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Intercropping for sustainability: Research developments and their application

Species choice and N fertilisation influence the biodiversity effect and its components in intercrops

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Summary

Loreau & Hector, (2001) proposed a framework to estimate the net biodiversity effect (over- or under-yielding) on the productivity of plant communities and to further decompose this effect into dominance and complementarity effects. Here we applied this method to analyse the performance of eight cereal-legume intercropping experiments grown in diverse environmental conditions in France, with three combinations of species mixtures: i) durum wheat/faba bean ii) soft wheat/pea and iii) durum wheat/pea. For each species mixture, we tested whether N fertilisation influenced dominance or complementarity effects using a Bayesian approach. Our results showed that the Biodiversity Effect (BE) was positive in the three intercrops under unfertilised conditions, mainly thanks to complementarity effect. The relative importance of BE and both of its components depends on the species intercropped. Finally, we showed that the impact of N fertilisation on BE of intercrops strongly depends on the competitive ability of the species intercropped.

Key Words: Complementarity effect, dominance effect, biodiversity effect, N fertilisation, intercropping

Introduction

Plant diversity promotes primary production through complementarity and dominance effects, both involved in the net biodiversity effect (BE; Loreau & Hector, 2001). Dominance effect measures the part of the BE due to the excessive competition of one given species, whereas the complementarity effect measures the part of the BE due to niche complementarity and/or facilitation. In intercrops, these effects were already demonstrated, highlighting that productivity is higher in cereal-legume intercrops, mainly due to complementarity effect (e.g. Pelzer *et al.*, 2012 on durum wheat/pea intercrops). However, the influence of the choice of the species intercropped or of the agronomic practices on these effects is not well understood.

In this study, we aimed to quantifying the BE and its components (i.e. complementarity and dominance effects) in three cereal-grain legume intercrops in unfertilised conditions (durum wheat/pea, soft wheat/pea and durum wheat/faba bean), and to test whether differences exist depending on the species intercropped. For this purpose, we used a database containing eight field experiments located at two sites (Angers and Auzeville) in France. We then studied how nitrogen (N) fertilisation influenced these effects.

Materials and Methods

Field experiments

In order to explore the net BE in intercrops, we gathered eight factorial experiments in two locations in France (Angers, Auzeville), covering a wide range of climate conditions and agricultural managements. The data were formatted (Wickham, 2014), homogenised and pooled in the same database.

Environmental conditions

Climate conditions of each experiment were characterised using variables retrieved from the NASA POWER API, i.e. the sum of precipitation (mm) and the mean temperature (°C) during the crop cycle (from sowing to harvest date). The experiments involved winter crops, with precipitation ranging from 286.4–712.5 mm and mean temperature ranging from 7.3–11.3°C during the crop cycle.

Agricultural management

All the experiments included cereal-grain legume intercrops of two annual crop species and their corresponding sole crops for which grain yield was measured (t ha^{-1}). Cereals were represented by two species: durum wheat (*Triticum turgidum* L.) and soft wheat (*Triticum aestivum* L.); legumes were represented by two species: faba bean (*Vicia faba* L.) and pea (*Pisum sativum* L.). Finally, we had three intercrop combinations: durum wheat/faba bean, soft wheat/pea and durum wheat/pea. Intercropped species were sown and harvested at the same time. Within an experiment, the different treatments differed in i) the number of genotypes cropped by species (from one to five genotypes), ii) the relative sowing densities of each species, sole crops being characterised by densities of 1 or 0.5 relatively to the recommended density, and intercrops being characterised by densities ranging from 0.33–1 and iii) the nitrogen (N) fertilisation, with unfertilised and N-fertilised treatments (from 30–180 kg N ha^{-1}).

89% of the intercrops were grown in a substitutive design (i.e. when the relative sowing densities of the two species intercropped sum to 1) and 11% of the intercrops were grown in an additive design (i.e. when the relative sowing densities of the two species intercropped sum higher than 1). Considering all these variations, the database contained 70 intercrop experimental units (site × year × mix of genotypes × relative densities × N-treatment), among which eight were in additive design and 62 in substitutive design, and 69 sole crop experimental units. The dataset was unbalanced because the experiments gathered were made for different purposes (i.e. different number of observations between groups) regarding many factors (N-treatment, mixture design, etc.). This heterogeneity constrained the statistical analyses we made.

Components of intercrop performance

For each experimental unit, we computed BE as the difference between the observed and expected yield in intercrops (Eq. 1):

$$BE = YO_C + YO_L - (YE_C + YE_L) \text{ (Eq. 1)}$$

where YO_C (resp. YO_L) is the observed yield of the cereal (resp. legume) grown in intercrop, and YE_C (resp. YO_L) is the expected yield of the cereal (resp. legume) grown in intercrop.

Expected yield was assessed from the yield of the species in sole crop weighted by the scaled relative density in intercrop (Eq. 2):

$$YE_C = M_C \frac{RD_C}{RD_C + RD_L} \text{ and } YE_L = M_L \frac{RD_L}{RD_C + RD_L} \text{ (Eq. 2)}$$

where Mc (resp. M_L) is the yield of the cereal (resp. legume) grown in sole crop and RD_C (resp. RD_L) is the relative density (i.e. the density of each species in the intercrop relatively to the sowing density in the reference sole crop) of the cereal (resp. legume) in intercrop.

In the case of substitutive designs, the expected yield is simply for cereal (resp. for legume):

$$YE_C = M_C RD_C \text{ (resp. } YE_L = M_L RD_L\text{) (Eq. 3)}$$

BE can be partitioned into dominance effect (DE, Eq. 4) and complementarity effect (CE, Eq. 5) (Loreau & Hector, 2001; Li *et al.*, 2020, where:

$$DE = \frac{1}{2}\left(\left(\frac{Y_C}{M_C} - \frac{RD_C}{RD_C+RD_L}\right) - \left(\frac{Y_L}{M_L} - \frac{RD_L}{RD_C+RD_L}\right)\right) \times (M_C - M_L) \text{ (Eq. 4)}$$

$$CE = \frac{M_C+M_L}{2} \times \left(\frac{Y_C}{M_C} - \frac{RD_C}{RD_C+RD_L} + \frac{Y_L}{M_L} - \frac{RD_L}{RD_C+RD_L}\right) = \bar{M} \times (LER - 1) \text{ (Eq. 5)}$$

A positive DE means that the species with the greater yield in sole crop benefits the most from intercropping. On the opposite, a negative DE means that the species with the lowest yield in sole crop has a higher relative yield gain. In the definition of CE, we introduced the classical Land Equivalent Ratio

$$LER = \frac{Y_C}{M_C} + \frac{Y_L}{M_L}$$

(Willey & Rao, 1980). Hence, CE is equal to the LER minus 1, multiplied by the average yields $(\bar{M})$ in sole crops. Thus, the CE measures the part of the BE due to niche complementarity and or facilitation, without being able to disentangle these processes (Loreau & Hector, 2001) .

Data processing and analysis

All analyses were done under the Bayesian approach. Bayesian inference is based on the reallocation of credible values for a parameter (posterior distribution), given the prior knowledge (prior distribution) and the adequacy of the data to the model (likelihood). Under the Bayesian approach, it is possible to get information about the probability of a hypothesis being true given the data (*P* (hypothesis/data)). Bayesian estimation for the difference of group means (Kruschke, 2013) is an alternative to the classical Student's *t* test to compare the means of two groups. This method allows to get a posterior distribution for the values of mean differences between the two groups, and to derive a 95% highest density interval (HDI), described as the 95% most credible values of the parameter (Kruschke, 2018).

For each species mixtures, we carried out Bayesian estimation for the difference of group means between the values of the components of the BE in fertilised and unfertilised treatments. We defined the null hypothesis (H0) as the hypothesis of equality of the mean BE components between fertilised and unfertilised intercrops. We applied the following decision rule according to the position of the null value (0) relatively to the position of the 95% HDI: reject H0 if 0 is completely outside the 95% HDI vs do not reject H0 if 0 falls inside the 95% HDI.

All indicator computations and statistical analyses were carried out with R 4.0.0 software (R Core Team, 2020). The data was ordered, reshaped and homogenised using the collection of R packages *tidyverse* (Wickham *et al.*, 2019). Bayesian statistical analyses were performed using the R package *BEST* (Kruschke & Meredith, 2020).

Results

Species choice influenced BE and its components in unfertilised conditions

The BE was positive in 100% of the cases (Table 1). The average BE of intercropping was equal to 0.67 ± 0.11 t ha^{-1} (mean ± standard error). This was mainly due to the complementarity effect which represented in average 77% of the BE. The remaining 23% of the BE was due to the dominance effect. The relative contribution of complementarity and dominance effects in BE differed between the species intercropped (Table 1) but complementarity effect was predominant in all unfertilised intercrops.

Table 1. *Biodiversity effect, complementarity effect and dominance effect in all intercropping conditions, and especially in intercrops of durum wheat (*Triticum turgidum *L.)/pea (*Pisum sativum *L.), soft wheat (*Triticum aestivum *L.)/pea and durum wheat/faba bean (*Vicia faba *L.), in unfertilised conditions (mean ± standard error). The relative contribution (%) of complementarity and dominance effects to the biodiversity effect was precised. For each experimental unit, we averaged yield values across all replicates of the treatment (two to four replicates by treatment)*

	Biodiversity effect (t ha^{-1})	Complementarity effect (t ha^{-1})	Dominance effect (t ha^{-1})	No. experimental units
All intercrops	0.67 ± 0.11	0.83 ± 0.11 (77%)	-0.17 ± 0.05 (23%)	28
Durum wheat/pea	0.52 ± 0.08	0.75 ± 0.07 (77%)	-0.22 ± 0.06 (23%)	18
Soft wheat/pea	1.21 ± 0.51	1.03 ± 0.61 (69%)	0.18 ± 0.17 (31%)	4
Durum wheat/faba bean	0.76 ± 0.21	0.99 ± 0.29 (83%)	-0.23 ± 0.09 (17%)	6

N fertilisation influenced BE and its components depending on species intercropped

Biodiversity effect and its components were not influenced by N fertilisation in the same way depending on crop mixture (Fig. 1).

Considering durum wheat/pea mixtures, 0 was outside the 95% HDI (0.19; 0.74) for the values of mean BE differences between the unfertilised and N-fertilised treatments. Thus, BE was higher in unfertilised treatments, resulting from both an effect of dominance and complementarity. For the dominance effect, 0 was outside the 95% HDI (-0.5; -0.21) for the values of mean differences between the unfertilised and N-fertilised treatments, meaning that N fertilisation increased the dominance effect. For the complementarity effect, 0 was outside the 95% HDI (0.57;1.07), meaning that N fertilisation decreased the complementarity effect. Hence, in unfertilised durum wheat/pea mixtures, the complementarity effect compared to N-fertilised crops was balanced by the higher complementarity effect, leading to a greater BE.

Conversely, considering soft wheat/pea mixtures, 0 was included in the 95% HDI for the difference of means of BE between unfertilised and N-fertilised treatments meaning that N fertilisation had no significant influence on BE. Moreover, N fertilisation had no significant influence neither on the complementarity effect nor on the dominance effect, the null value being inside the 95% HDI.

In the same way, considering durum wheat/faba bean mixtures, N fertilisation had no significant impact on the BE or complementarity effect. Null value was also a credible value for the difference of means dominance effect between N-fertilised and unfertilised treatments. A trend was distinguishable in the posterior distribution of the difference of means, 93% of the posterior values of μ_N being greater than μ_{N0}, meaning that N fertilisation tended to increase the dominance effect.

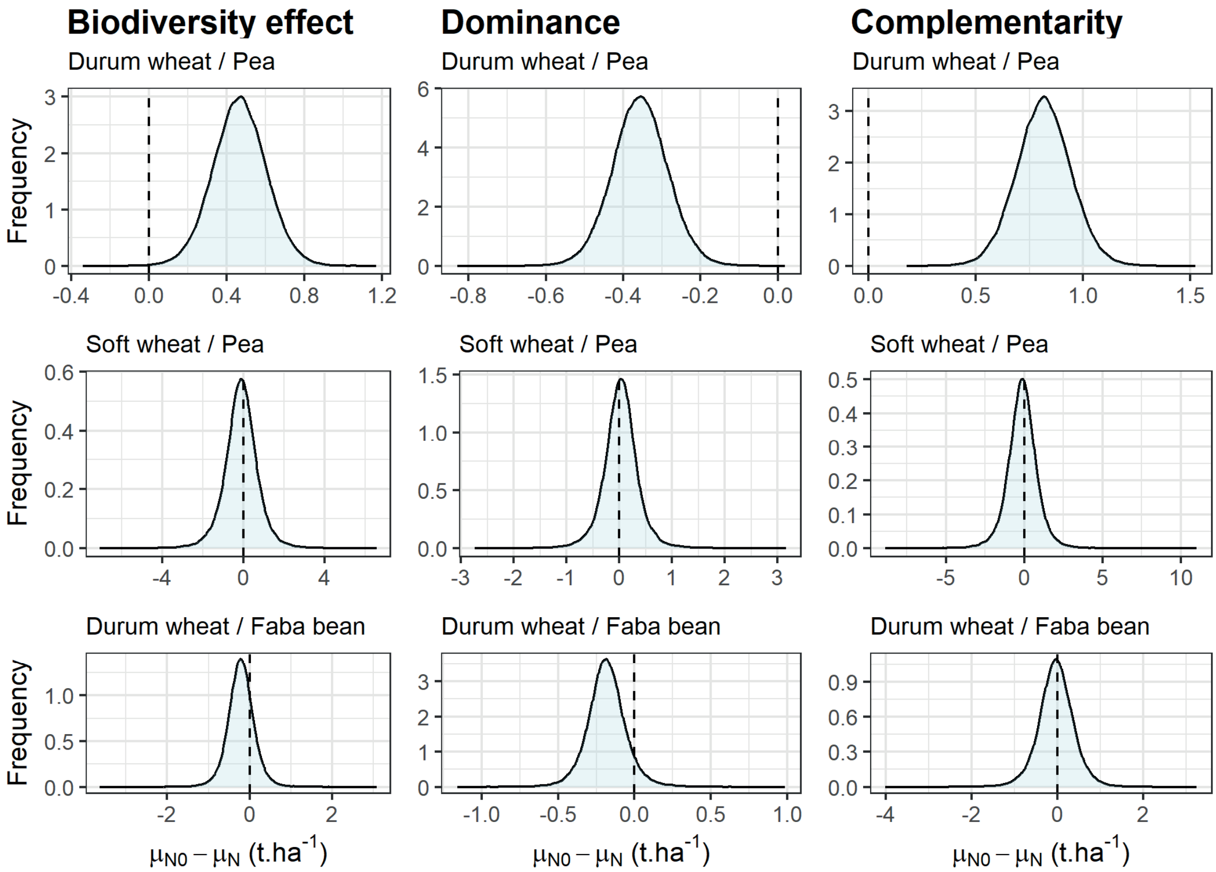

Fig. 1. Posterior distribution of the difference of mean biodiversity effect (left panels), dominance effect (center panels) and complementarity effect (right panels) between unfertilised (µN0) and fertilised (µN) intercrops of durum wheat (*Triticum turgidum* L.)/pea (*Pisum sativum* L.), soft wheat (*Triticum aestivum* L.)/pea and durum wheat/faba bean (*Vicia faba* L.). The dotted lines represent the null value of the posterior difference of means.

Discussion and Conclusion

In this study, we showed that the overall biodiversity effect of unfertilized cereal-legume intercrops was positive (pooling together all experimental units), mainly due to complementarity effect (77%), meaning that intercrops were more efficient considering yield than their corresponding sole crops, which is in accordance with previous findings (e.g. Li et al., 2020; Pelzer et al., 2012; Yu et al., 2016). However, this effect strongly depends on species intercropped and on N fertilisation management.

The results of Bayesian estimations of group means showed that N fertilisation increased dominance effect and decreased complementarity effect in durum wheat/pea mixtures, which is a behaviour typically highlighted in existing literature for cereal-legume intercrops (e.g. Corre-Hellou *et al*., 2007; Naudin *et al*., 2010). In unfertilised conditions, the superior competitive ability of the cereal forces the legume to rely more on its atmospheric N-fixing ability (Ghaley *et al*., 2005). The complementarity for the use of N increased as the symbiotic N_2 fixation of the legume is enhanced leaving more mineral N for the cereal (Corre-Hellou *et al*., 2007). In fertilised conditions, dominance is boosted because durum wheat takes a competitive advantage over the legume. Our results showed, however, that if we change one of the species in the intercrop and the fertilisation conditions, we can move away from this textbook case.

Replacing durum wheat by soft wheat in wheat/pea mixtures, N fertilisation did not influence the components of the BE of the intercrop anymore. This could be due to a lower competitive ability of soft wheat compared to durum wheat. However, such a conclusion has to be tempered as N fertilisation levels in soft wheat/pea mixtures were lower than those of durum wheat/pea mixtures

(40 kg N ha^{-1} *vs* 60–140 kg N ha^{-1}), and also globally lower to conventional N fertilisation levels in wheat crops (170 kg N ha^{-1}; Mercier-Poirier, 2014)). Thus, the amount of N brought by fertilisation might be insufficient to upset complementarity and dominance occurring in unfertilised conditions.

Finally, when replacing pea by faba bean in the mixtures, we showed a tendency to an increase of dominance effect without decreasing complementarity effect in N-fertilised intercrops (in contrast to durum wheat/pea mixtures). The absence of impact of N fertilisation on the complementarity effect could be due to a stronger competitive ability of the faba bean compared to the pea in unfertilised conditions and/or to a lack of N availability for the cereal, even with the presence of the symbiotic fixation of the faba bean.

Therefore, our study highlighted that BE was positive in the three unfertilised cereal-legume intercrops considered, mainly thanks to complementarity effect. However, the relative importance of BE and both of its components depends on the species intercropped. Using a Bayesian alternative to the *t test*, we showed that the impact of N fertilisation on BE of intercrops strongly depends on the competitive ability of the species intercropped.

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