variables were generated and the corresponding models were fitted to the data. The BIC and BIC-weight were then calculated for each model from the outputs of the *lme* R function. When p explanatory variables were available, $q=2^p$ variable combinations, and therefore q regression models, were fitted by the maximum likelihood method. BIC-weight was calculated for the m^{th} regression model as:

$$W_m = \frac{e^{-0.5(BIC_m - BIC_{min})}}{\sum_{m=1}^{q} e^{-0.5(BIC_m - BIC_{min})}} \tag{11}$$

where BIC_m is the BIC of the m^{th} regression model, and BIC_{min} is the lowest BIC of any of the regression models.

The models were fitted with the same subset of data, including the six most tested species and mixtures only, to avoid confounding effects. These analyses were also restricted to the trials for which data were available for all covariates (the numbers of data used for the analyses are displayed in Table 2), because the BMA approach does not accept missing data.

Table 2. Relative importance (W_X) of the variable for explaining the variability of the effects of rapeseed-CP intercropping before winter. W_X values greater than 0.2 are in shown in bold font. The analyses include only the trials for which all the descriptors were available (*n* = the number of data used for the analysis/the total number of data available in the dataset; T = the number of trials used for the analysis/the total number of trials in which the measurement was made). When not pertinent, explanatory variables are not included in the models, and a "-" is indicated in the table.

Variable	Factor levels (for qualitative variables)	Before winter							
		CP dry mass accumulation		Rapeseed dry mass ratio		Rapeseed NNI ratio		Weed ratio	
		n = 213/267		n = 210/272		n = 176/180		n = 68/87	
		T = 54/67		T = 53/68		T = 45/47		T = 18/22	
		W_X	Estimates	W_X	Estimates	W_X	Estimates	W_X	Estimates
(Intercept)	–	**1.00**	4.19E + 01	**1.00**	−7.30E − 03	**1.00**	−1.09E − 02	**1.00**	−2.03E + 00
Soil texture	Clay (intercept)		0.00E + 00		0.00E + 00		0.00E + 00		0.00E + 00
	Loamy	0.01	2.28E − 01	0.02	−1.35E − 03	0.05	−2.87E − 03	0.03	−1.21E − 02
	Sandy		6.04E − 01		−4.43E − 03		−6.16E − 03		−1.23E − 02
Soil depth	–	0.15	−2.74E + 00	0.07	−7.81E − 04	0.08	6.45E − 04	0.14	1.81E − 02
Soil N richness at sowing	–	0.11	−1.39E + 00	**0.23**	−1.77E − 02	0.08	−1.02E − 03	0.13	1.63E − 02
Rainfall in the fall	–	**0.30**	8.52E − 02	0.07	5.46E − 06	0.08	−6.92E − 06	**0.21**	9.31E − 04
Radiation in the fall	–	**0.25**	6.01E − 04	0.07	−4.08E − 08	0.07	−1.97E − 08	0.17	3.88E − 06
Evapotranspiration in the fall	–	**0.26**	−2.50E − 01	0.08	6.44E − 05	0.08	1.05E − 05	0.13	1.60E − 04
Temperature in the fall	–	**0.21**	2.82E − 02	0.09	1.94E − 05	0.09	−6.99E − 06	**0.27**	6.71E − 04
Tillage type	Plowing (intercept)		0.00E + 00		0.00E + 00		0.00E + 00		0.00E + 00
	Direct sowing	**0.25**	1.66E + 01	0.01	1.76E − 04	0.01	−2.22E − 04	0.02	−2.98E − 03
	Reduced tillage		1.50E + 01		−1.20E − 03		−9.63E − 05		−3.65E − 03
Type of rapeseed cultivar	Hybrid (intercept)	**0.76**	0.00E + 00	0.07	0.00E + 00	0.08	0.00E + 00	**0.38**	0.00E + 00
	Inbred line		4.60E + 01		−1.55E − 03		1.72E − 03		3.08E − 01
CP species	Faba bean (intercept)		0.00E + 00		0.00E + 00		0.00E + 00		0.00E + 00
	Faba bean + lentil		−1.74E + 01		−4.02E − 03		−1.11E − 04		5.61E − 05
	GFL	**1.00**	−5.80E + 01	0.04	−2.78E − 03	0.00	−2.79E − 04	0.00	−1.04E − 04
	Lentil		−5.54E + 01		−5.56E − 03		−2.60E − 04		−1.23E − 04
	Field pea		3.23E + 00		−9.75E − 03		−2.57E − 05		−2.28E − 05
	VVC		−2.80E + 01		−3.90E − 03		−1.37E − 04		−5.86E − 05
CP dry mass at winter	–	–	–	**0.54**	−6.23E − 04	**0.78**	4.50E − 04	0.17	−2.00E − 04
CP species × CP dry mass interaction	Faba bean × CP dry mass				−4.98E − 04		1.00E − 04		−2.61E − 06
	Faba bean + lentil × CP dry mass		–		−1.23E − 03		6.16E − 05		4.15E − 07
	GFL × CP dry mass	–	–	**0.93**	−1.37E − 03	**0.43**	−3.79E − 04	0.00	−9.10E − 06
	Lentil × CP dry mass		–		−1.35E − 03		−1.63E − 04		−8.51E − 06
	Field pea × CP dry mass		–		−1.96E − 03		1.05E − 04		−2.48E − 06
	VVC × CP dry mass		–		−1.44E − 03		−8.41E − 06		−8.79E − 06

The relative importance of a given explanatory variable *X*, denoted W_X, was calculated as the sum of BIC-weights across all models including *X*. For each performance indicator, the larger the value of W_X, the more important *X* was considered among the set of explanatory variables.
The regression parameter values θ_r, $r = 1, \ldots, p$ (*p* is the number of variables considered in the regression model) were estimated as the sum of the maximum likelihood estimators weighted by BIC-weight:

$$\bar{\theta}_r = \sum_{m=1}^{q} W_m \hat{\theta}_{rm} \quad (12)$$

If a covariate X led to a BIC-weight greater than 0.2, an interaction term (CP species × X) was added to the BMA procedure. In this case, a single interaction term (CP species × dry mass at winter) was considered, because the inclusion of other interaction terms led to a BIC weight below 0.2.

3. Results

The M2 model outperformed M1 (according to the Bayesian information criterion, BIC) only for *Δyield* when intercropped rapeseed and sole rapeseed crops received the same amount of N fertilizer (Appendix D, Table D1 in the Supplementary material). The effects presented here are those calculated for M1, except for this last variable, for which M2 estimates are provided.

3.1. Accumulation of CP dry mass before winter

Non-legume and legume CPs had accumulated 109 and 81 g m^{-2} dry mass, respectively, before winter (about 5–10 t ha^{-1} fresh matter) (Fig. 2). This difference between non-legume and legume CPs was not significant. Field pea had accumulated the largest amount of dry mass before winter of any of the six most tested legume species and mixtures of species with 116 g m^{-2}, followed by faba bean (108 g m^{-2} of dry mass), faba bean + lentil, VVC, lentil and GFL. The results obtained for field pea, faba bean and faba bean + lentil differed significantly from those obtained for lentil and GFL. These results, as well as the indicators presented below were summed up in radar charts to provide a holistic view of rapeseed performance when intercropped with different types or species of CP (Fig. 3).

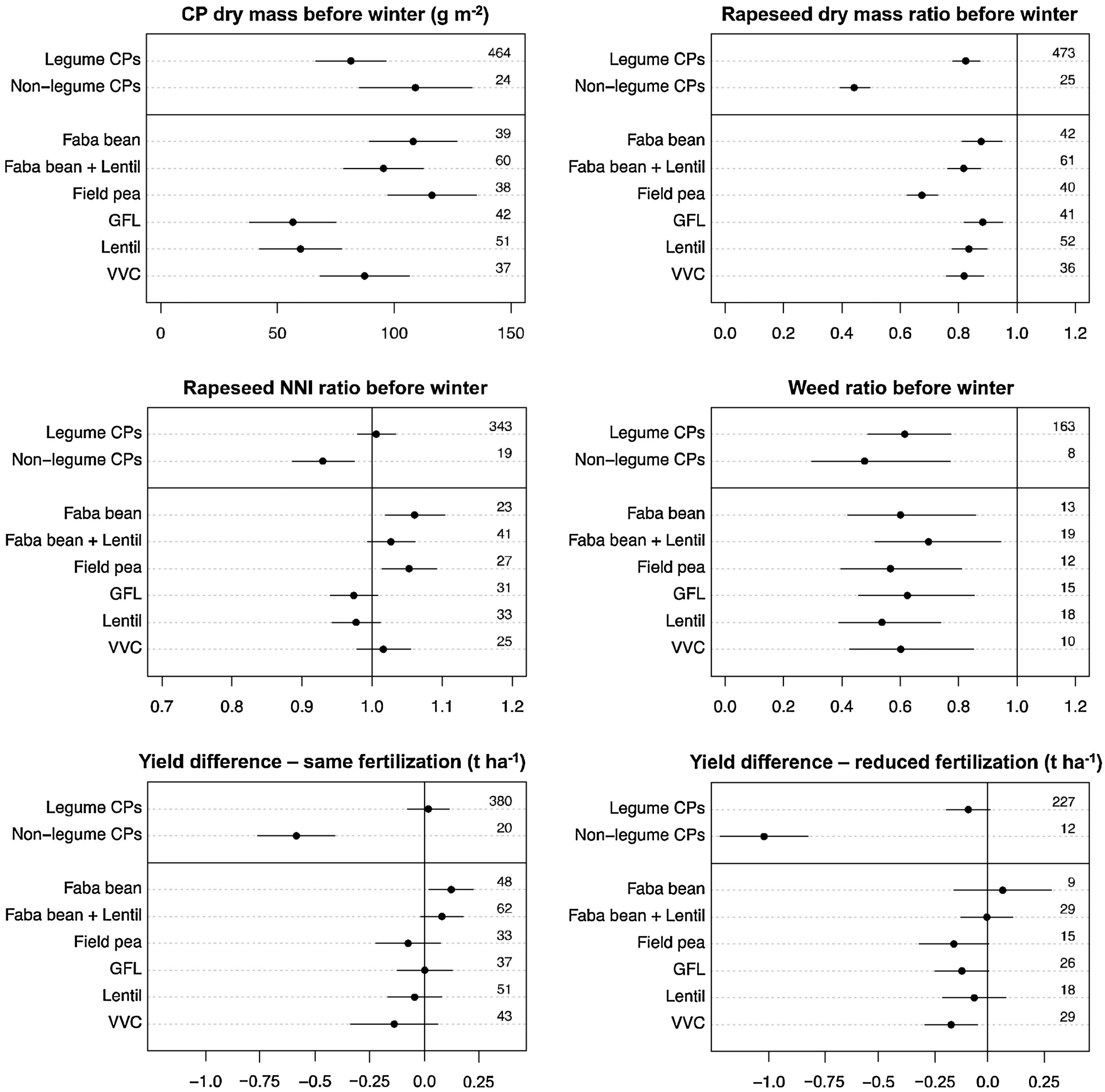

Fig. 2. Mean effects and 95% confidence intervals for the various indicators evaluated before winter or at harvest. These effects were estimated with model M1, except for "Yield difference – same fertilization", for which model M2 was used as it outperformed model M1 (lower BIC for M2 than for M1). The numbers on the right are the numbers of data for each treatment.

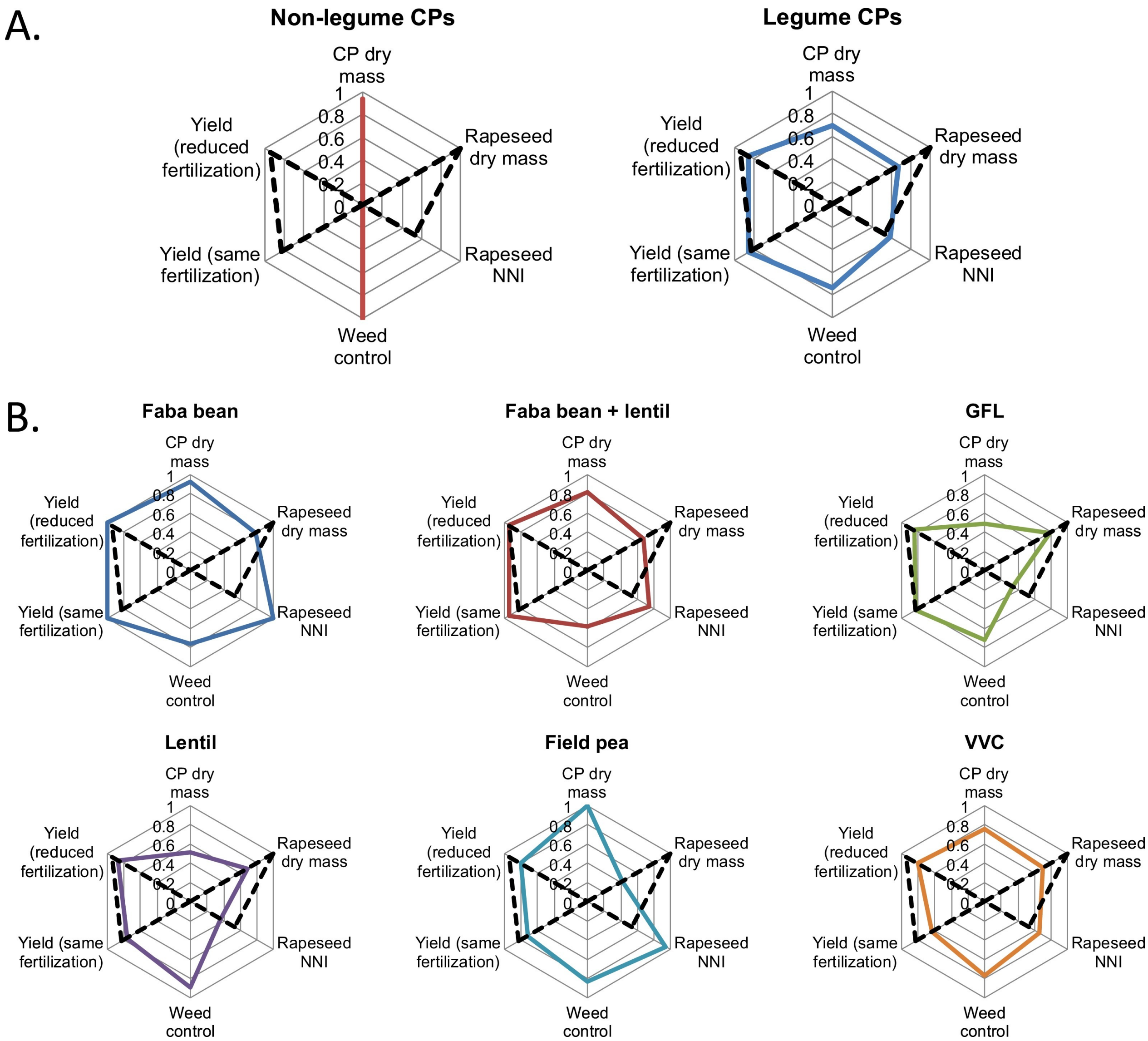

Fig. 3. Radar chart of the performance of the companion plant families (A) and species (B) intercropped with rapeseed (full line), relative to sole rapeseed crop (dashed line). The effects were normalized as described by Ramírez-García et al. (2015). Intercrop performances were best for the values towards the periphery of the chart, indicating a maximal provision of services to the rapeseed crop.

Bayesian model averaging showed that the amount of CP dry mass accumulation before winter was explained principally by CP species and then by the type of rapeseed cultivar, with a higher CP biomass for inbred line cultivars (Table 2). CP dry mass also increased with rainfall, radiation and temperature in the fall, but decreased with increases in potential evapotranspiration. Direct sowing and reduced tillage tended to be associated with a higher CP dry mass than plowing.

3.2. Rapeseed dry mass at winter

Rapeseed dry mass at winter was significantly lower in intercrops than for sole crops, by 18% and 56% for intercropping with legume and non-legume CPs, respectively (Fig. 2). For the six most tested treatments, the difference in rapeseed dry mass relative to the sole crop was greatest for field pea. This was the only species for which a significant difference relative to the other species was identified.
The lower levels of rapeseed dry mass in intercrops were explained primarily by CP dry mass before winter, alone or in a two-way interaction with CP species, which had a negative effect (Table 2). Field pea had the strongest negative impact on rapeseed dry mass, whereas faba bean had the weakest effect.

Secondarily, soil N richness at sowing had a relatively small, negative impact on intercropped rapeseed dry mass.

3.3. Rapeseed nitrogen nutrition index before winter

Non-legume CPs decreased rapeseed NNI by 7%, on average, whereas legume CPs had no impact on rapeseed NNI (Fig. 2). Faba bean and field pea increased rapeseed NNI by 6% and 3% relative to sole crops of rapeseed, whereas the other treatments had no significant effect. CP dry mass at winter was associated with a higher rapeseed NNI in intercrops (Table 2). CP species × dry mass interaction had different effects, depending on the CP species. For faba bean, field pea, and faba bean + lentil, a high dry mass was associated with a higher rapeseed NNI, whereas, for lentil, GFL and VVC, a high dry mass was associated with a lower rapeseed NNI.

3.4. Weed control before winter

Both non-legume and legume CPs significantly decreased weed infestations, by 52% and 38%, respectively. There was no significant difference between the six species and mixtures of legumes tested (Fig. 2).
The between-trial variability was poorly explained by the descriptors we tested (Table 2). Hybrid rapeseed cultivars had a negative effect on weed ratio, resulting in better weed suppression. Higher cumulative temperature and rainfall during the fall decreased the efficacy of weed control by intercrops relative to rapeseed as a sole crop. CP dry mass made very little contribution to weed control in intercrops.

3.5. Rapeseed yield

If identical amounts of fertilizer were applied on sole crops of rapeseed and intercropped rapeseed, intercropping with non-legume CPs resulted in a significantly lower rapeseed yield, by 0.58 t ha^{-1}, whereas intercropping with legume CPs had no effect on rapeseed yield (Fig. 2). The difference in yield between intercropped rapeseed and rapeseed grown as a sole crop was significant only for faba bean, with a yield gain of 0.12 t ha^{-1}. Non-significant minor rapeseed yield losses were observed for field pea, lentil and VVC. The yield gain decreased with increasing soil richness at sowing, and increased with CP biomass accumulation before winter (Table 3).

Table 3. Relative importance (W_X) of the variable for explaining the variability of the effect of rapeseed-CP intercropping on rapeseed yield. W_X values greater than 0.2 are in shown in bold font. The analyses include only the trials for which all the descriptors were available (*n* = the number of data used for the analysis/the total number of data available in the dataset; T = the number of trials used for the analysis/the total number of trials in which the measurement was made).

Variable	Factor levels (for qualitative variables)	At harvest			
		Yield difference (same fertilization) n = 166/274 T = 31/52		Yield difference (reduced fertilization) n = 101/126 T = 24/29	
		W_X	Estimates	W_X	Estimates
(Intercept)	–	**1.00**	3.71E − 02	**1.00**	4.12E − 01
Soil texture	Clay (intercept)	0.02	0.00E + 00	0.11	0.00E + 00
	Loamy		−2.10E − 03		6.08E − 03
	Sandy		−5.24E − 03		–
Soil depth	–	0.10	−5.88E − 03	0.10	1.68E − 03
Soil N richness at sowing	–	**0.23**	−2.99E − 02	**0.90**	−2.13E − 01
Tillage type	Plowing (intercept)	0.01	0.00E + 00	0.03	0.00E + 00
	Direct seeding		−3.70E − 04		−2.96E − 03
	Reduced tillage		3.23E − 04		2.28E − 03
Type of rapeseed cultivar	Hybrid (intercept)	0.08	0.00E + 00	0.15	0.00E + 00
	Inbred line		3.27E − 03		2.12E − 02
CP species	Faba bean (intercept)	0.02	0.00E + 00	0.01	0.00E + 00
	Faba bean + lentil		−6.01E − 04		−1.25E − 03
	GFL		−2.52E − 03		−3.22E − 03
	Lentil		−2.02E − 03		−2.47E − 03
	Field pea		−2.84E − 03		−3.44E − 03
	VVC		−4.19E − 03		−4.20E − 03
CP dry mass at winter	–	**0.71**	6.89E − 04	0.13	5.23E − 05
CP species × CP dry mass interaction	Faba bean × CP dry mass	0.00	2.26E − 06	0.00	2.86E − 07
	Faba bean + lentil × CP dry mass		2.81E − 06		5.92E − 07
	GFL × CP dry mass		−1.00E − 06		−6.88E − 07
	Lentil × CP dry mass		1.76E − 06		8.94E − 08
	Field pea × CP dry mass		−2.94E − 07		−9.73E − 08
	VVC × CP dry mass		−1.99E − 06		−7.46E − 07
Fertilizer reduction	–	0.05	4.52E − 06	0.16	−2.28E − 03

If the amount of fertilizer applied on intercropped rapeseed was decreased by 30 or 40 kg ha^{-1} relative to recommendations, intercropping with non-legume CPs caused a significant yield reduction of 1.00 t ha^{-1}, whereas intercropping with legume CPs caused a non-significant yield reduction of 0.09 t ha^{-1}. VVC, field pea and GFL caused significant yield losses of 0.17, 0.15 and 0.12 t ha^{-1}, respectively. No significant difference was found between the six most tested CP species and mixtures of species. With this lower level of fertilizer application, the yield difference between intercropped rapeseed and rapeseed grown as a sole crop decreased with increasing soil N richness at sowing.

3.6. Interactions between CP species and trial

The interactions between CP species and trial had different effects on CP species and performance indicators. The comparison of models M1 and M2 revealed significant interactions only for the indicator *Δyield* when intercropped rapeseed and sole rapeseed crops received the same amount of N fertilizer (lower BIC for M2 than for M1 for this variable, results not shown). For this variable, the effect of CP species on rapeseed yield was strongly related to trial effect (in Fig. 4, the dots are scattered along the *x*-axis), with significant high correlation coefficients for the relationship between the deviation due to trial conditions and the deviations due to CP species (Fig. 4), especially for field pea and the VVC mixture. Correlation coefficients were also relatively high for the other *Δyield* variable (when intercropped rapeseed received less fertilizer than sole rapeseed) and for the rapeseed dry mass ratio at winter, suggesting that these indicators were more subject to CP species × trial interactions than the other indicators, such as CP dry mass, for which the correlation coefficient was lower (Appendix D, table D2 in the Supplementary material).

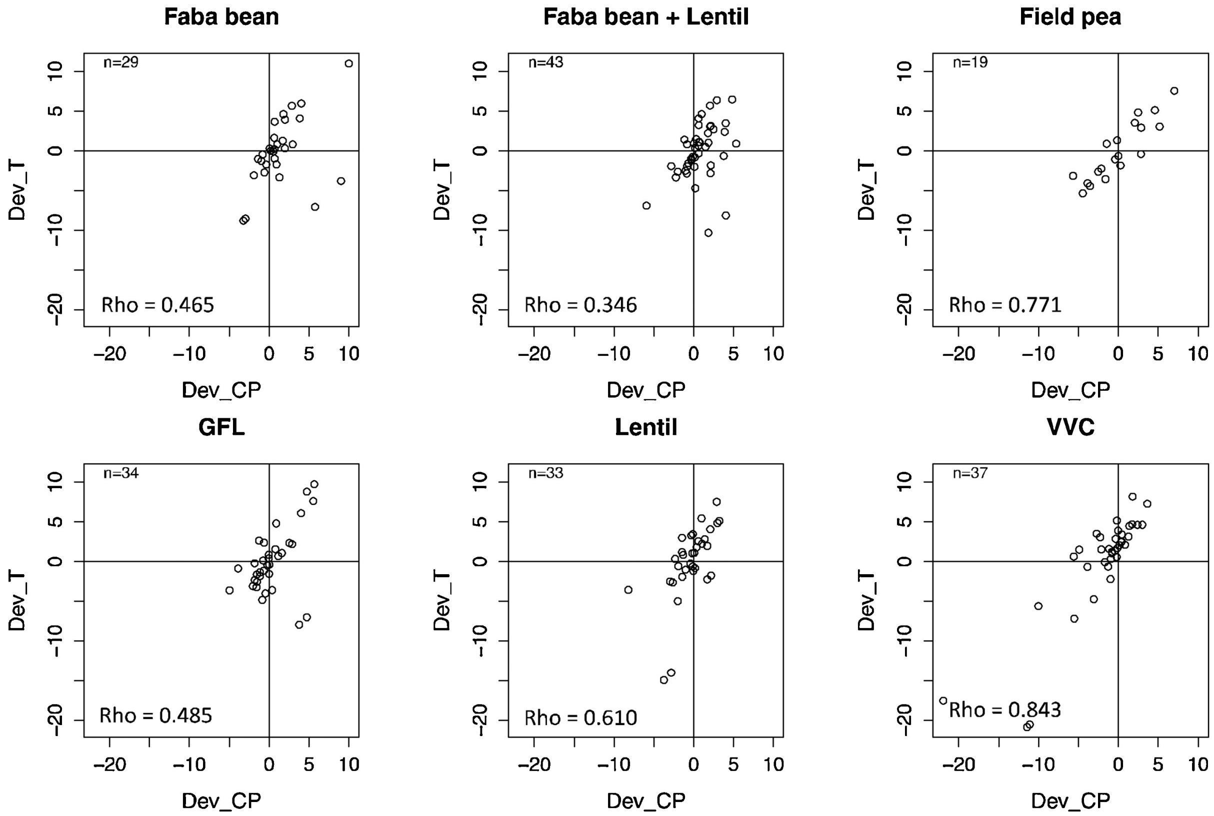

Fig. 4. Representation of the effects of CP species and of the trials on the deviation of the yield difference (same fertilization rate for the intercropped rapeseed and sole rapeseed). Each dot represents one trial. The x-axis is the deviation of the yield difference for one CP species in one trial from the mean of all CP species in the same trial (*Dev_CP*). The y-axis is the deviation of the yield difference of one CP species in one trial from the mean of all trials for that CP species (*Dev_T*). "Rho" values are the Pearson correlations coefficients between *Dev_CP* and *Dev_T*.

For the six performance indicators, field pea, VVC mixture and faba bean had the highest correlation coefficients overall (Appendix D, Table D2 and Figures D1 to D5 in the Supplementary material), indicating that the performance of these species was more subject to interactions depending on trial conditions than that of the GFL and faba bean + lentil mixtures, for which lower correlation coefficients were obtained.

4. Discussion

4.1. Performance of CP families and species in intercrops

In the fall, before their death, the CPs competed with rapeseed for resources, resulting in a lower rapeseed dry mass in intercropping situations. Non-legume species were more competitive than legumes when intercropped with rapeseed, probably because non-legumes are entirely dependent on soil mineral N for their nutrition. Field pea was the most competitive legume species, as it was associated with the lowest rapeseed biomass at winter. In the trials, this species produced the largest amounts of biomass and had a branched architecture and leaf functional traits values favoring light interception, at the expense of rapeseed (Lorin et al., 2015, Tribouillois et al., 2015). Faba bean, which also accumulated large amounts of biomass, was not as competitive as field pea, as indicated by a very low "CP species × CP dry mass" interaction term effect on rapeseed dry mass. This species have an erect habit and little branched architecture that would have intercepted less light than field pea, for a given biomass (Lorin et al., 2015).

The intercropping of rapeseed with a CP also affected the nitrogen nutrition of the rapeseed. NNI analyses revealed that this effect could be positive or negative, depending on CP family and species. As indicated by the lower rapeseed NNI before winter, non-legume CPs competed with rapeseed for N resources, whereas both faba bean and faba bean + lentil mixtures increased rapeseed NNI, thus having a facilitation effect on rapeseed. This process was not investigated further here, but it seems likely that faba bean, with its strong, deep taproot, modifies the rooting system of rapeseed, enabling it to explore a larger volume of soil and to obtain more nitrogen (Jamont et al., 2013). Génard et al. (2016) demonstrated that nitrogen transfer from a legume CP to the intercropped rapeseed can make a relevant contribution to rapeseed nitrogen nutrition. They showed that white lupin and crimson clover, two legume species not tested here, made a positive contribution, of 2 and 3%, respectively, to rapeseed total nitrogen.

We show here that CPs are useful for weed control, with a tendency for non-legume CPs (52% decrease in weed amount) to outperform legume CPs (38% decrease in weed amount). However, no legume species was identified as significantly more effective than any other for weed control. Weed suppression by the CP has been reported in many previous studies; it mostly involves competition for light and for nitrogen in the case of non-legume CPs (Liebman and Dyck, 1993, Verret et al., 2017).

Non-legume CPs strongly hindered rapeseed growth. This effect of competition was observed from the fall onwards, through the rapeseed dry mass and yields at harvest. This was not the case for CPs of the legume family, for which the weaker competition observed in the fall did not generally result in lower rapeseed yields. However, two legume species did have an impact on rapeseed yield: faba bean and VVC, which were associated with a yield gain and a yield loss, respectively, relative to rapeseed grown as a sole crop. Surprisingly, these two species displayed similar levels of competition with rapeseed in the fall. Vetches were not always fully killed by frost or herbicide in the spring in these trials, and this species was therefore sometimes found alive in the canopy at harvest. This may account for the small, but significant yield loss observed with VVC. By contrast, field pea, which had the highest competitive impact on rapeseed growth at winter, had no significant effect on final yield.

The effects of competition before winter and the application of 30–40 kg N ha^{-1} less fertilizer were compensated by the facilitation effects of intercropping. The processes potentially underlying this facilitation, particularly for faba bean, may include: (i) better rapeseed nitrogen nutrition in the fall, as demonstrated here, improving growth conditions in the second part of the crop cycle, (ii) higher levels of soil biological activity and organic matter mineralization (Cheng et al., 2014, Nakamoto and Tsukamoto, 2006), (iii) lower levels of insect damage, due to a modification of visual cues, with tall plants impeding the recognition of rapeseed by insects before winter (Finch and Collier, 2000, Parker et al., 2013), (iv) the spring mineralization of CP residues (up to 80 kg N ha^{-1}), a fraction of which may subsequently be available to the rapeseed (Lorin et al., 2016).

We obtained a global overview of CP performance by plotting on radar charts the effects of the two types of CP family (legume and non-legume) and the six most tested legume species or mixtures of species on the performances of the intercrops relative to sole-crop rapeseed (Fig. 3). Overall, for weed control, rapeseed competition, nitrogen nutrition and grain yield, the analysis of a large dataset for 79 trials covering a large range of soil and climate conditions in the northwestern half of France showed that legumes gave better results than non-legumes for intercropping with rapeseed. Rapeseed intercropped with legume CPs performed at least as well as sole crops of rapeseed, for all six indicators considered. Faba bean and faba bean + lentil were the legume species with the best performances, whereas VVC and GFL had the poorest performance of the six treatments tested.

4.2. Effects of the CP species × trial interaction on intercrop performances

We investigated interactions between CP species and trial with the M2 model. The higher BIC values for model M2 than for model M1 indicated that these interactions were generally not important, except for the yield differences between intercropped rapeseed and sole rapeseed crops receiving the same amounts of N fertilizer. The interactions were strongest for field pea and the VVC mixture, indicating that the effect on yield was not stable and was very sensitive to trial conditions for these CP species.
More generally, even interactions were strongest for field pea, the VVC mixture and faba bean for the six performance indicators considered (especially for rapeseed dry mass ratio and yield differences), most of these interactions did not improve the BIC of model M2 relative to that of model M1. This highlights the general weakness of CP species × trial interactions for these variables in these intercrops, due essentially to (1) the mostly additive effects of CP species and trial conditions, independently of climate, soil conditions and agricultural techniques in each trial, or (2) difficulties detecting significant interactions over our dataset.

4.3. Effect of trial characteristics on intercrop performances

We also analyzed the impact of the pedoclimatic conditions and agricultural practices in each trial on intercropped rapeseed performance. The variables describing agricultural practices had the highest weights, with the choice of CP species being the most important. CP species, and, often, the interaction with CP dry mass before winter, seemed to be the most important factors accounting for the effects of intercropping on rapeseed dry mass, NNI and yield. As expected, CP dry mass before winter affected several performance indicators (Table 2 and Table 3). Surprisingly, CP dry mass before winter had a weaker effect than CP species on weed suppression, despite the widespread use of this variable as an indicator of the weed suppression performance of cover crops (Uchino et al., 2009, Mohammadi, 2010, Lorin et al., 2015, Vrignon-Brenas et al., 2016). This may be due to interactions with the trial conditions at each site, such as weeding operations, potentially modifying competition relationships between rapeseed, the CP and weeds. CP species × CP dry mass accumulation interactions were found for rapeseed dry mass and NNI ratios. Thus, particular species traits probably influence the performance of the ecological functions involved in such processes (Garnier and Navas, 2012, Wood et al., 2015). Other previously identified CP species × trial interactions could not be explored more deeply by Bayesian model averaging, because the dataset was unbalanced. The choice of a hybrid or inbred line rapeseed cultivar affected rapeseed × CP × weed interactions. Inbred line cultivars were associated with higher levels of CP biomass accumulation before winter than hybrid cultivars, probably because inbred lines are less vigorous and less competitive than hybrids (Mr S Cadoux 2017, pers. comm.).
N-rich soils also minimized the benefits of intercropping in terms of yield gain relative to rapeseed as a sole crop. Similar results have been reported for cereal-legume intercrops, which have been shown to be particularly suitable for low-nitrogen input systems (Bedoussac et al., 2015). Rapeseed dry mass ratio was, unexpectedly, lower in N-rich soils. Biological nitrogen fixation rates are lower in such conditions (Voisin et al., 2002), and we hypothesize that the legume species may have competed with the rapeseed for soil mineral nitrogen. In N-rich soils, rapeseed sole crops perform well, accumulating large amounts of biomass before winter, through efficient soil nitrate capture and weed suppression (Dejoux et al., 2003, Valantin-Morison and Meynard, 2008), and CP intercropping may be unlikely to improve the growing conditions for rapeseed further in such conditions. Thus, in cropping systems with regular organic manure spreading, the intercropping of rapeseed with CP would probably not increase grain yield or weed control, although other services, not investigated here, might be enhanced in these conditions (e.g. insect pest regulation (Cadoux et al., 2015)). Soil texture and depth had relatively low weights in the averaged models.
Climate descriptors made a major contribution to explaining CP biomass accumulation, which was favored by abundant rainfall, radiation and high temperatures in the fall. These growing conditions may have also favored the development of weeds, slightly limiting their suppression by the CP.

4.4. Limitations

The collection of data from a large network entailed several difficulties. Some trials did not include all the measurements in their design, whereas others had missing information for trial descriptors. This restricted the statistical analyses to different subsets of trials for each indicator. The experimental design of the trials was adapted to match local practices, in terms of tillage, weeding operations, and choice of species for rapeseed intercropping. We tried to limit confounding of effects by focusing our analysis on a subset of treatments assessed at most sites, with the results confirmed by direct comparisons. However, the large number of trials in this dataset and the use of statistical methods derived from meta-analysis ensure that our conclusions about the impact of CPs on the rapeseed crop can be generalized.

5. Conclusion

Intercropping rapeseed with non-legume and legume CPs reduced weed amounts by 52% and 38% respectively, with no difference between CP species. Non-legumes decreased the nitrogen nutrition index of rapeseed in fall by 7%, whereas pea and faba bean increased this index by 6% and 3%, respectively. Non-legume CPs decreased rapeseed yield at harvest by 0.58 t ha^{-1}, whereas faba bean and faba bean + lentil increased yield by more than 0.12 t ha^{-1}, when fertilized at the recommended rate. CP species differed in their competitiveness and their facilitation effects on rapeseed crops, but faba bean and a mixture of faba bean + lentil had the best overall performances. CP dry mass accumulated before winter was the variable most frequently influencing intercrop performance, and its effect on rapeseed dry mass and NNI depended on CP species. Other than for rapeseed yield performance, CP species performances did not interact with trial conditions, indicating that our results may be valid over a wide range of agricultural and environmental conditions.

This study showed that environmental and agricultural conditions interfered with intercrop performance, with the type of rapeseed cultivar, followed by fall temperature and rainfall on the one hand, and the soil mineral nitrogen at sowing on the second hand, being the most important variables to explain the variability of CP dry mass and yield differences, respectively. We therefore recommend intercropping rapeseed in soils with low nitrogen content, with an early sowing date in the late summer, to maximize legume CP dry mass accumulation due to a high cumulative temperature and radiation levels, at sites at which precipitation does not limit CP establishment and growth. A reduction of nitrogen application by 30–40 kg ha^{-1} is possible with no significant decrease in rapeseed yield. Non-legume species may be useful for weed control and CP dry mass accumulation, but should be used only at low sowing densities, in mixtures with legume CPs, to limit deleterious effects on yield.

Finally, economic, social and environmental analyses should be carried out to evaluate the extent to which the intercropping of legume CPs with winter rapeseed can improve the sustainability of cropping systems (Craheix et al., 2016).

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