A meta-analysis of relative crop yields in cereal/legume mixtures suggests options for management

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Abstract

Intercrops of cereals and legumes are grown worldwide, both in smallholder agriculture in developing countries and in organic farming systems in developed countries. The competitive balance between species is a key factor determining productivity in mixtures. Management factors, e.g. sowing time, sowing density and rate of N fertilizer, affect the relative competitiveness and performance of intercropped species. There is a need for an overarching analysis to elucidate general principles governing the relative performance of legumes and cereals in mixtures. We therefore conducted a meta-analysis of published studies to explore how the relative yield of legumes and cereals in mixtures responds to relative sowing time, relative density and nitrogen fertilizer.

An index for relative sowing time, RST, was developed to quantify the relative difference in sowing time between the intercropped species. RST is defined as the amount of time that a species is sown earlier or later than its companion species, relative to the length of its own growing period. RST is smaller than zero if a species is sown earlier than its companion species and greater than zero if it is sown later. Relative performance of a species was characterized by its relative yield (or partial land equivalent ratio, PLER) in the intercrop compared to the yield in the sole crop.

In 409 out of 552 cases, the cereal had a greater relative yield than the legume. Sowing a species earlier than its companion increased its relative yield, and vice versa. An increase in density of a species increased its relative yield and decreased the relative yield of the companion species. The relative yield of cereals increased and that of legumes decreased with the amount of N fertilizer. The negative effect of N on the relative yield of legumes was mitigated if the legume was sown before the cereal.

The study shows how the performance of cereals and legumes in an intercrop is affected by sowing densities, relative sowing times, and nitrogen fertilizer. Growers can

exploit these relationships to manage competition between cereals and legumes in mixtures and enhance species complementarity, total productivity and economic profit.

Keywords: cereal/legume mixtures; competition; PLER; agronomic managements; meta-analysis

Introduction

Intercropping (i.e. the mixed cultivation of crop species) is a traditional agronomic practice that is widely used by smallholder farmers in Asia, Africa and Latin America (Vandermeer, 1992; Lithourgidis et al., 2011). Intercropping is also drawing increasing interest as a strategy for increasing productivity and sustainability of mechanized western crop production systems, e.g. through incorporation of legumes in cereal production systems (e.g. Dhima et al., 2007; Lithourgidis et al., 2007; Bedoussac and Justes, 2010; Pelzer et al., 2012). There are many types of intercrops, including mixtures of two cereals, mixtures of two legumes, as well as mixtures of a cereal and a legume or non-legume broadleaf species (Li et al., 2013; Yu et al., 2015). Mixtures of a cereal and a legume are by far the most common type of intercrop (Rao et al., 1987).

Cereal/legume intercrops have been shown advantageous over sole crops in many respects. Most frequently reported, cereal/legume intercrops use the land more efficiently than sole crops (e.g. Ofori and Stern, 1987a). If resource conversion efficiency of plants is equal between intercrops and sole crops, the increased land use efficiency by intercropping implies that plants in intercrops acquire more growth resources e.g. light, water or nutrients than in sole crops. Indeed, it has been reported that compared to sole crops, higher land use efficiency in cereal/legume intercrops was associated with greater light capture (Marshall and Willey, 1983; Watiki et al., 1993, Zhang et al., 2008; Gou et al. under review) or complementary nutrients acquisition (e.g. Hauggaard-Nielsen et al., 2009). The complementarity in nitrogen acquisition between cereals and legumes has received considerable attention in scientific literature, though, also enhanced phosphorous use efficiency has been reported (Li et al., 2007). Cereals and legumes are complementary in their acquisition of nitrogen because legumes can fix nitrogen from air through symbionts in addition to using soil N, while cereals acquire nitrogen only from the soil (Jensen, 1996; Hauggaard-Nielsen and Jensen, 2001; Chu

et al., 2004; Corre-Hellou et al., 2006). Nitrogen fixation from air is critical if there is little N available from the soil. Acquisition of soil N by the cereals may reduce the availability to the legumes and trigger the legumes to fix more N from the air (Lambers et al., 2008). Nitrogen fixation from the air is also seen as a step in making agriculture more sustainable because it circumvents the need for industrial nitrogen fixation based on fossil energy (Courty et al., 2015; Duc et al., 2015).

The different N acquisition strategies of the cereals and the legumes offer opportunity for complementarity, which could result in a high relative yield for each species (little reduction from competition), and a high relative yield total of the mixture. The relative yield of each species is considered a useful index for the extent to which each species has realized its potential growth, given the conditions and the competition from the other species, while the relative yield total is a useful index for the total niche realized in mixture (Vandermeer, 1992). The extent to which this relative yield total exceeds one is an indicator for complementarity.

The land equivalent ratio (LER) is widely used to characterize the land use efficiency in intercropping. LER is calculated as the sum of the relative yields of intercropped species in an intercrop, as compared to their sole crops (Mead and Willey, 1980). The value of LER may be interpreted as the land area required to produce the same yields in sole crops as obtained from a unit area of intercrop. An LER greater than one implies that intercropping makes a more efficient use of the land than sole cropping. The partial land equivalent ratio (PLER) is the relative yield of an intercropped species compared to its yield in a sole crop (Ofori and Stern, 1987a). PLER can be interpreted as a measure for the contribution of each species to the efficiency of land use by the system as a whole.

In older literature (e.g. Mead and Riley, 1981), a distinction is made between relative yield (total) and (partial) land equivalent ratio. The premise is that relative yield total should

be measured in experimental settings with replacement designs in which the relative density total is one (e.g. De Wit's replacement series; De Wit, 1960), whereas land equivalent ratios are measured in experimental settings with a much wider set of designs, including additive designs with a relative density total of two, and augmentative designs that have a relative density total between one and two. Relative yield (RY) is calculated in the same way as partial land equivalent ratio, while the relative yield total (RYT) is calculated in the same way as the land equivalent ratio. Therefore the distinction between RY and PLER, and between RYT and LER is nowadays seldom made, and we consider it unnecessary and obsolete.

According to the stress gradient hypothesis (SGH) (Brooker et al., 2008), plant-plant interactions depend on the environmental context with negative interactions (competition) dominating under favorable conditions, and positive interactions (facilitation) prevailing under unfavorable conditions. The SGH predicts that at high doses of nitrogen fertilizer, interspecific competition would be dominant in intercrops, whereas at low nutrient inputs, complementary use of N would be dominant. In cereal/legume intercropping, under low nitrogen input conditions, the complementary acquisition of nitrogen from different sources would be dominant (Jensen, 1996) while at high nitrogen input, interspecific competition would lead to a dominance of cereals in the mixture due to the stronger competitiveness of cereals as compared to the companion legumes (Ofori and Stern, 1987a).

The competitiveness of individual species in mixtures might be affected by differences in sowing date. The first-sown species will get a competitive advantage while the second-sown species is likely to have a competitive disadvantage. However, if the sowing delay of the second species is very large, such that its growth period is to a large extent after the growth period of the first species (as in relay intercropping), the suppression on the second species might be minor or transient (Zhang and Li, 2003). The strength of interspecific competition could also be determined by relative plant densities of the mixed species (Ofori

and Stern, 1987a; Vandermeer, 1992). Increased density of one intercropped species is likely to increase its competitiveness in the intercrop, and suppress the performance of the associated species (De Wit, 1960; Braakhekke, 1980; Gardiner and Craker, 1981; Fawusi et al., 1982). Although the effects of these agronomic practices (rate of N fertilizer, sowing time and sowing density of intercropped components) on competitiveness of the species in mixtures have been reported, there is a large variation in these effects across studies. There is a lack of quantitative assessment across studies of the extent to which these agronomic practices can influence the performance of individual species in mixtures. Besides, it is not clear how species performance in mixtures is affected by the interplay between these factors.

In this study we conduct a meta-analysis to investigate how performance of cereals and legumes is affected by sowing time, sowing density, rate of N fertilizer and the interactions between these factors in cereal/legume intercrops. PLER is taken as a measure of performance of intercropped species. As PLER is the ratio of yield of one species in an intercrop over yield in the respective sole crop, low yields in sole crops might result in high PLERs. We therefore also explore whether high PLERs are associated with low yields of the sole crops.

Materials and methods

Paper and data selection

Data on yields in cereal/legume intercrops used here are a subset of records from a database built by Yu et al. (2015). From the original database, all data records of cereal/legume intercrops (552) were extracted, representing data from 144 experiments out of 77 publications. Each data record provides the PLER of both the cereal and the legume. An experiment was defined as a unique combination of site and year. Within experiments, data

records were defined by treatment, including crop species combination, sowing dates, rate of fertilizer application and crop densities. Data were entered into the database using identifiers for the publications, and the experiments, and listing all relevant inputs and outputs (Appendix: Table A1). Among the 552 data records of cereal/legume intercrops, 485 were grain cereal/grain legume intercrops, 14 were combinations of grain cereal/fodder legume, and 53 were fodder cereal/fodder legume intercrops. Not all data records reported all variables mentioned in Table A1. There were some missing values for density of crops (5 out of 552 records) and rate of N fertilizer (92 out of 552 records; Table A1). Data records with missing values of a variable were excluded only from those analyses that required that variable.

Response and explanatory variables

In all analyses, partial land equivalent ratio (PLER), was taken as response variable. PLER is defined as:

$$\text{PLER} = \frac{Y}{M} \quad (1)$$

where Y and M represent yield of a species in intercrop and sole crop respectively.

In this meta-analysis, we used four explanatory variables, i.e. (i) relative sowing time (RST, continuous, see Eq. 2 below), (ii) relative density (RD, continuous, see Eq. 3 below), (iii) rate of N fertilizer application in the intercrop (N, continuous), and (iv) Crop type (0 for cereal or 1 for legume). Rates of N fertilizer application and crop type were extracted from the publications while relative sowing time and relative density were calculated.

In many studies, rates of N fertilizer are different between intercrops and sole crops. A categorical variable “**N strategy**” with four levels was defined according to the comparative amounts of N applied in intercrops and sole crops. In strategy 1, all treatments receive the same amount of N applied in intercrops and sole crops. In strategy 1, all treatments receive the same amount of N fertilizer ($n = 243$). In strategy 2, the rate of N fertilizer in the intercrop is

intermediate between that in the two respective sole crops ($n = 43$), while in strategy 3, the N rate in the intercrop is equal to the lowest N rate in sole crops ($n = 67$), and in strategy 4, the N rate in intercrop is equal to the highest N rate used in sole crops ($n = 107$). For N strategies 2-4, sole cropped cereals usually received more N fertilizer than sole cropped legumes (215 cases out of 217).

Relative sowing time of a species is calculated as the ratio of the difference of sowing time of that species and its companion species divided by its own growing period:

$$RST_a = \frac{S_a - S_b}{H_a - S_a} \quad (2)$$

where RST_a represents relative sowing time of species a with respect to species b . In the analysis, a can represent either the cereal or the legume, while b represents the companion species. S_a and S_b represent sowing times of species a and b in Julian day number, respectively. H_a represents harvesting time of species a in Julian day number (Fig. 1). The magnitude of RST_a is the ratio of the difference in sowing time between species a and the species it is intercropped with to the growing period of species a . For the earlier sown species $RST < 0$, while for the later sown species $RST > 0$. RST measures the time, relative to the total growing period, that a species is growing before (after), and therefore without (with) competition from, the companion species. This index is expected to be a useful predictor of the relative yield in the intercrop.

Fig. 1 Illustration of calculation of relative sowing time. The upper bar represents the growing period of the first-sown species (species *a*) and the lower bar represents the growing period of the second-sown species (species *b*). The arrows represent sowing and harvesting time of each species in days after sowing of the first sown species. Relative sowing time is calculated as: $RST_a = (S_a - S_b) / (H_a - S_a)$. $RST_a < 0$ means species *a* is sown earlier than species *b*, and vice versa. In the analysis, *a* can represent either the cereal or the legume, while *b* represents the companion species.

Relative density of a species is calculated as the ratio between the density of that species in intercrop and in its sole crop:

$$RD_a = \frac{d_{ic,a}}{d_{sc,a}} \quad (3)$$

where $d_{ic,a}$, and $d_{sc,a}$ are densities of species *a* in the intercrop and sole crop, respectively.

Density of a species in intercrop is defined as number of plants of a species per land area of the intercrop. Relative density of an analyzed species is denoted by RD , relative density of the companion species is denoted by $RD_{associated}$.

Statistical analysis

Relationships between PLER and explanatory variables, i.e. relative sowing time, relative density and rate of N fertilizer, were estimated for cereals and legumes using mixed effects

modelling to account for correlation between data belonging to the same experiment and/or publication (Pinheiro and Bates, 2000; Zuur et al., 2009). Six mixed effects models were formulated (Table 1, models 2-7). All these six models were fitted to the dataset of 1104 (i.e. $2 * 552$) PLER records. All analyses were conducted in R (R Core Team, 2013). Mixed effects models were fitted using R function *lme* from R package *nlme* (Pinheiro et al., 2015). Mixed effects models were also used to estimate the relationships between PLERs of cereals and the associated legumes (Table 1, model 1) and between PLER and yield of the corresponding sole crop (Table 1, model 8). The assumption of equal variance for mixed effects models was checked by analyses of quantile plots and plots of residuals against fitted values (Zuur et al., 2009). No violations of assumptions were observed. Figures were made using R packages *plotrix* and *graphics* (Lemon, 2006; R Core Team, 2013).

The PLERs of the cereal and the legume from the same data record might be correlated and have a negative correlation due to the interspecific competition. Therefore, a negative correlation structure of data between the cereal and the legume from the same data record was added in the mixed effects models to account for the correlation using R function *corCompSymm* for the argument of *correlation* in *lme* (Pinheiro and Bates, 2000).

A mixed effects model (Table 1, model 9) was fitted to the data to detect whether the effect of N fertilizer on PLER differed between N strategies. The relationship between PLER of the cereals and PLER of the legumes might be non-linear, and PLER of the cereal should be one when PLER of the legume is zero (i.e. sole crop of cereal) and *vice versa*. Therefore, a non-linear model which could reveal this feature of the relationship between PLER of the cereals and PLER of the legumes (Table 1, model 10) was fitted to the data using R function *gnls* (Pinheiro et al., 2015). The non-linear model is

$$PLER_{cereal,ijk} = \frac{q(1 - PLER_{legume,jk})}{1 + (q - 1)(1 - PLER_{legume,ijk})} + \varepsilon_{ijk} \quad (4)$$

A comparison of goodness of fit between the linear mixed effects model (model 1) and the non-linear model (model 10) was conducted with Akaike information criterion (Zuur et al., 2009). In this meta-analysis, we did not use the inverse variance of LER as a weight since there were too few publications reporting measures of variance of yields.

Table 1 List of models fitted to data. The indices i , j and k represent publication, experiment and treatment respectively. In all mixed effects models (models 1-9), a_i is a random publication effect. b_{ij} is a random experiment effect nested within the i th publication. a_i and b_{ij} are assumed normally distributed with constant variances. ε_{ijk} is a residual error associated with the k th observation in the j th experiment in the i th publication. assumed normally distributed with constant variance. The variances of a_i , b_{ij} and ε_{ijk} are all assumed independent. The relationship between PLER of the cereal and PLER of the legume was also analyzed using a simple non-linear model (model 10). In the non-linear model, ε_{ijk} is a residual error assumed normally distributed with constant variance.

Model	Explanatory variables	Equation
1	PLER _{legume}	$PLER_{cereal,ijk} = \beta_0 + \beta_1 * PLER_{legume,ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
2	RST, Crop type	$PLER_{ijk} = \beta_0 + \beta_1 * RST_{ijk} + \beta_2 * Crop\ type_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
3	RD, RDassociated, Crop type	$PLER_{ijk} = \beta_0 + \beta_1 * RD_{ijk} + \beta_2 * RDassociated_{ijk} + \beta_3 * Crop\ type_{ijk} + \beta_4 * RD_{ijk} * RDassociated_{ijk} + \beta_5 * RD_{ijk} * Crop\ type_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
4	N, Crop type	$PLER_{ijk} = \beta_0 + \beta_1 * N_{ijk} + \beta_2 * Crop\ type_{ijk} + \beta_3 * N_{ijk} * Crop\ type_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
5	RD, RST, Crop type	$PLER_{ijk} = \beta_0 + \beta_1 * RD_{ijk} + \beta_2 * RST_{ijk} + \beta_3 * Crop\ type_{ijk} + \beta_4 * RD_{ijk} * Crop\ type_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
6	RST, N, Crop type	$PLER_{ijk} = \beta_0 + \beta_1 * N_{ijk} + \beta_2 * RST_{ijk} + \beta_3 * Crop\ type_{ijk} + \beta_4 * RST_{ijk} * N_{ijk} + \beta_5 * N_{ijk} * Crop\ type_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
7	RD, N, Crop type	$PLER_{ijk} = \beta_0 + \beta_1 * N_{ijk} + \beta_2 * RD_{ijk} + \beta_3 * Crop\ type_{ijk}^1 + \beta_4 * RD_{ijk} * Crop\ type_{ijk}^1 + \beta_5 * N_{ijk} * Crop\ type_{ijk}^1 + a_i + b_{ij} + \varepsilon_{ijk}$
8	Yield_sc	$PLER_{ijk} = \beta_0 + \beta_1 * Yield_sc_{ijk} + \beta_2 * Crop\ type_{ijk} + \beta_3 * Crop\ type_{ijk} * Yield_sc_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
9	N, N strategy*, Crop type	$PLER_{ijk} = \beta_0 + \beta_1 * N_{ijk} + \beta_2 * N\ strategy_{ijk}^2 + \beta_3 * N\ strategy_{ijk}^3 + \beta_4 * N\ strategy_{ijk}^4 + \beta_5 * Crop\ type_{ijk} + \beta_6 * N_{ijk} * N\ strategy_{ijk}^2 + \beta_7 * N_{ijk} * N\ strategy_{ijk}^3 + \beta_8 * N_{ijk} * N\ strategy_{ijk}^4 + \beta_9 * N_{ijk} * Crop\ type_{ijk} + \beta_{10} * N\ strategy_{ijk}^2 * Crop\ type_{ijk} + \beta_{11} * N\ strategy_{ijk}^3 * Crop\ type_{ijk} + \beta_{12} * N\ strategy_{ijk}^4 * Crop\ type_{ijk} + \beta_{13} * N_{ijk} * N\ strategy_{ijk}^2 * Crop\ type_{ijk} + \beta_{14} * N_{ijk} * N\ strategy_{ijk}^3 * Crop\ type_{ijk} + \beta_{15} * N_{ijk} * N\ strategy_{ijk}^4 * Crop\ type_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$

$$10 \quad \text{PLER}_{\text{legume}} \quad \text{PLER}_{\text{cereal}, ij} = q * (1 - \text{PLER}_{\text{legume}, ij}) / (1 + (q-1) * (1 - \text{PLER}_{\text{legume}, ij})) + \varepsilon_{ij}$$

* N strategy is a categorical variable with four levels. N strategy 1: intercrop and both sole crops receive the same amount of N fertilizer, N strategy 2: the rate of N fertilizer in the intercrop is intermediate between that in the two respective sole crops, N strategy 3: the N rate in the intercrop is equal to the lowest N rate in sole crops, N strategy 4: the N rate in intercrop is equal to the highest N rate in sole crops. The superscript of N strategy in model 10 distinguishes the estimates of parameters for each level of N strategy.

Results

Characteristics of cereal-legume intercrops

On average, intercrops were more efficient in land use than the corresponding sole crops, with 434 out of 552 calculated LER values larger than 1 (Fig. 2a). The median LER was 1.16 (Fig. 2b), the mean 1.17 and the standard deviation 0.24, indicating substantial variation of LER over treatments, experiments and publications. More than 90 percent of the intercrops in the database received less than 100 kg/ha N fertilizer (Fig. 3a) and about 80 percent of the intercrops were sown simultaneously, i.e. RST equal to zero (436 out of 552 cases, Fig. 3b, c). Each data record provides yield and relative yield of both cereal and legume. Among the 116 cases with an RST not equal to zero, the cereals were sown earlier than the legumes in 71 cases, and in 45 cases the cereals were sown later than the legumes (Fig. 3b, c).

Fig. 2 Cumulative frequency (a) and frequency distribution (b) of land equivalent ratios (LER) for cereal/legume mixtures. The vertical lines in panel **b**, indicate values of the first quartile, median and the third quartile of LER.

Competitiveness of individual species in cereal/legume intercrops

PLER of the cereals was greater than that of the legumes in ~75% of the cases (409 out of 552 cases) indicating that the competitiveness of cereals is normally higher than that of legumes in a mixture. A high PLER of the cereal corresponded with a low PLER of the legume and *vice versa* (Fig. 4). We chose a linear model to represent the relationship between PLER of the cereal and the legume since the goodness of fit of the linear model (model 1) was better than that of the non-linear model (model 10) according to Akaike's information criterion. One unit increase of PLER of the legume resulted in 0.605 unit decrease of PLER of the cereal (model 1, $\beta_1=0.605$, $SE=0.035$, $P<0.001$, Fig. 4).

Fig. 3 Frequency distribution of the rate of N fertilizer on intercropping (a) and relative sowing time of the cereal (b) and the legume (c) in intercropping. (Note the broken y-axis.)

Fig. 4 Scatter plot of partial land equivalent ratio (PLER) of the cereal against PLER of the legume in analyzed intercrops. The broken line represents a theoretical negative relationship with a slope of 1 between the two PLERs, the solid line represents the observed relationship between $PLER_{cereal}$ and $PLER_{legume}$ as fitted by mixed effects model 1: $PLER_{cereal,ijk} = \beta_0 + \beta_1 * PLER_{legume,ijk} + a_i + b_{ij} + \epsilon_{ijk}$.

Effect of relative sowing time on PLER

Earlier sowing as compared to the companion species increased PLER for both the cereals and the legumes (Fig. 5). The effect of relative sowing time on PLER was not significantly different between the cereals and the legumes. Therefore, a model with a common slope for cereals and legumes (model 2) was fitted to the data. Increase of one unit in relative sowing time resulted in an decrease of 0.7 unit of PLER (model 2, $\beta_1 = -0.7$, $SE = 0.15$, $P < 0.001$) for both cereals and legumes.

Fig. 5 Effect of relative sowing time (RST) on partial land equivalent ratio (PLER) of cereals (black circles) and legumes (red squares). The solid and broken lines respectively represent relationships between PLERs of cereals and legumes and their relative sowing time fitted by mixed effects model 2: $PLER_{ijk} = \beta_0 + \beta_1 * RST_{ijk} + \beta_2 * Crop\ type_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$.

Fig. 6 Linear functions relating partial land equivalent ratio (PLER) of cereals (a) and legumes (b) to relative densities of both cereals and legumes fitted by mixed effects model 3: $PLER_{ijk} = \beta_0 + \beta_1 * RD_{ijk} + \beta_2 * RD_{associated\ ijk} + \beta_3 * Crop\ type_{ijk} + \beta_4 * RD_{ijk} * RD_{associated\ ijk} + \beta_5 * RD_{ijk} * Crop\ type_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$. The colors of dots represent relative density of the companion species, i.e. either legume (a) or cereal (b), from low (blue) to high (red).

Effect of relative density on PLER

A significant positive effect of relative density on PLER was observed for both cereals (model 3, $\beta_1 = 0.35$, $SE = 0.06$, $P < 0.001$) and legumes (model 3, $\beta_1 + \beta_5 = 0.22$, $SE = 0.06$, $P < 0.001$). The effect of relative density on PLER was stronger in cereals than in legumes (model 3, $\beta_5 = -0.13$, $SE = 0.04$, $P = 0.002$). On the other hand, there was a negative relationship between PLER of a species and the relative density of the associated species in both cereals and legumes (model 3, $\beta_2 = -0.36$, $SE = 0.06$, $P < 0.001$, Fig. 6), i.e. increasing relative density of one species decreased PLER of the associated species. There was no difference in this negative effect between cereals and legumes. This result supports the hypothesis that increasing density of one species in a mixture increases its relative yield while decreasing the relative yield of the associated species.

There was a significant positive interaction between the relative density of an analyzed species and the relative density of the associated species on PLER of the analyzed species (model 3, $\beta_4 = 0.16$, $SE = 0.07$, $P = 0.03$). This positive interaction indicates that the negative effect of relative density of the associated species on PLER of the analyzed species is mitigated by increased relative density of the analyzed species.

Effect of N fertilizer application on PLER

We found a significant negative effect of N fertilizer application rate on PLER of legumes (model 4, $\beta_1 + \beta_3 = -0.0013$, $SE = 0.0002$, $P < 0.001$, Fig. 7). PLER of legumes decreased 0.13 unit when the rate of N fertilizer application was increased with 100 kg/ha. PLER of cereals increased slightly with N fertilizer (model 4, $\beta_1 = 0.00058$, $SE = 0.00023$, $P = 0.01$, Fig. 7). This finding is in line with the hypothesis that increasing the rate of N fertilizer leads to an increase in the relative performance of the cereals but a decrease for the legumes.

The effect of N was not expected to be different between different N strategies. However, the results showed some pattern in cereals (Fig. A1a). There was a slight positive effect of N on PLER of the cereals for strategies 1 (equal rate of N in intercrop and sole crops) and 2 (N in intercrop intermediate between sole crops). However, for strategy 3 (N in intercrop equal to lowest level in sole crops), there was a strong positive effect of N fertilizer on PLER while there was a strong negative effect of N fertilizer on PLER with strategy 4 (N in intercrop equal to the highest level in sole crops) (Fig. A1a). This pattern is mainly due to confounding between the rate of N and the relative density of cereals in strategies 3 and 4. For strategy 3, low N plots of the cereals were also those with low relative density, the apparent N effect was therefore driven by the relative density. The reverse held for strategy 4 where a low rate of N was associated with a higher relative density of the cereals compared to the treatments receiving higher rates of N. The effect of N fertilizer on PLER of the legumes was consistently negative (Fig. A1b).

Fig. 7 Effect of N fertilizer application on partial land equivalent ratios (PLER) of cereals (circles) and legumes (squares). The solid and broken lines respectively represent relationships between PLER and rate of N fertilizer application for cereals and legumes fitted

by mixed effects model 4: $PLER_{ijk} = \beta_0 + \beta_1 * N_{ijk} + \beta_2 * \text{Crop type}_{ijk} + \beta_3 * N_{ijk} * \text{Crop type}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$.

Fig. 8 Linear functions relating the partial land equivalent ratio (PLER) to the relative sowing time and relative density for cereals (a) and legumes (b) fitted by a mixed effects model 5: $PLER_{ijk} = \beta_0 + \beta_1 * RD_{ijk} + \beta_2 * RST_{ijk} + \beta_3 * \text{Crop type}_{ijk} + \beta_4 * RD_{ijk} * \text{Crop type}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$. The colors of dots represent relative densities from low (blue) to high (red).

Interactions between factors

No interaction between RST and RD was found for either cereals or legumes. A model with RST and RD but without interaction was therefore fitted to the dataset (model 5). For cereals (Fig. 8a) and legumes (Fig. 8b), both the effects of RD ($\beta_1 = 0.39$, $SE = 0.03$, $P < 0.001$ and $\beta_1 + \beta_4 = 0.29$, $SE = 0.03$, $P < 0.001$ respectively) and of RST ($\beta_2 = 0.58$, $SE = 0.07$, $P < 0.001$) were positive and significant. These results indicate that relative sowing time and relative density of the species in mixtures may be adjusted to achieve desired PLERs of the cereals and the legumes according to production aims.

A negative interaction effect of N rate and relative sowing time on PLERs of cereals and legumes was expected. In other words, we expected that the positive effect of N fertilizer on competitiveness of cereals would be enhanced by sowing cereals earlier than legumes

while the negative effect of N on competitiveness of legumes would be alleviated by sowing legumes earlier than cereals. Indeed, a negative interaction between the relative sowing time and the rate of N fertilizer was found in both the cereals and the legumes (model 6, $\beta_4 = -0.0051$, $SE = 0.0021$, $P = 0.017$, Fig. 9). For the cereals, there was a slight positive effect of N fertilizer on PLER when the two intercropped species were sown simultaneously, i.e. $RST = 0$ (model 6, $\beta_1 = 0.00064$, $SE = 0.00022$, $P = 0.003$). The negative interaction between RST and the rate of N fertilizer for the cereals indicates that sowing legumes later than the cereals enhances the positive effect of N fertilizer on PLER of cereals. For legume species, there was a negative effect of N fertilizer on PLER when the legumes were sown simultaneously with the cereals (model 6, $\beta_1 + \beta_5 = -0.0014$, $SE = 0.00022$, $P < 0.001$). However, this negative effect was mitigated by sowing the cereals later than the legumes.

Fig. 9 Relationships of partial land equivalent ratio (PLER) to relative sowing time and rate of N fertilizer application for cereals (a) and legumes (b). Relationships were analyzed by fitting mixed effects model 6: $PLER_{ijk} = \beta_0 + \beta_1 * N_{ijk} + \beta_2 * RST_{ijk} + \beta_3 * Crop\ type_{ijk} + \beta_4 * RST_{ijk} * N_{ijk} + \beta_5 * N_{ijk} * Crop\ type_{ijk} + a_i + b_{ij} + \epsilon_{ijk}$. The colors of dots represent N fertilizer rates from low (blue) to high (red).

Fig. 10 Relationships of partial land equivalent ratio (PLER) with relative density and rate of N fertilizer for cereals (a) and legumes (b). Relationships were analyzed by fitting mixed effects model 7: $PLER_{ijk} = \beta_0 + \beta_1 * N_{ijk} + \beta_2 * RD_{ijk} + \beta_3 * Crop\ type_{ijk} + \beta_4 * RD_{ijk} * Crop\ type_{ijk} + \beta_5 * N_{ijk} * Crop\ type_{ijk} + a_i + b_{ij} + \epsilon_{ijk}$. The colors of dots represent N fertilizer rates from low (blue) to high (red).

We expected that increasing N fertilizer in intercrops would enhance the positive effect of relative density on relative performance of the cereals but decrease the density effect for the legumes. However, the results showed no interaction between relative density and rate of N on PLER for either the cereals or the legumes (model 7, Fig. 10).

Relationship between PLER and yield of corresponding sole crops

A negative relationship between PLERs of both the cereals and the legumes and yields in sole crops was hypothesized, as low yields of sole crops would result in high PLERs. For the cereal species, indeed, a slight negative effect of sole crop yield on its PLER was observed (model 8, $\beta_1 = -0.007$, $SE = 0.0024$, $P = 0.04$, Fig. 11a) however this did not seem to be related to a high PLER at low sole crop yields, but rather to a low PLER with some extremely high sole crop yields of C4 fodder cereals e.g. maize or millet, harvested as whole plants. For the legume species there was no effect of sole crop yield on PLER (model 8, $\beta_1 + \beta_3 = 0.0023$,

SE = 0.0029, $P = 0.44$, Fig. 11b). Our results indicate therefore that in the sampled intercropping literature, PLER was not biased by low yield of sole crops.

Fig. 11 Relationships between partial land equivalent ratio (PLER) of cereals (a) or legumes (b) and yield of their respective sole crops. The lines represent relationships between PLER and sole crop yields fitted by mixed effects model 8: $PLER_{ijk} = \beta_0 + \beta_1 * Yield_sc_{ijk} + \beta_2 * Crop\ type_{ijk} + \beta_3 * Crop\ type_{ijk} * Yield_sc_{ijk} + a_i + b_{ij} + \epsilon_{ijk}$.

Discussion and conclusion

This is the first meta-analysis to quantitatively assess the effects of agronomic management levers (sowing date, density, N fertilizer) on the relative performance of the cereals and legumes in mixtures. We showed that sowing time is a key factor determining species competitiveness. Sowing one species earlier increases its competitiveness and decreases the competitiveness of the later sown species. Besides, we confirmed the hypothesis that increasing relative density of a species increases its performance while decreasing the performance of the associated species in a mixture. Furthermore, we showed that application of N in cereal/legume intercrops increases the competitiveness of the cereals but decreases that of the legumes. A negative interaction between relative sowing time and rate of N

fertilizer was found for both the cereal and the legume. For the cereals, the negative interaction means that sowing the cereals earlier enhances the positive effect of N fertilizer, while for the legumes the negative interaction means that sowing the legumes earlier mitigates the negative effect of N fertilizer. Finally, we showed that partial land equivalent ratio values were not biased by low yields of sole crops.

Competitive balance in species mixtures

In species mixtures, competition between species is always present as the plants require the same growth resources, e.g. water, nutrient and light. While nutrients and water may be supplied at a level that they are no longer limiting, competition for them being negligible, the same is not true for light, because the interception of light by one species in a closed stand goes inevitably at the expense of light interception by another species. The strength of competition depends on the similarity of the patterns of resource acquisition in time and space between the species in the mixture. The species of similar spatial and/or temporal niche tend to compete intensively, which in turn, would result in reduced biomass and seed production of the relatively weaker species. In natural systems this could lead to extinction of the weaker species (Vandermeer, 1992), while in agricultural systems this could mean failure of one of the two crops. The competitive balance, i.e. equal/similar competitiveness of the mixed species plays an important role in maintaining high productivity of the community (Yachi and Loreau, 2007) and LER values greater than one in intercrops. Therefore, understanding how the competitiveness of the mixed species changes with the environment is important for achieving a high productivity in a mixture.

In this study, we showed that in general, the cereals achieve higher relative yields than the legumes in cereal/legume intercrops. This balance depends on the sowing times of the species relative to one another (relative sowing time, RST). We showed that separating the

growing period of the cereals and the legumes results in a stronger competitiveness of the early sown species and a weaker competitiveness of the late sown one as compared to the corresponding species in an intercrop in which two species are sown simultaneously. Therefore, to maintain the competitive balance in cereal/legume intercrops, sowing the legumes earlier than the cereals would be one option, though other agro-ecological demands of the species (e.g. a difference in optimal growth temperature in relation to the spring-summer sequence) should obviously also be considered.

Many studies have shown that application of N fertilizer in cereal/legume intercrops would increase the competitiveness of the cereals, very likely leading to a competitive imbalance and a failure of legumes in mixtures (Ofori and Stern, 1986; Ofori and Stern, 1987b; Cowell et al., 1989; Tobita et al., 1994; Pelzer et al., 2014). This meta-analysis confirmed the negative effect of N fertilizer on competitiveness of the legumes. The negative effect of N fertilizer on the legumes might be one of the reasons that researchers state that intercropping is mainly important in low-input agriculture (e.g. (Brooker et al., 2015). However, we show there are options to combine higher N rates with maintained production gains of intercropping because of the negative interaction between relative sowing time and N fertilizer. This interaction indicates that the negative effect of N fertilizer on the legumes can be mitigated by sowing the legumes before the cereals. This finding may be used to further integrate legumes in modern high-input agricultural systems.

Implications for the design of productive intercrops

This study shows how an increase in competitiveness of one species results in a decrease in competitiveness of the companion species. To increase productivity of intercrops, it is important to achieve a greater increase in performance of one species associated with a smaller decrease in performance of the companion species resulting overall in

complementarity within the system. The results of this study suggest possibilities for achieving higher intercropping productivity by manipulating the agronomic practices including sowing time, sowing density and rate of N fertilizer in cereal/legume intercrops.

In this study, we showed an identical effect of relative sowing time on PLER for cereals and legumes. The positive effect of sowing one species earlier on its relative yield is canceled out by the negative effect of delayed sowing of the companion species, which results in an overall null effect on productivity of the system as a whole. However, this is only true when the span of growing periods of intercropped species are identical. For instance, in a cereal/legume intercrop, the growth period of both the cereal and the legume is 150 days. Sowing the legume 50 days earlier than the cereal results in a relative sowing time of -0.33 ($50/150$) for the legume and 0.33 for the cereal. According to the estimated relationship between RST and PLER (model 2, Fig. 5), PLER of the legume increases 0.23 while PLER of the cereal decreases 0.23 with RST, which would suggest no effect on the total productivity (LER). However, if a species with a short growing period is grown together with a species with a longer growing period, sowing the former before the latter would result in an increase in the total productivity of the intercrop due to the greater negative RST for the species with the short growing period as compared to the positive RST for the species with the longer growing period.

It has been shown that application of N in cereal/legume intercrops decreases LER of the intercrop when the cereals and the legumes are sown simultaneously (Yu et al., 2015), because the legumes suffer more from the competition with cereals. The finding of a negative interaction between relative sowing time and N rate indicates that combining an early sown short growing period legume with a later sown longer growing period cereal is an option for high-input cropping systems.

Our results show that the relative yield of a species is increased by increasing its density, but at the expense of the relative yield of the companion species. On average, the positive effect of increasing the relative density of the cereal on its relative yield was stronger than the negative effect on the companion legume. The findings altogether imply that increasing density of the cereal species in a cereal/legume intercrop would not only increase the productivity of the cereal but also increase the productivity of the intercrop as a whole.

Conclusion

In this study, we quantitatively assessed how the performance of each species in cereal/legume intercrops is affected by agronomic practices including sowing time, sowing density and rate of N fertilizer as well as the interplay between these factors. These three factors play important roles in determining the relative performance of individual species in cereal/legume intercrops and overall system performance. These findings can be used to design cereal/legume intercrops by fitting the competitive balance with production aims that farmers have related to intercrop productivity. Such aims are related to prices of inputs and outputs and the uses farmers may have for the two products. A next step would be to translate our findings to decision support tools rather than to set rules simply to optimize total yield.

Acknowledgement

We thank staff from the crop systems analysis and plant production systems groups of Wageningen University for suggestion on how to improve this study. The financial support by China Scholarship Council (CSC) and the National Science Foundation of China (grant numbers: 31210103906, 31461143025) are gratefully acknowledged.

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