Yield gain, complementarity and competitive dominance in intercropping in China: A meta-analysis of drivers of yield gain using additive partitioning

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ABSTRACT

Intercropping is known to increase the efficiency of land use, but no meta-analysis has so far been made on the yield gain of intercropping compared to sole cropping in terms of absolute yield per unit area. Yield gain could potentially be related to a relaxation of competition, due to complementarity or facilitation, and/or to the competitive dominance of the higher yielding species. The contributions of competitive relaxation and dominance were here estimated using the concepts of complementarity effect (CE) and selection effect (SE), respectively. We compiled a dataset on intercropping of grain-producing crops from China, a hotspot of strip intercropping in the world. We quantified the yield gain and its components and analysed the contribution to yield gain of species traits (C3, C4, legume, non-legume), complementarity in time and nutrient input. Total yield in intercrops exceeded the expected yield, estimated on the basis of sole crop yields, by 2.14 ± 0.16 Mg ha^{-1} (mean $\pm$ standard error). Ninety percent of this yield gain was due to a positive CE while the remaining 10 % was due to SE. The net yield gain increased with temporal niche differentiation (TND) which is the proportion of the total growing period of the crop mixture during which species grow alone. The mechanism underlying yield gain shifted from competitive dominance of the higher yielding species when there was more overlap in growth period between the two species, to competitive relaxation when there was less overlap, while competitive relaxation remained the major component of the yield gain. The yield gain was substantially greater in intercrops with maize than in intercrops without maize, but there was no difference in yield gain between systems with and without legumes. The yield gain increased with nitrogen (N) input in maize/C3-cereal intercrops but not in cereal/legume intercrops, illustrating the ability of legumes to compensate for low N input, and highlighting the need for N input for high productivity in intercropping systems without legumes. Yield gain did not respond to phosphorus (P) input. We conclude that competitive relaxation is the main contributing factor to yield gain in the investigated Chinese intercropping systems, which were mostly relay strip intercropping systems. The underlying drivers of yield gain were related to presence of maize and species complementarity in time, but we did not find strong evidence for the selection effect.

1. Introduction

Biodiversity is a major determinant of productivity, functioning and stability in natural ecosystems (Tilman et al., 2014). Likewise, on-farm biodiversity can contribute to more sustainable agro-ecosystems (Loreau et al., 2012; Bommarco et al., 2013; Geertsema et al., 2016). Intercropping is the planned combination of multiple crop species in one field (Willey, 1990). It aims to increase yields, improve resource capture, and lower production risks (Vandermeer, 1992; Lithourgidis et al., 2011). Intercropping results in natural suppression of pests and diseases (Zhu et al., 2000; Zhang et al., 2019) and it increases soil nitrogen and carbon due to increased biomass input into the soil and better nutrient retention (Cong et al., 2015). Intercropping has been practiced in China for over 2000 years, and there are contemporary

hotspots of intercropping in the southwest and northwest of China, e.g. in the provinces Sichuan, Yunnan and Gansu (Zhang and Li, 2003; Hong et al., 2017).

The land equivalent ratio (LER) is a commonly used index to assess yields in intercropping compared to sole crops (Mead and Willey, 1980). It is numerically the same as the relative yield total (RYT; De Wit, 1960; Weigelt and Jolliffe, 2003). The LER represents the relative land area needed under sole crops to obtain the same yields as are obtained on a unit area of intercrop (Mead and Willey, 1980). Yu et al. (2015) found an average LER of 1.22 ± 0.02 in a database of 100 intercropping studies while Martin-Guay et al. (2018), using an independent selection of 126 papers from the literature, found an average LER of 1.30 ± 0.01. The LER does not directly relate to absolute yield levels because it is defined as the sum of relative yields of component crops in the intercrop as compared to the sole crops. LER is an indicator for the comparative land use efficiency of intercrops and sole crops as it represents the area of sole crops that is required to produce the yield that are obtained from a unit area of intercropping. LER is not a suitable indicator for productivity.

Here we present an analysis focusing on the yield advantage in intercropping in absolute terms (grain yield per unit area). Loreau and Hector (2001) proposed additive partitioning as a statistical method to analyse productivity benefits in plant species mixtures. This method defines the net effect (NE) as the difference in yield or biomass between the mixture and the (weighted) average of the sole crops, and partitions the NE into two components: a complementarity effect (CE) and a selection effect (SE). The CE is the overall gain in relative yield in a mixture (RYT-1) multiplied by the average yield or biomass of the sole crops (Loreau and Hector, 2001). The SE measures the association between sole crop yield of species and their change in relative yield in the mixture (Loreau and Hector, 2001). It is a measure for how much of the yield gain is due to overyielding of component species with high versus low sole crop yield. A positive CE can arise if species are complementary or facilitative with respect to resource acquisition in the mixture such that the total resource capture in the mixture is greater than expected from the sole crops (Loreau and Hector, 2001). Complementarity results in competitive relaxation and increased production according to what Vandermeer (1989) called the "competitive production principle". The value of SE characterizes to which extent the dominance of the more productive species in terms of biomass or space occupancy is responsible for overyielding in the mixture. Additive partitioning can be used to assess whether intercropping advantage is achieved in a situation where, on average, the species do relatively better in the mixture than in sole crop (high CE) or, alternatively, this advantage is achieved by competitive dominance of the species with the highest sole crop yield (high SE), or a combination of high CE and SE. Malézieux et al. (2009) pointed out that the additive partitioning method could be used to analyse the yield increases that might be obtained by cultivating N species as a polyculture instead of cultivating them on N separate fields. However, only few empirical studies have been made to date on how the complementarity and selection effects contribute to overyielding in intercrops (Zhang et al., 2014; Giles et al., 2016; Li et al., 2018), and no overarching analysis of data from multiple studies has so far been made.

LERs of intercrops can be increased by combining species with different functional traits, e.g. a C3 with a C4 species (Yu et al., 2015). Moreover, cereal/legume intercropping is popular in low-input agriculture because of functional complementarity for N uptake (Bedoussac and Justes, 2010; Pelzer et al., 2012). C3 and C4 species differ in photosynthesis-light response, water use efficiency and N use efficiency (Li, 1993; Vogan and Sage, 2011), growing period and temperature response. These trait differences between C3 and C4 species may synergize to maximize canopy functioning (Anten and Hirose, 1999; Chimonyo et al., 2015). Because of their differences in adaptation to climate factors, C3 and C4 species are suitable for combining in relay intercropping where each species is sown at an appropriate time to

optimize its performance. In China, widely used relay intercropping are wheat/maize (Li et al., 2001; Hong et al., 2019), maize/soybean (Yan et al., 2010, 2015) and maize/pea (Hu et al., 2016). Relay intercropping allows for niche partitioning and competitive relaxation between component species due to time differences in resource capture. An index for temporal niche differentiation (TND) was first defined by Yu et al. (2015). This index is the proportion of the total growing period of an intercropping system that species are growing alone, without the companion (competitor) crop.

Maize is a commonly cultivated C4 species in intercrops. The peak of its growth rate is later in the season than that of C3 crops such as small grains (e.g. wheat) and legumes (e.g. soybean or peanut). Sowing maize later reduces shading of the less competitive C3 species by maize but also reduces maize performance early in the growing season when it is shaded by an earlier sown C3 species (Li et al., 2001; Gou et al., 2016). However, maize can continue to grow after harvest of the C3 species and compensate for the early-season growth reduction (Li et al., 2001; Gou et al., 2016). Our first hypothesis is that C3/C4 intercrops show a greater NE and CE than intercrops with only C3 species, because greater differences in functional traits allow greater complementarity in resource capture. We also expect a greater SE in C3/C4 intercrops than in C3/C3 intercrops due to the tendency of tall C4 species to be competitively dominant and high yielding which could result in a positive SE.

Cereal and legume species differ in N acquisition and rhizosphere-related traits: Legumes are able to fix N_2 from air, hence cereal/legume intercrops can show a complementary use of N sources (Jensen, 1996; Fan et al., 2006). Therefore our second hypothesis is that CE is greater in intercrops including legumes than in intercrops without legumes, especially under low N conditions. Legumes are furthermore expected to facilitate P acquisition of intercropped cereals through exudation of phosphatases and carboxylates in the rhizosphere (Li et al., 2014). This would also lead to a positive contribution of mixing cereals and legumes to the CE.

Yu et al. (2015) showed that the LER of intercropping increases with TND. Therefore, our third hypothesis is that CE increases with TND, but the SE may decrease with TND because the SE is driven by competitive interactions which may be mitigated by niche differentiation in time, as characterized by TND.

There has been no meta-analysis on the occurrence of CE in intercropping in relation to nutrient availability. The stress gradient hypothesis (Maestre et al., 2009; He et al., 2013) predicts that positive interactions between species (associated with high CE) are more common under conditions with higher abiotic stress (Roscher et al., 2016). In agreement with this hypothesis, the yield advantage (as measured by LER) of cereal/legume intercrops was greatest with no N fertilization and was reduced when N fertilizer was applied (Hauggaard-Nielsen and Jensen, 2001). However, overyielding of cereal/cereal intercrops can also be attained with adequate N fertilizer input (Li et al., 2011) and the level of P fertilization did not affect the LER of cereal/legume intercrops such as durum wheat/faba bean intercrop (Tang et al., 2016). Our last hypothesis is that species complementarities between cereals and legumes are greatest at low nutrient availability (N and P) while sole crop yields are greater at high nutrient availability. With CE being the product of average relative yield gain and average sole crop yield, CE could then show a quadratic response to nutrient input. The SE quantifies the dominance of species with high yield in sole cropping because of their capacity to capture more light and nutrients. Competitive dominance for light is related to leaf growth, which is promoted by high nutrient input, hence we expect a greater selection effect at higher nutrient input.

Intercropping is still prevalent in China (Hong et al., 2017), and many studies on productivity of intercrops have been done in China over the past 30 years. This has resulted in a wealth of suitable data from China, both in the international and Chinese literature. We therefore focus this meta-analysis on data from intercropping studies

conducted in China. In summary, we did a meta-analysis to address three research questions: (1) How large is the yield gain of intercropping in units of grain yield per hectare? (2) What is the contribution of the CE and SE to the yield gain in various intercropping systems, and (3) What are the effects of species trait combination, TND, and N and P input on the NE, CE and SE?

2. Materials and methods

2.1. Data collection

A literature search was conducted on the Chinese National Knowledge Infrastructure. We used the search terms "intercrop" and "yield" in the topic field and "field experiment" in the full text. An additional literature search was conducted on Web of Science using the search terms "intercrop" and "yield" and "field experiment" in the topic field and "China" in the author address. The two datasets were combined and doubles were removed. The papers were then checked on extractable data on crop yields in intercrops and sole crops, information to calculate the land shares of species in the intercrop, sowing dates and harvest dates, and information on management, based on original field experiments (Table 1; see also Methods A1). A total of 69 publications (24 in English and 45 in Chinese, Methods A2) were retained during this selection. Data were extracted from tables or from figures using GetData software (http://getdata-graph-digitizer.com/).

The final dataset included data from 100 experiments, i.e. 100 unique combinations of site and year, and 426 data records. Each data record contained yield data on the intercrop and the corresponding sole crops at the same management such as fertilizer input, sowing dates and harvest dates. If an experiment reported data on intercropping and sole crops at different levels of fertilizer input, the data at each nutrient input level was recorded in separate records. If the N and P fertilizer in the intercrop were given separately for each species, the total N and P fertilizer input in intercropping was calculated according to the land share of each species in the intercrop (Methods A3).

In this database, most of the experiments concerned strip intercropping (414 out of 426 records), in which two species were cultivated in alternative strips and at least one strip includes more than one row. (Of those, 14 records had one of the species in single strips while the other species was arranged of multiple rows in strips.) There were only 12 records of row intercropping (1 record of maize (*Zea mays*)/peanut (*Arachis hypogaea*), 4 records of wheat (*Triticum aestivum*)/faba bean (*Vicia faba*), 7 records of maize/soybean (*Glycine max*)), in which two species were cultivated in alternate rows. There were three main groups of species combinations (Table 2): C4-cereal/C3-cereal (118 records), C4-cereal/legume (252 records) and C3-cereal/legume intercrops (36 records). The C4-cereal/C3-cereal intercrops were dominated by

Table 2
Contingency table for frequency (data records) of intercrops including C3, C4, cereal, legume or other species.

	Cereal/ cereal	Cereal/ legume	Cereal/ others	Legume/ legume	Legume/ others	Total
C3/C3	0	36	0	1	5	42
C3/C4	118	252	12	0	0	382
C4/C4	2	0	0	0	0	2
Total	120	288	12	1	5	

Note: The three main combinations are C3-cereal/legume, C4-cereal/C3-cereal and C4-cereal/legume.
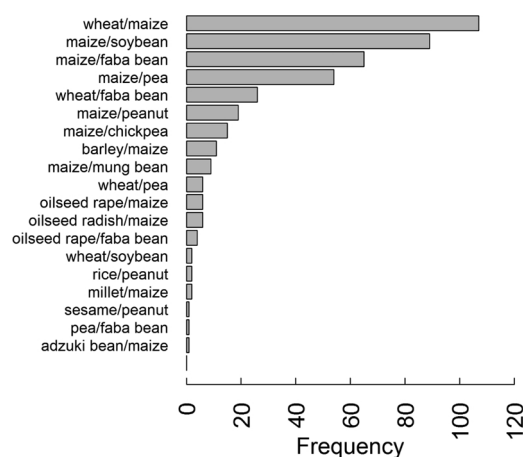

Fig. 1. Frequency of occurrence (data records) of species combinations in the dataset.

maize/wheat and maize/barley (*Hordeum vulgare*), while the C4-cereal/legume intercrops comprised maize intercropped with a variety of legume species, such as soybean, faba bean, peanut and pea (*Pisum sativum*). If a C4 cereal was present, it was almost always maize. There were two data records on maize/millet (*Setaria italica*) (Fig. 1).

2.2. Calculation of an index for temporal niche differentiation (TND)

An index for temporal niche differentiation was calculated using sowing dates and harvest dates of each species in the intercrop (Yu et al., 2015):

$$\text{TND} = \frac{P_{\text{system}} - P_{\text{overlap}}}{P_{\text{system}}} = 1 - \frac{P_{\text{overlap}}}{P_{\text{system}}} \tag{1}$$

Table 1
Variables extracted from publications.

Variable	Definition	Data type/Unit
Title	Title of publication	Text
Authors	Authors of publication	Text
Journal name	The name of the journal	Text
Year of publication	Year	Text
Latitude and longitude	Latitude and longitude of experimental site	Decimal Degrees
Species	Name of crop species	Text
Plant density	Density of each species in sole crops and in the intercrop	Plants ha^{-1}
Row numbers, row distance and plant distance in intercropping	Number of rows, row distance and plant distance of each species in the sole crop and intercropping, and row distance between two species in intercropping or strip width of each species in intercropping, to calculate the strip width, relative density and land share	Number/cm
Sowing dates and harvest dates	Sowing dates and harvest dates of intercropped species or information on total period and overlap period of intercrops to calculate TND	Dates
Functional-trait species combinations	Trait combinations: (C3, C4) × (cereal, legume): C4-cereal/C3-cereal, C4-cereal/legume, C4-cereal/C4-cereal, C3-cereal/C3-cereal, C3-cereal/legume (Table 2, Fig. 1).	Categorical
Yield	Grain yield (dry grain weight) of both sole crops and intercrops	Mg ha^{-1}
Amount of N and P fertilizer	Amount of N and P fertilizer applied to sole crops and to intercrops	kg ha^{-1}

Table 3

List of final best models fitted to the data. The indices, *i, j* and *k* represent publication, experiment and treatment, respectively. In all mixed models, a_i is a random publication effect and b_{ij} is a random experiment effect. a_i and b_{ij} are assumed normally distributed with constant variances. ε_{ijk} is a residual random error assumed normally distributed with constant variance. The variance terms a_i, b_{ij} and ε_{ijk} were all assumed independent.

Model	Equations	Data
1	$(NE, CE, SE)_{ijk} = \beta_0 + a_i + b_{ij} + \varepsilon_{ijk}$	All data
2	$(NE, CE, SE)_{ijk} = \beta_{TC}(TC_{ijk}) + a_i + b_{ij} + \varepsilon_{ijk}$	Only for maize/C3-cereal, maize/legume and C3 cereal/legume intercrops
3	$(NE, CE, SE)_{ijk} = \beta_{TND} TND_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$	All records with information on TND
4	$(NE, CE)_{ijk} = \beta_{TC}(TC_{ijk}) + \beta_{TND}(TC_{ijk}) TND_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$	Only for maize/C3-cereal, maize/legume and C3 cereal/legume intercrops
5	$SE_{ijk} = \beta_{DV1}(DV1_{ijk}) + \beta_{TND}(DV1_{ijk}) TND_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$	Only for maize/C3-cereal, maize/legume and C3 cereal/legume intercrops
6	$(NE, CE, SE)_{ijk} = \beta_N N_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$	All records with information on N input
7	$(NE, CE)_{ijk} = \beta_{TC}(TC_{ijk}) + \beta_N(TC_{ijk}) N_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$	Only for records with information on N input concerning maize/C3-cereal, maize/legume and C3 cereal/legume intercrops
8	$SE_{ijk} = \beta_{DV2}(DV2_{ijk}) + \beta_N(DV2_{ijk}) N_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$	Only for records with information on N input concerning maize/C3-cereal, maize/legume and C3 cereal/legume intercrops

Note: TC (Trait combination) is a categorical variable with three levels representing maize/C3-cereal, maize/legume and C3-cereal/legume intercrops. The intercept $\beta_{TC}(TC_{ijk})$ can take three values, depending on species combinations such as maize/C3-cereal, maize/legume, C3-cereal/legume. DV1 and DV2 are categorical variables with two levels (dummy variables). DV1 indicates whether the intercrop includes maize: (0) intercrops with maize (maize/C3-cereal and maize/legume); (1) intercrops without maize (C3-cereal/legume). DV2 indicates whether the intercrop includes a legume: (0) with a legume; (1) without a legume. After model selection (Method A8), models 4, 5, 7 and 8 were selected to estimate the different responses of three species trait combinations to TND or N input.

Where $P_{overlap}$ represents the period of overlap between the growing periods of the intercropped species, while P_{system} represents the duration of the whole intercrop. TND = 0 means simultaneous intercropping, with full overlap of two species (both species are sown and harvested at the same time). TND = 1 would mean no overlap, i.e. double cropping (the second species is sown after the first is harvested). Double cropping was not included in our analysis. Most of the intercrops in the dataset had a value of TND greater than zero (296 out of 326 data records with TND > 0), and only 30 data records had TND = 0. Thus, most of the intercrops were relay intercrops.

2.3. Additive partitioning method to calculate net effect, complementarity effect and selection effect

The net effect (NE) is defined as the difference between the observed yield and the expected yield (Loreau and Hector, 2001).

$$NE = (Y_1 + Y_2) - (EY_1 + EY_2) \tag{2}$$

Y_1 and Y_2 are the observed yields of species 1 and 2 in intercrop, EY_1 and EY_2 are the expected yields (EY) of two species, which were calculated as the products of the yield of each sole crop and its land share (see Methods A4).

The NE is equal to the sum of two components, which have been coined the complementarity effect (CE) and the selection effect (SE) (Loreau and Hector, 2001):

$$NE = CE + SE = N \times \bar{\Delta RY} \times \bar{M} + N \times cov(\Delta RY, M) \tag{3}$$

Here, $\bar{\Delta RY}$ is the average relative yield gain of the two species, $\bar{M}$ is the average yield of sole crops, and $cov(\Delta RY, M)$ is the covariance between the relative yield gain in the intercrop and the sole crop yield. N is the number of species, which is in all cases of the dataset $N = 2$.

Relative yield gain is mathematically defined as:

$$\Delta RY_i = RY_i - RY_i^0 \tag{4}$$

where RY_i is the actual relative yield of a species and RY_i^0 is the expected relative yield. Actual relative yield is the yield in the intercrop (per unit area of the whole crop) divided by the yield in the sole crop. It is for each species defined as (De Wit, 1960):

$$RY_i = Y_i / M_i \tag{5}$$

Expected relative yield is based on the land share of a species in the intercrop. This land share can be calculated on the basis of the densities of a species in the intercrop and the sole crop or on the basis of row or plant arrangement (Methods A4).

For a two-species intercropping system, CE can be written as

$$CE = (RYT - 1) \times \bar{M} \tag{6}$$

Thus, CE is equal to the relative yield total (or LER) minus 1, multiplied by the average yield of sole crops. SE can be written as (Methods A5):

$$SE = 2 \times cov(\Delta RY, M) = \frac{1}{2} \times (\Delta RY_1 - \Delta RY_2) \times (M_1 - M_2) \tag{7}$$

SE is positive if the species with the highest sole crop yield (presumably a competitive species) is overyielding more strongly (greater ΔRY) in intercropping than the species with the lowest sole crop yield. SE is negative if the species with the lowest sole crop yield has a higher relative yield gain. Therefore, the sign of SE indicates whether the high or low-yielding species profits most (in terms of relative yield gain) from intercropping. Positive SE would arise if the more productive species dominates the mixture in terms of biomass or space occupancy (Barot et al., 2017).

The additive partitioning method was proposed for multi-species systems with *N* species (Loreau and Hector, 2001; Malézieux et al., 2009). However, all components in the additive partitioning formula (Eq. 3), including the covariance term (Eq. 7), can be readily calculated with only two species in the mixture, as is well known from analyses of grassland biodiversity studies, where the species number $N = 2$ represents one of the levels of biodiversity that is considered (Loreau and Hector, 2001).

2.4. Statistical analysis

All analyses were conducted in R (R Core Team, 2014). Linear regression with mixed effects models (R package *nlme*; Pinheiro et al., 2015) was used to quantify the relationships of NE, CE, and SE with the explanatory variables (species trait combinations, TND, N and P input). We assumed normal error structure and homoscedasticity and validated the model assumptions by checking residuals (Zuur et al., 2009). We used publication and experiment within publication as random effects to account for differences between the studies (publications) and between experiments (sites * years) within studies. The best random effects structure was identified by fitting different structures and comparing them using Akaike's information criterion (R functions anova() and AIC()) (Bolker, 2008). We finally selected eight mixed effects models to present in this paper (Table 3).

We used the anova() function to check the significance of quadratic or linear effects (e.g. nutrient input) or interactions between TND or nutrient input and a categorical variable for functional-trait species combinations (Three levels: maize/C3-cereal, maize/legume, and C3-
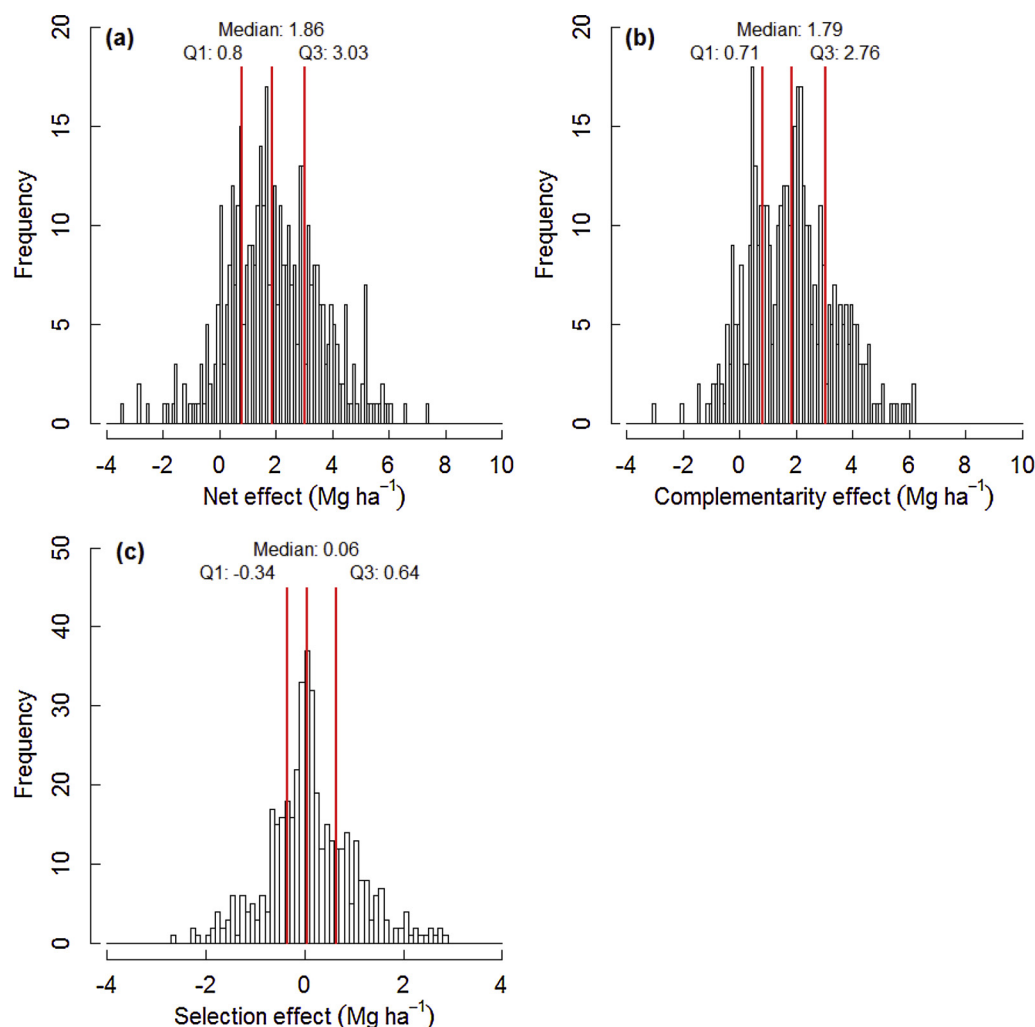
Fig. 2. Frequency distribution of (a) the net effect (NE), (b) the complementarity effect (CE) and (c) the selection effect (SE). Vertical red lines in the panels a–c indicate the first quartile (Q1), median and third (Q3) quartile of the NE, CE and SE (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

cereal/legume intercrops (Table 1)). The AICs of models with the same or different intercept or slope among the three groups were compared (Methods A6). The best models were presented in Table 3, and only the regression lines of the models with P values lower than 0.05 are shown in the figures.

We made funnel plots (Duval and Tweedie, 2000) for the NE, CE and SE to assess publication bias (Methods A7). For each funnel plot, we plotted average NE, CE and SE in each of the 69 studies against the total number of experimental units (replicates) in the study as a proxy for study accuracy. There were 341 out of 426 data records without standard error or standard deviation reported. We therefore did an unweighted analysis in which all studies had an assumed equal variance, consistent with earlier meta-analyses on yield advantages in intercropping (Yu et al., 2015; Martin-Guay et al., 2018).

3. Results

3.1. Frequency distribution of the net effect and its components

The average NE of intercropping was 2.14 ± 0.16 Mg ha^{-1} grain yield (mean $\pm$ standard error) with a median of 1.86 Mg ha^{-1} (Fig. 2a, model 1). The NE was negative in only 9 % of the data records. Most of the yield gain (90 %) was due to the CE: the average CE was 1.94 ± 0.15 Mg ha^{-1} with a median of 1.79 Mg ha^{-1} (Fig. 2b). The SE

was a minor component (10 %) of the yield gain: the average SE was 0.18 ± 0.08 Mg ha^{-1} with a median SE of 0.06 Mg ha^{-1} (Fig. 2c), indicating that overyielding of the species with the greater sole crop yield made only a minor contribution to the NE.

3.2. Effects of species trait complementarity on the net effect and its components

The NEs of maize/C3-cereal and maize/legume intercrops were similar: 2.25 ± 0.22 Mg ha^{-1} and 2.43 ± 0.18 Mg ha^{-1} ($P = 0.44$, Fig. 3a), respectively. The NE in C3-cereal/legume intercrops was 0.44 ± 0.40 Mg ha^{-1}, not significantly different from zero, and significantly lower than in mixtures containing maize and another cereal or a legume (both $P < 0.001$). There was no difference in CE whether maize was intercropped with a C3-cereal (2.27 ± 0.20 Mg ha^{-1}) or a legume (2.08 ± 0.16 Mg ha^{-1}). The CE in C3-cereal/legume intercrops was 0.14 ± 0.35 Mg ha^{-1}, not significantly different from zero, and significantly lower than in mixtures containing maize and another cereal or a legume (both $P < 0.001$). When maize was intercropped with a legume, the SE was higher than when intercropped with a C3 cereal (difference in SE = 0.47 ± 0.13 Mg ha^{-1}, model 2, $P < 0.001$, Fig. 3b). Summarizing, the NEs and CEs of intercrops with maize were substantially higher than those of intercrops without maize, while the SE was slightly greater when maize was intercropped with a legume
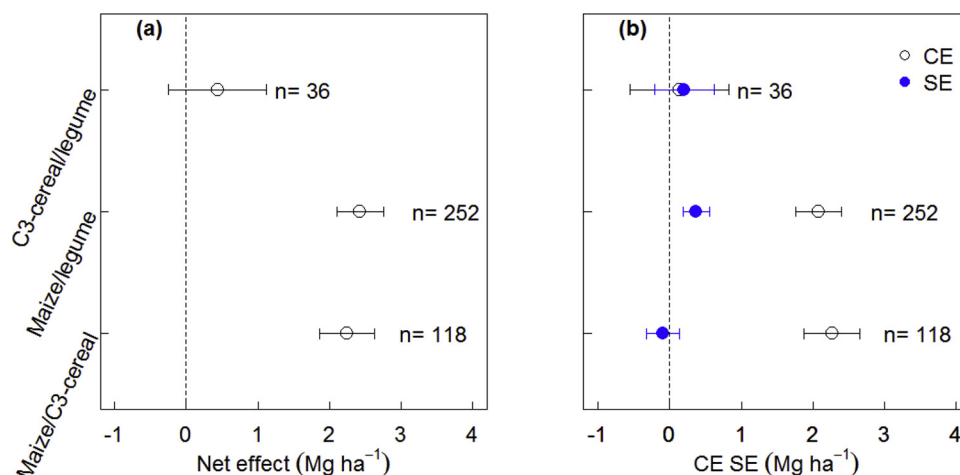
Fig. 3. The net effect (a), complementarity effect (CE) and selection effect (SE) (b) of intercropping for maize/C3-cereal, maize/legume and C3-cereal/legume combinations. The horizontal bars represent 95 % confidence intervals; n = number of entries.

than when it was intercropped with a C3 cereal.

3.3. Effect of temporal niche differentiation on the net effect and its components, and the interaction with species combinations

When using the full dataset, the NE increased 0.81 ± 0.40 Mg ha^{-1} per unit of TND (model 3, $P = 0.04$, Fig. 4a). The CE increased with 2.65 ± 0.33 Mg ha^{-1} per unit TND ($P < 0.001$, Fig. 4c) while the SE decreased 1.73 ± 0.22 Mg ha^{-1} per unit TND ($P < 0.001$, Fig. 4e), but the decrease of SE was smaller than the increase of CE, the NE therefore increased with TND. When only using data for the subsets of maize/C3-cereal, maize/legume and C3-cereal/legume, we did, however, not identify a significant positive relationship between TND and NE (model 4, Fig. 4b). Only the CE of maize/legume intercrops increased with TND (2.51 ± 0.36 Mg ha^{-1}, $P < 0.001$, Fig. 4d), but the CEs of the other two species combinations were independent of TND. The presence of maize in intercropping was associated with a decrease in SE with greater TND. The SE of intercrops with maize decreased with TND but the SE of intercrops without maize was independent of TND (Fig. 4f). The results indicate that in maize/legume intercrops, the SE had a slightly larger contribution to the net effect at low TND (high overlap in time between species) whereas the contribution of CE was bigger at higher TND.

3.4. Effect of N input on the net effect and its components, and the interaction with species combinations

We hypothesized that the NE and CE might show quadratic responses to N fertilizer input, however, in model selection (Methods A6), the linear models were better than the quadratic models. Both the NE and CE increased with N fertilizer input (model 6, $P < 0.001$, Fig. 5a and c). The NE increased 2.75 ± 1.33 kg ha^{-1} per kg of N fertilizer per ha, and the CE increased 2.66 ± 0.58 kg ha^{-1} per kg of N fertilizer per ha. The SE was independent of N input (model 6, $P = 0.77$, Fig. 5e). Thus, the yield gain and competitive relaxation of intercrops depend on N fertilizer input. N fertilizer input had no influence on the SE.

The NE of maize/C3-cereal intercrops increased 7.33 ± 0.88 kg ha^{-1} per kg of N fertilizer per ha (model 7, $P < 0.001$, Fig. 5b), and the CE of maize/C3-cereal intercrops increased 5.79 ± 0.83 kg ha^{-1} per kg of N fertilizer per ha (model 7, $P < 0.001$, Fig. 5d), but NE and CE of intercrops with legumes did not respond to N input. The SE of maize/C3-cereal intercrops was close to zero and slightly increased with N input (model 8, $P < 0.01$; Fig. 5f). However, there were no significant responses of SE to N fertilizer input in intercrops with legumes (i.e. maize/legume and C3-cereal/legume).

3.5. Effect of P input on the net effect and its components, and the interaction with species combinations

The NE and its components did not respond to P fertilizer input, and regressions for different functional intercrop groups did not identify any significant relationships (Fig. S1).

4. Discussion

Our study showed that the yield gain of intercropping in the present dataset was 2.14 Mg grain per hectare. This yield gain was largely due to the CE, with a small contribution from the SE. Temporal niche differentiation increased the yield gain by increasing the contribution of CE to the net effect and decreased the contribution of SE. A greater yield gain and CE were found in intercrops with maize (e.g. maize/C3-cereal or maize/legume) compared to intercrops without maize (e.g. C3-cereal/legume). The SE was significantly positive in maize/legume intercrops. The yield gain increased with N input in maize/C3-cereal intercrops but not in cereal/legume intercrops. This increase in yield gain was largely due to the positive response of maize to N input in relay strip intercropping. The NE and its components were independent of P input.

4.1. Using absolute gains to better appreciate the yield benefit of intercropping

The choice of indicators is essential to appreciate the yield benefit of intercropping (Bedoussac and Justes, 2011). This is the first meta-analysis using the net effect of intercropping to analyse yield advantage. The advantage of net effect is that it expresses intercropping benefit in real terms of Mg ha^{-1}. The information provided by NE and its components is complementary to that provided by LER. Where LER characterizes the land use efficiency of intercropping, the NE indicates how much more yield is obtained per unit area than expected from the sole crop yields and species land shares. Relative yield can be high if the absolute yields in the intercrop and the sole crop(s) are low, but in the case of NE, the value is not likely to be substantial at low yield levels. Partitioning the net yield gain of intercrops into complementarity and selection effects with additive partitioning method helps to analyse the drivers of yield gain of intercropping. In particular, additive partitioning helps to ascertain whether intercropping advantage is predominantly due to overyielding of the species with the highest sole crop yield (in many studies maize) or due to overall functional complementarity between the species, such that the sum of relative benefits is greater than zero ($\Delta RY > 0$). Our analysis shows that 90 % of the
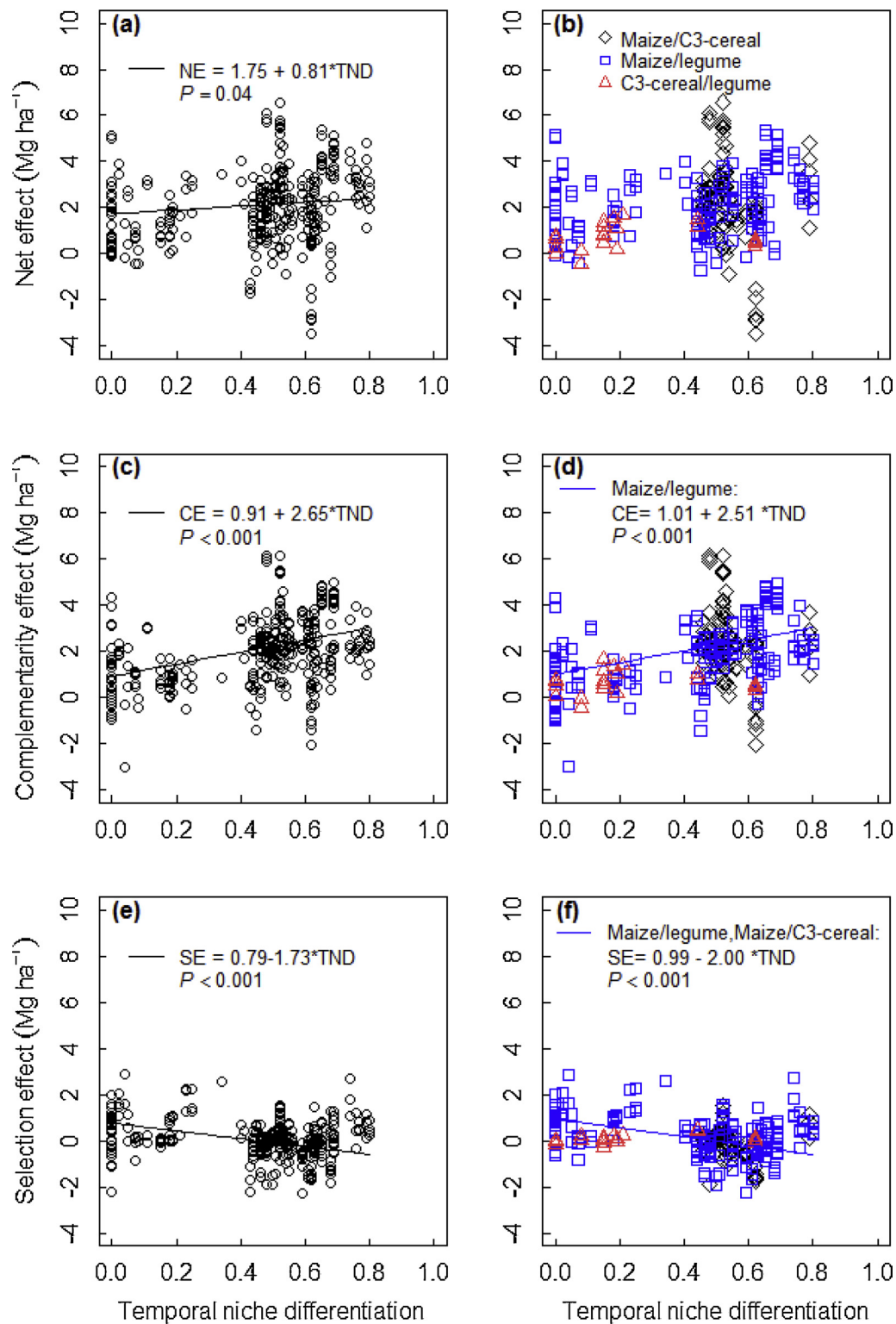
Fig. 4. Relationship between (a) the net effect, (c) complementarity effect (CE) and (d) selection effect (SE) and temporal niche differentiation (TND) for all intercrops, and relationship between (b) the NE, (e) CE, (f) SE and TND for maize/C3-cereal, maize/legume and C3-cereal/legume intercrops. Only regressions with P < 0.05 are presented in the panels.

intercropping advantage is due to complementarity as captured by CE. Furthermore, the effect size of more than 2 tons of grain per ha is substantial and of great agronomic relevance.

4.2. Components of net yield gain in different intercropping groups

In line with our first hypothesis, the NE and CE were greater in C3/C4 intercrops (mainly maize with a C3-cereal or legume) than in intercrops with only C3 species, predominantly C3-cereal/legume mixtures (Fig. 3). This might be explained by differences in functional traits
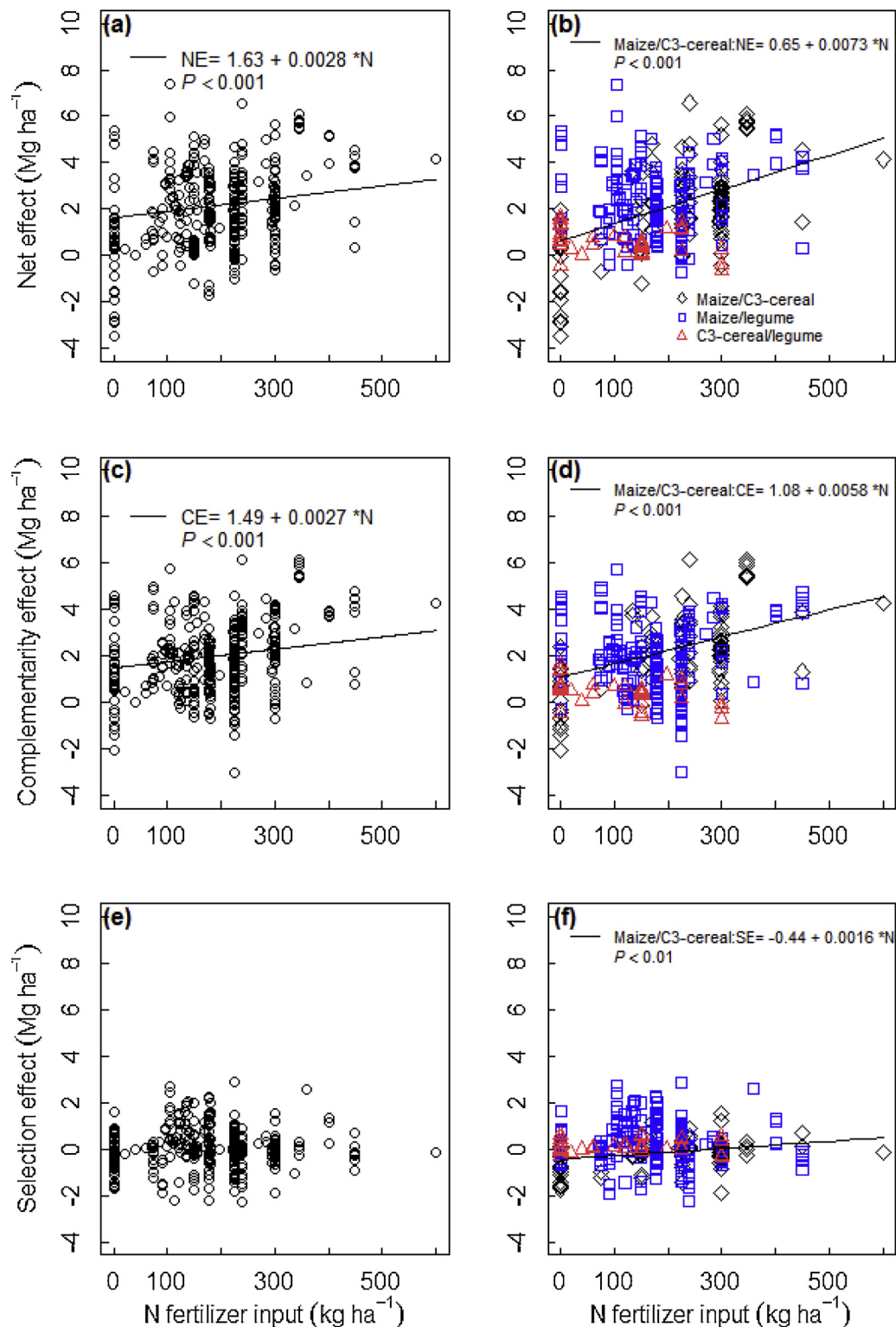
Fig. 5. Relationship between (a) the net effect, (c) complementarity effect (CE) and (d) selection effect (SE) and N input for all intercrops, and relationship between (b) the NE, (e) CE, (f) SE and N input for maize/C3-cereal, maize/legume and C3-cereal/legume intercrops. Only regressions with P < 0.05 are presented in the panels.

and temporal niche differentiation between maize and C3 species. Large differences in growing period and contrasting temperature responses between maize and C3 species allow greater complementarity in resource capture (light, water and nutrients) to be achieved over a growing season, particularly if sowing and harvesting of the species is staggered in time. The larger TND of intercrops with maize (Fig. S2)

also explained the higher NE and CE of intercrops with maize than without maize. As a C4 species, maize is more adapted to high temperatures than C3 species, enabling niche differentiation between species in crop mixtures over time, resulting in better exploitation of seasonal patterns in light and temperature (Anten and Hirose, 1999).

The hypothesis that the SE would be greater in intercrops with

maize, was not confirmed. The SE of maize/C3-cereal intercrops was not significantly different from 0. In this dataset, maize/C3-cereal intercrops included maize/wheat and maize/barley (Fig. S3), and these intercrops had high TND (Fig. S2) because maize, which is the better competitor, was always sown later than wheat and barley. We infer that due to this temporal differentiation, maize was not strongly competitive to its companion species, and hence, SE was zero.

Contrary to the second hypothesis, we found no differences in NE and CE between maize intercropped with a C3 cereal or a legume (Fig. 3). This was unexpected because the literature assigns a great importance to the complementary uptake of N by cereals and legumes (e.g. Lithourgidis et al., 2011). It is possible that the potential synergy between cereals and legumes did not reach its full potential in the dataset due to high fertilization levels (Fig. S4) (Hauggaard-Nielsen and Jensen, 2001). It would have been interesting to compare C3-cereal/C3-cereal and C3-cereal/legume intercrops, but there was no data on C3-cereal/C3-cereal intercrops in the dataset (Table 2). The comparatively larger SE of maize/legume intercrops as compared to maize/C3-cereal intercrops (Fig. 3b) is in line with the well-established low competitiveness of legumes with respect to cereals (Yu et al., 2016). With stronger competitiveness of maize towards legumes than to other cereals, a larger SE was expected in mixtures with legumes, and the analysis confirmed this. Maize plants are generally tall (though there is high genotypic variability for this) resulting in severe shading of legumes in mixtures if these are sown at the same time as maize. This highlights the subordinate role that legumes have in mixtures with maize as a result of competition for light (Liu et al., 2017, 2018).

4.3. Temporal niche differentiation as a mechanism underlying the complementarity and selection effects

We obtained confirmation of the third hypothesis that CE increases with TND (Fig. 4). If two species are sown and harvested at the same time (TND = 0), taller species can outcompete shorter species, since competition for light between species is size asymmetric (Weiner, 1990; DeMalach et al., 2016; Huang et al., 2017). With less overlap in time between the two species (high TND), temporal and spatial complementarity in light interception becomes more important. Similarly, the shorter co-growth period allows species to acquire water and nutrients at different times. The later species may also benefit from N mineralisation from decomposing roots of the earlier species. In relay intercropping (high TND), crops can take up N over a longer period of time. The relatively low density of species during the time that they are growing without the companion species relaxes competition for both aboveground and belowground resources, resulting in increased CE with greater TND (Fig. 4c). Since the NE was greatly contributed by the CE which was positively related to TND, the NE therefore increased with greater TND.

The CE increased with TND in maize/legume intercrops (Fig. 4d) but the yield gain and component effects were independent of TND in C3-cereal/legume intercrops (Fig. 4b, d, f). The range of TND in maize/legume intercrops (0–0.80) was larger than in the other two groups (Fig. 4). While TND is evidently a factor contributing positively to CE in maize/legume intercrops, other factors may be involved, such as the higher temperature optimum for growth in maize, or the possibility of a more favourable light distribution in the co-growth stage when mixing plants with different architecture and temporal complementarity. Further work is needed to elucidate the role of different plant traits in the complementarity in maize/legume systems with temporal niche differentiation.

4.4. Complementarity effect and selection effect in relation to N and P input

Contrary to our last hypothesis, we found a linear response rather than a quadratic response of the NE or CE of maize/C3-cereal intercrops to the N fertilizer input (Fig. 5b, d). The positive response of NE to N

input in maize/C3-cereal intercropping systems is likely due to the positive response of maize in relay intercropping systems to sufficient N availability during its recovery after harvest of the C3-cereal (Li et al., 2001; Gou et al., 2016).

We found that the NE and CE of intercrops with legumes (i.e. maize/legume, C3-cereal/legume intercrops) were independent of N fertilizer input. Similarly, the LER of cereal/legume intercrops was independent of N fertilizer input in other meta-analysis studies (Pelzer et al., 2014). However, results of Yu et al. (2015, 2016) indicate that LER in simultaneous cereal/legume intercrops decreases with N input. While we had hypothesized a quadratic response to N input in cereal/legume intercrop, we found in our meta-analysis no significant response at all. This is not contradicting our initial reasoning. On the one hand, we expected that N input would tend to increase yield level, and thereby NE, which was confirmed (Fig. S5). On the other hand, the complementarity between cereals and legumes for N acquisition would diminish in importance as N input increased, shown as lower LER (also confirmed, Fig. S5), which would tend to decrease NE. The overall effect was no effect of N input on NE in cereal/legume intercropping. On the other hand, N input increased both yield level and LER in maize/C3-cereal intercropping (Fig. S5). Hence the effect of N input on NE in maize/C3-cereal intercrops was positive.

Available N is not entirely driven by fertilizer as N can also be mineralized from soil organic matter. We conducted an additional analysis using as an explanatory variable the total N supply calculated as the sum of N derived from fertilizer (accounting for recovery fraction) and N from soil organic matter (Methods A8; Sattari et al., 2014). This analysis indeed yielded a curvilinear response of NE to N supply (Fig. S6, S7). However, the response of CE to N supply was linear while SE showed no response to N supply, which is inconsistent with the curvilinear response of NE. We consider this analysis of the influence of N supply less robust than the analysis of N input because (1) the analysis of the effect of N supply was based on unverified assumptions in the calculation of supply (e.g. the recovery fraction) and (2) the dataset was considerably (37 %) smaller than the full dataset used for the analysis of N input. All in all, both analyses show that a trade-off exists between the effects on yield level and intercropping advantage of N input and soil N supply; on the one hand, N input increased N availability and yield level, but on the other hand, higher levels of soil N decrease relative intercropping advantage due to N capture complementarity in cereal/legume mixtures. In maize/C3-cereal mixtures, both the yield level and the relative intercropping advantage increased with N input.

SE was independent of N input in cereal/legume intercrops (Fig. 5f). This contradicts our hypothesis and several empirical studies showing that application of N fertilizer in cereal/legume intercrops increases the competitiveness of cereals thereby increasing the competitive inequality between cereals and legumes (Bedoussac and Justes, 2010; Andersen et al., 2014; Pelzer et al., 2014; Yu et al., 2016). A possible explanation is that most of the intercropping systems in our database were strip intercropping systems. In these systems, the competitive interactions between species are less intense than in the row intercropping or completely mixed intercropping systems that were conducted in Europe or worldwide. Both experiments and simulations with plant models have shown that competitive dominance effects are aggravated if the strips are narrow or consist of single rows (Yu, 2016).

Contrary to our expectation and the stress gradient hypothesis, yield gain and its component effects were independent of P input. The reason may be that soil P levels in the synthesized studies were not limiting yield. The average Olsen-P in the studies in this dataset was $12.3 \pm 2.5 \, \mathrm{mg \, kg^{-1}}$ (Fig. S8), which was in the range of soil Olsen-P for optimal crop yield ($10.9–21.4 \, \mathrm{mg \, kg^{-1}}$) (Bai et al., 2013). Accordingly, there was no response of maize yield in sole crop to the P input of sole maize in the dataset (Fig. S9b) (382 out of 426 data records include maize in the intercrop). Similar to our results, Li et al. (2018) did not find any consistent effect of P input on CE across four species combinations in intercropping. Positive interactions between intercrops that

involve P-mobilizing exudates require root proximity (Hinsinger et al., 2011), but our dataset mostly comprised data on strip intercropping. Altogether, this meta-analysis gives no support for the notion that the level of P input is an important factor driving yield advantages in Chinese intercropping.

5. Conclusions

Our study highlights that net effects of Chinese intercropping on yield are highly dependent on the presence of maize and that temporal niche differentiation is key to competitive relaxation through an increase of the complementarity effect. The results indicate that yield gain by intercropping is sustained under high nutrient availability. Yield gains are similar regardless whether maize is intercropped with a C3 cereal or a legume. The yield gains of maize/C3-cereal intercrops depend on N input, while the yield gains in cereal/legume intercrops were independent of N input.

The results confirm that intercropping is a promising pathway for ecological intensification of agriculture (Lithourgidis et al., 2011; Brooker et al., 2015) which demands for design of optimized cropping systems that are highly productive and resource use efficient (Malézieux et al., 2009; Gaba et al., 2014). Our findings indicate that these systems might be conceived with high yielding C4 species such as maize that are tall, fast-growing during the later growing season and can recover from early competition with an earlier sown species.

Acknowledgements

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.eja.2019.125987.

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