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REGULAR ARTICLE

Intercropping legumes and cereals increases phosphorus use efficiency; a meta-analysis

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Abstract
Aims Intercropping cereals with legumes may achieve high crop yields at reduced input levels. Several studies have indicated that intercropping increases phosphorus use efficiency but no overarching analysis exists on the role of species traits and input levels. Here we synthesize the available information on P use efficiency in cereal/legume intercropping.
Methods Global data on yields, P uptake and nutrient input in cereal/legume mixtures were extracted from the literature and statistically analyzed. Co-variables explaining P uptake efficiency and yield were considered.
Results P uptake was substantially increased with an average value of LER_P, the land equivalent ratio for P uptake, of 1.24, and an average NE_P (observed P uptake minus expected P uptake) of 3.67 kg P ha^{-1}. The conversion efficiency of P uptake to biomass decreased with P uptake and was lower in intercrops than in sole crops but the conversion efficiency to yield was not affected by intercropping. The P fertilizer requirement was 21% lower in intercrops than in sole crops for the same yields.
Conclusions Substantial improvements in land use efficiency and P uptake are obtained by cereal/legume intercropping. Cereal/legume intercropping has therefore potential to increase P fertilizer use efficiency in agriculture.

Keywords Cereal/legume intercrops · Meta-analysis · P uptake · P conversion efficiency · P fertilizer equivalent ratio

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Introduction

Intercropping is the cultivation of two or more crop species simultaneously in the same field during a significant part of their growing periods (Willey 1979; Ofori and Stern 1987; Hauggaard-Nielsen and Jensen 2005). Intercropping has been used for millennia by smallholder farmers in Asia, Africa and Latin American and is currently attracting attention because of its ability to produce high yields at lower inputs (e.g. nitrogen fertilizer) and its potential for land sparing (Yu et al. 2015; Martin-Guay et al. 2018; Li et al. 2020a, b). Furthermore, intercropping suppresses pests and diseases (Trenbath 1993; Boudreau 2013; Zhang et al. 2019) and it can increase soil organic matter and

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retention of N in agricultural systems (Cong et al. 2015). Therefore, intercropping could play a role in the sustainable intensification of agriculture (Tilman 2020). Mixtures of a cereal and a legume are by far the most common type of intercrop cultivated worldwide (Rao et al. 1987; Gaba et al. 2015; Yu et al. 2015; Martin-Guay et al. 2018; Li et al. 2020a, b).

Cereal/legume intercropping has been advocated particularly for the complementary acquisition of N, with both the cereal and legume acquiring N from the soil solution, but only the legume fixing N in addition from the air through symbiosis with nitrogen fixing bacteria in root nodules (Pelzer et al. 2014). At low soil N supply, cereals perform better in a mixture with a legume than in a sole stand due to reduced competition for N because legumes obtain part of their nitrogen from the air. Intercropping legumes with cereals can also increase the proportion of nitrogen that legumes obtain from air (e.g. Cowell et al. 1989; Hauggaard-Nielsen et al. 2001). Thus, intercropping a cereal and a legume at low N input reduces nitrogen stress of the cereal and strengthens the biological capture of atmospheric nitrogen by the legume (Hauggaard-Nielsen and Jensen 2001).

The benefits of cereal-legume intercrops for P uptake and yield depend on species combination (He et al. 2013), soil P availability, and P input levels (Tang et al. 2016; Darch et al. 2018). Intercropping of a species with P mobilizing traits and a species without such traits may result in facilitation of the species without the traits by the species with the traits. Several examples of such facilitation have been described in cereal/legume intercropping (Betencourt et al. 2012; Tang et al. 2014, 2016). However, the consequences of facilitation of P uptake are not necessarily clear-cut because plant species are competing for other resources at the same time, particularly light, water, and nutrients. Also, facilitation due to release of P mobilizing chemicals by the roots of one of the species is likely to be unapparent if the soil has high P availability.

Apart from facilitation, P uptake in intercrops could be enhanced by complementarity. Complementarity can occur due to different root traits, e.g. rooting depth, and can be also related to differences in species growing periods (Yu et al. 2015). No overarching analysis has been made to date of P uptake in intercropping in response to species combinations and level of P or N input. Thus, there is a need for critical analysis of literature to synthesize the existing knowledge and ascertain the general P uptake benefits attained in intercrops, its variation across studies, and the factors affecting the P uptake efficiency, such as species combinations and P input levels.

The land equivalent ratio (*LER*) is commonly used to assess the yield advantage of intercropping. The *LER* is defined as the sum of relative yields of the component crops (Mead and Willey 1980). The *LER* is best interpreted as the relative land area needed by sole crops to produce the same yields as those obtained in a unit area of intercrop. A *LER* greater than one implies that intercropping makes a more efficient use of the land than sole cropping. The worldwide average *LER* in cereal-legume intercrops is well above 1, around 1.2–1.3 (Yu et al. 2015; Yu et al. 2016a, b; Martin-Guay et al. 2018; Xu et al. 2020; Li et al. 2020a, b). The LER does not directly relate to absolute yield levels. The relative yield advantage could be large at low input levels (e.g. low N or P input), but the absolute yield advantage could be lower at low input levels than at higher input levels, even if the LER would be higher at a low input level. It is therefore important to base an analysis of use efficiency of P in intercropping not only on the relative efficiency in intercropping and pure stands, as captured by the LER, but also on the absolute yield advantage.

The absolute yield advantage in intercropping can be assessed by the "net effect" which is defined as the yield (or biomass) difference between the observed total yield in intercrops (e.g. the total grain yield or biomass) and the expected total yield considering the component crop yields (biomasses) in the pure stands and the species proportions in the mixture (Loreau and Hector 2001; Li et al. 2020a, b). The net effect can also be determined for P uptake in the biomass. Using as a metric for complementarity for P uptake the net effect for P yield has the advantage that it expresses the gains in phosphorus uptake (actual minus expected) in physically meaningful units (kg P ha^{-1}), which helps making an interpretation that makes sense in real world terms. We use both LER and NE in our analysis because they provide complementary insight. LER indicates on a proportion scale how much more land is required in pure stands than in intercrops to generate a certain yield, biomass or P uptake (as obtained in intercropping) while NE indicates per ha of intercrop how much greater the yield, biomass or P uptake is than expected, expressed in kg ha^{-1}.

Legumes can mobilize P from chemically bound forms in the soil on the basis of root exudates such as

enzymes, organic acids and protons. Species differ in their ability to mobilize P. Table 1 summarizes key information for common species in studies on P uptake in intercropping.

We hypothesized that intercrops comprising legumes with a stronger ability to mobilize sparingly soluble P in the soil (particularly faba bean and chickpea) would support greater increases in P acquisition in intercropping (indicated by LER_P) than species with a weaker ability to mobilize P (e.g. soybean) when species grow in a low-P environment (low soil P and low P input).

Here, we synthesized the globally available published information on P uptake, biomass and yield in cereal-legume mixtures, based on field trials. We excluded pot experiments because they can only address principles and do not correctly represent effect sizes that are to be expected in the field when root systems are not confined. The study addresses four questions 1) Does cereal/legume intercropping increase P uptake, biomass, and yield as compared to sole crops? 2) How do species traits affect the complementarity for P uptake, biomass and yield in intercropping? 3) How do P input, N input and differences in growing period between species affect the effect of intercropping on P uptake, biomass and yield? 4) What is for cereals and legumes in sole crops and intercrops the relationship between P uptake and biomass or yield (internal use efficiency)?

Materials and methods

Meta-analysis-data sources, extraction and analysis

Data on P uptake in intercropping were obtained through computer searches in Google scholar, ISI Web of Science and the China National Knowledge Infrastructure (www.cnki.net). We used the following key-words alone or in combination: intercrop*, phosphorus, and cereal* and legume*. We found 17 papers (including publications, MSc theses and PhD theses) that satisfied the following criteria: (i) the study quantified biomass and P uptake or P concentration of sole crops and intercrops with the same management (e.g. level of fertilizer input) under field conditions; (ii) it reported the rate of N and P fertilizer; (iii) it reported the plant density in sole crops and intercrops (this information is needed to calculate the net effect). Compared to the large number of studies on intercropping (~3000), the number of retrieved studies was limited because less than 1% of the published studies reported P uptake or concentration in the plant material. For each study, data were extracted from tables, the text, or from figures using GetData 2.24 software. Data were entered into a database using identifiers for the publications and the experiments, and listing all relevant inputs and outputs. The 17 studies resulted in a data file with 97 data records (Tables S1, S2). A single study could yield several data records for the meta-analysis because it might contain data from multiple experiments or data from multiple treatments within an experiment. If an experiment had treatments, each treatment was represented by a separate line in the data file. There were some missing values for LER (16 out of 97 records), crop biomass (45 out of 97) and LER_P (22 out of 97). Some studies provided biomass data and P concentration data, while some other studies provided P uptake data but no biomass data. Data records with missing values of a variable were excluded from analyses that required that variable.

Textbooks on meta-analysis (Gurevitch and Hedges 1999), especially in the medical sciences, recommend extracting standard errors of the measurements in order to conduct a weighted analysis. We did an unweighted analysis because several papers did not provide the data in a form that would allow estimating the SE with confidence. We reasoned that conducting an unweighted analysis for a large set of data would give more reliable results than conducting a weighted analysis for a smaller set of data (Cf. Li et al. 2018; Porre et al. 2020). Furthermore, agronomic experiments, unlike medical trials, have to a large extent similar population sizes, e.g. three or four replicate plots per treatment. Hence, the effect of weighting is not expected to be important and certainly much less important than in the medical sciences where study sizes (number of subjects) may vary by orders of magnitude. Unweighted analyses have been successfully used in previous intercropping meta-analyses (Yu et al. 2015, 2016a, b; Martin-Guay et al. 2018; Xu et al. 2020; Li et al. 2020a, b).

Response variables

We used six response variables in the current study. These include three versions of the LER, viz for yield, aboveground biomass and P-uptake in above ground biomass (LER_Y, LER_B and LER_P, respectively) and three versions of the net effect, viz for yield, aboveground biomass and P uptake in above ground biomass (NE_Y, NE_B and NE_P, respectively).

Table 1 The capacity of legumes to mobilize soil P based on their ability of exudation of organic acid, acid phosphatase and rhizosphere acidification

Legume species	Indices for P mobilization activity	P mobilizing ability	Reference
Cowpea	Acid phosphatase activity (+)	Moderate	Fernandez and Ascencio 1994 Makoi et al. 2010
Pea	Acid phosphatase activity (no)	no	Hauggaard-Nielsen et al. 2001 Launay et al. 2009
Soybean	Acid phosphatase activity (no) Organic acid (+) Rhizosphere acidification (+)	no	Li et al. 2001 Li et al. 2007 Zhang et al. 2016
Faba bean	Acid phosphatase activity (++) Organic acid (++) Rhizosphere acidification (++)	Strong	Li et al. 2007
Chickpea	Acid phosphatase activity (++) Rhizosphere acidification (++)	Strong	Li et al. 2003 Li et al. 2004 Betencourt et al. 2012

no means no effect; + means significant activity; ++ means highly significant activity

The LER for yield is defined as:

$$LER_Y = \frac{Y_1}{M_1} + \frac{Y_2}{M_2} \quad (1)$$

where Y_1 and Y_2 are the yields (per unit of total area of the intercrop) of the cereal and the legume in the intercrop, while M_1 and M_2 are the yields of the cereal and legume in the sole crops (per unit area of the sole crop). The same equation was used to calculate the land equivalent ratio for biomass or P uptake. In the case of LER_B (biomass), we used the biomass per species for quantifying Y_1, Y_2, M_1 and M_2, while in the case of LER_P, we use the P uptake (whole biomass) per species to quantify Y_1, Y_2, M_1 and M_2. The LER_Y, LER_B and LER_P can be used to assess whether the realized yields, biomasses and P uptake of each species are more efficiently (per unit land) realized in intercropping than in sole crops. The land equivalent ratio is useful for assessing the relative land use efficiency of intercropping as compared to pure stands for yield, biomass production, and taking up P in the biomass.

The net biodiversity effect for grain yield, NE_Y, was calculated as the difference between the observed total grain yield (Y_{obs}) and the expected total grain yield (Y_{exp}) (Loreau and Hector 2001):

$$NE_Y = Y_{obs} - Y_{exp} = \sum Y_i - \sum p_i \times M_i \quad (2)$$

Observed total yield was calculated as the sum of the species yields, while the expected total yield was calculated as the sum of the species yields multiplied by their proportion (p) in the mixture. Here, proportion should be understood as the expected share a species would take of the land area and resources in the intercrop. NE_B and NE_P are the net effect for biomass and P uptake and are calculated using the same principles.

If the intercrop had a replacement design, we used the relative density, RD_i, of a species in the intercrop as estimator for its proportion. Relative density is in that case defined as the density of a species in the intercrop (number of plants per unit area of the whole intercrop) divided by the density of the species in the sole crop (plants per m^2). If the intercrop did not have a replacement design, the RD_i was rescaled as:

$$RD_1 = \frac{RD_1}{RD_1 + RD_2} \quad (3)$$

$$RD_2 = 1 - RD_1 \quad (4)$$

(Li et al. 2020a).

Explanatory variables

In the analyses, we use four explanatory variables, i.e. 1) species type combinations (categorical: with maize or without maize; and according to the species of legume); 2) rate of P fertilization in intercrops (continuous); 3) rate of N fertilization in intercrops (continuous); 4) TND, an index for temporal niche differentiation between species (continuous; eq. 6 below). The first three variables were directly extracted from the publications,

while temporal niche differentiation was calculated from sowing and harvesting dates according to Eq. 5 (Yu et al. 2015).

$$\mathrm{TND} = \frac{P\mathrm{system} - P\mathrm{overlap}}{P\mathrm{system}} = 1 - \frac{P\mathrm{overlap}}{P\mathrm{system}} \quad (5)$$

where P_{overlap} represents the period of overlap of the growth period of the intercropped species, while P_{system} represents the duration of the whole intercrop from sowing of the first species to harvest of the second species in the intercrop. A TND value of 0 means the two species are sown and harvested simultaneously, while a TND value of 1 means no overlap, i.e. double cropping. Double cropping was not considered in the data set as it is not intercropping.

Statistical analysis

Relationships between response variables and explanatory variables were estimated via linear mixed effects modelling. Random effects were included to account for the possibility of correlation between data originating from the same experiment and/or publication (Pinheiro and Bates 2000; Zuur et al. 2009). Random effects associated with experiments and publications account for effects of location, year, and other aspects of the study or experiment that affect the results but are not accounted for by the explanatory variables (fixed effects). Interactions between explanatory factors were explored. We used the anova() function to check the significance of interactions in ANOVA. All fitted models are described in the Supplementary Information Table S3.

We fitted the relationship between P uptake and biomass with a two-parameter Monod equation:

$$B_{i,j,k} = \frac{s\,P_{i,j,k}}{1 + s\,P_{i,j,k}/B_{\max}} \quad (6)$$

(model 1 in Table S4), where B_{ijk} is the biomass (or yield) measured in study i, experiment j, observation k, P_{ijk} is the corresponding P uptake, $B_{\max}$ is the maximum biomass (or yield) across all studies, and s is the initial slope of the relationship between biomass (or yield) and P uptake. Model selection with Akaike's Information Criterion (Bolker 2008) was used to determine whether there were differences between cereals and legumes and between intercrops and sole crops in the parameters of these models (Table S5, S7). Non-linear regressions were fitted using the R function nls() and random effects were not included. To assess the effect of random "between study" effects, linear mixed effects models were also fitted to the relationship between P uptake and biomass. Figures were made using R packages *plotrix* and *graphics* (Lemon 2006, R Core Team, 2013).

Results

P uptake, biomass and yield benefits in cereal/legume intercrops

On average, intercrops had greater P uptake in the aboveground biomass than sole crops. The mean value of $\mathrm{LER_P}$ was 1.24 ± 0.04 (mean ± SE), with 60 out of 65 $\mathrm{LER_P}$ values larger than 1 (Fig. 1a, model 1). The value of 1.24 indicates that 24% more land would be needed when using sole crops to extract the same amount of P from the soil as a unit area of intercrop. Accordingly, intercrops took up 3.67 ± 1.00 kg/ha more P than expected from the sole crops, with 59 out of 66 calculated $\mathrm{NE_P}$ values larger than 0 (Fig. 1b, model 2).

On average, intercrops had higher land use efficiency for biomass than sole crops, with 71 out of 82 calculated $\mathrm{LER_B}$ values larger than 1 and a mean $\mathrm{LER_B}$ of 1.27 ± 0.04 (Fig. 2a, model 3). The population standard deviation of $\mathrm{LER_B}$ was 0.35, reflecting substantial variation in the literature. A positive net effect for biomass ($\mathrm{NE_B} > 0$) was observed in 41 out of 50 cases, with a mean net effect of 1.00 ± 0.55 t per ha (Fig. 2b, model 4).

The average land equivalent ratio based on yield ($\mathrm{LER_Y}$) was 1.27 ± 0.06, with 57 out of 65 $\mathrm{LER_Y}$ values larger than 1 (Fig. 3a, model 5). The $\mathrm{NE_Y}$ was positive in 87% of data records with a mean yield gain of 1.66 ± 0.14 t per ha (Fig. 3b, model 6).

Effect of species combinations

Mixtures with maize or without maize

Species traits are expected to affect complementarity in intercrops. The net effect for P uptake of systems with maize was significantly greater than 0, but the net effect for P uptake for systems without maize was not significantly greater than 0 (Fig. 4b). Intercrops with maize had significantly higher $\mathrm{LER_B}$ than intercrops without maize (Fig. 4b; model 9, $P < 0.05$). Systems without maize did not show $\mathrm{LER_Y}$

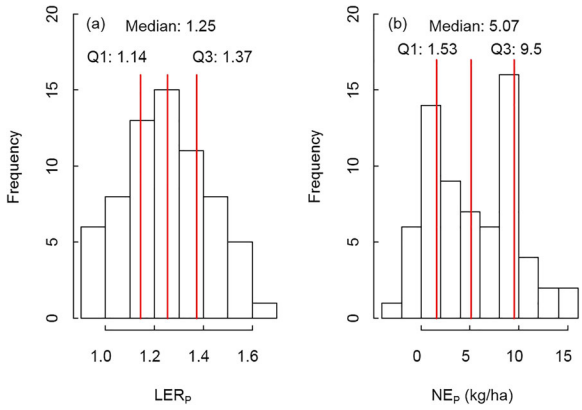

Fig. 1 Frequency distribution of the Land Equivalent Ratio for P uptake (LER_P) (**a**) and the net effect on P uptake (NE_P) (**b**) in cereal-legume intercropping. Vertical red lines in panels a and b indicate the first quartile (Q1), median and third (Q3) quartile of LER_P and NE_P

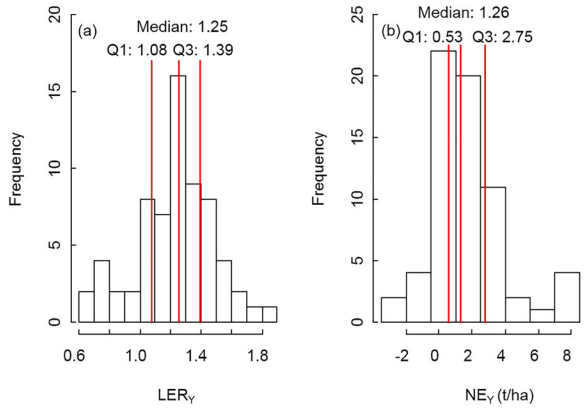

Fig. 3 Frequency distribution of the Land Equivalent Ratio for yield (LER_Y) (**a**) and the Net Effect on yield (NE_Y) (**b**) in cereal-legume intercropping. Vertical red lines in panels a and b indicate the first quartile (Q1), median and third (Q3) quartile of LER_Y and NE_Y

significantly greater than one or NE_Y significantly greater than zero, mostly due to few date records (Fig. 4e, f).

Effect of legume species on LER, NE of P uptake, biomass and yield

We hypothesized that intercrops comprising legumes with a stronger ability to mobilize sparingly soluble P in the soil (particularly faba bean and chickpea) would support greater increases in P uptake (indicated by LER_P and NE_P) than species with a weaker ability to mobilize P (e.g. soybean). LER_P was indeed significantly greater in systems with faba bean and chickpea than in systems with soybean (Fig. 5a; model 13). LER_B was significantly greater in intercrops with faba bean than in intercrops with soybean or chickpea (Fig. 5c, model 15). LER_Y was significantly greater in intercrops with faba bean or chickpea than in intercrops with soybean (Fig. 5e, model 17). There was no significant difference in any of the three net effects (for P uptake, biomass or yield) between intercrops with different legume species (Fig. 5b–f). Thus, intercrops with faba bean and chickpea had greater LER for P uptake, biomass and yield than intercrops with soybean, but in terms of net effect, no significant effect of legume species was found. Still, trends for NE were similar to those for LER.

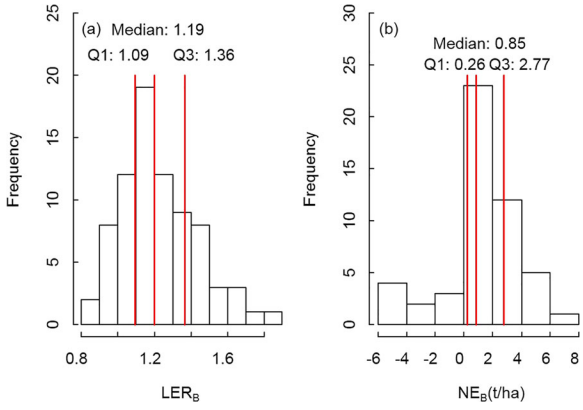

Fig. 2 Frequency distribution of the Land Equivalent Ratio (LER_B) (**a**) and the Net Effect (NE_B) on biomass (**b**) of cereal-legume intercropping. Vertical red lines in panels a and b indicate the first quartile (Q1), median and third (Q3) quartile of LER_B and NE_B

Effect of P fertilization

P fertilizer had a significant and positive effect on NE_P. This effect was characterized by a significant increase in the net effect of 3 kg P uptake/ha per 100 kg of P fertilizer per ha (model 19, $\beta_1 = 0.03$, $P = 0.026$, Fig. 6b). However, P fertilizer rate had no effect on LER_P (model 20, $\beta_1 = 0.03$, $P = 0.9$, Fig. 6a). We also found a significant negative effect of P fertilizer rate on LER_B (model 21, $\beta_1 = 0.11$, $P = 0.017$, Fig. 6c). LER_B decreased with 0.11 unit when the rate of P fertilizer was increased with 100 kg/ha. However, no response of NE_B to rate of P fertilizer was found (model 22, $\beta_1 = 0.03$, $P = 0.64$, Fig. 6d). The LER_Y and NE_Y showed no significant response to P input.

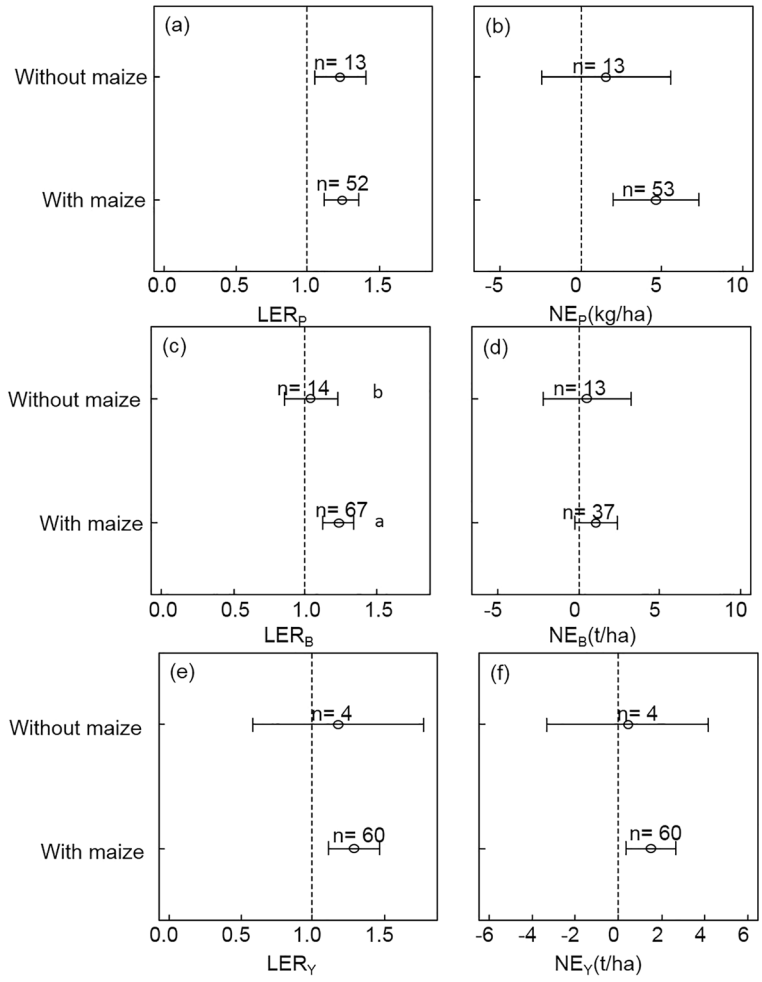

Fig. 4 Estimated means of LER_P (**a**), NE_P (**b**), LER_B (**c**), NE_B (**d**), LER_Y (**e**) and NE_Y (**f**) in mixtures with or without maize. The vertical dotted lines indicate the expected LER and NE in the absence of an intercropping effect, i.e. LER equal to 1 in panels on the left and NE equal to 0 in panels on the right; the horizontal bars represent 95% confidence intervals of estimates

Effect of N fertilization

The NE_P increased 3.0 ± 0.06 kg/ha per 100 kg of N fertilizer per ha (model 26, $\beta_1 = 0.03$, $P = 0.018$, Fig. 7b). N fertilizer rate had a significant and positive effect on NE_B (model 28, $\beta_1 = 0.01$, $P = 0.039$, Fig. 7d). The N fertilizer rate did not significantly affect the LER_Y and absolute yield gain (NE_Y) in intercrops.

Effect of TND

The absolute gain in P uptake (NE_P) due to intercropping increased by 6.87 kg/ha per unit TND (model 32, $\beta_1 = 6.87$, $P = 0.031$, Fig. 8b). The LER and NE for biomass and yield were independent of TND (results not shown).

Conversion efficiency of P uptake to biomass and yield (internal use efficiency)

Model selection using significance testing and AIC demonstrated a difference between mixtures and sole crops in the relationship between biomass and P uptake in both cereals and legumes (Fig. 9, Table S5, S6). The relationships were for cereals well described using the Monod model (model 1, Fig. 9a). Sole cereals had higher values for the initial slope and the maximum biomass per unit P uptake than intercropped cereals. Intercropped legumes and sole legumes also had a different biomass-P uptake relationship ($P < 0.001$; Table S5, S6). The best model for describing the relationship between biomass and P uptake in sole legumes was a curvilinear (model 1, Fig. 9b), while the best model in intercropped legumes was a linear model (model 2, Fig. 9b). The initial slope was higher in the

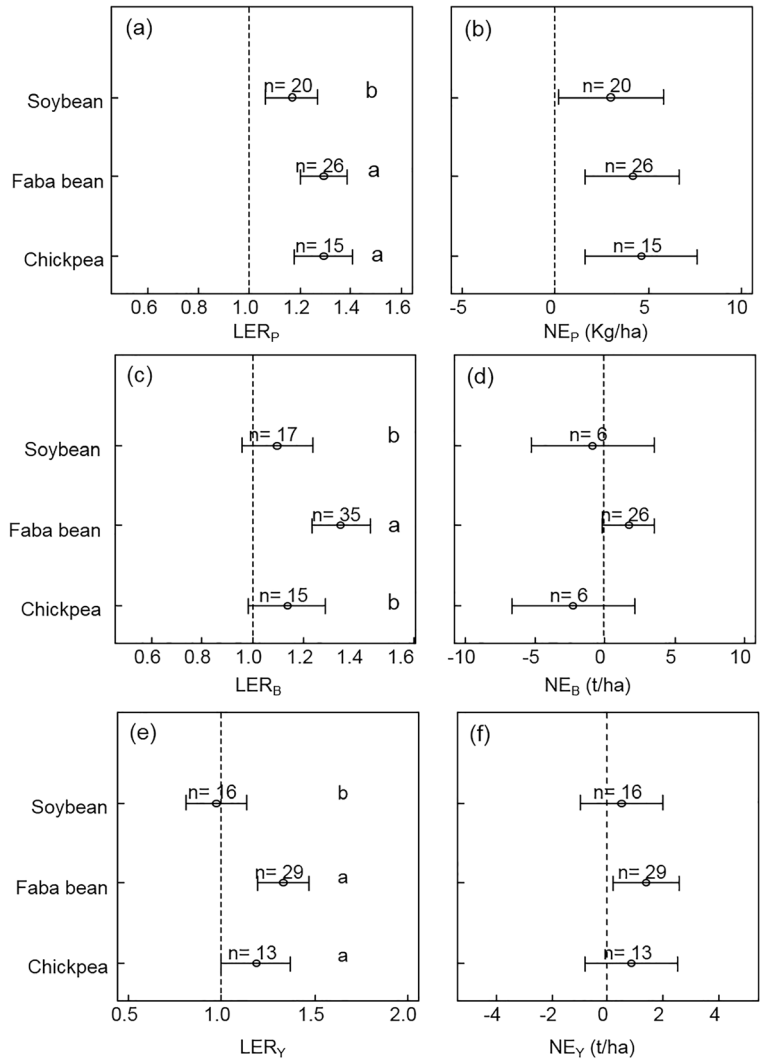

Fig. 5 Estimated means of LER_P (**a**), NE_P (**b**), LER_B (**c**), NE_B, (**d**), LER_Y (**e**) and NE_Y (**f**) across intercrops comprising different species of legumes. The vertical dotted lines indicate the expected LER and NE in the absence of an intercropping effect, i.e. LER equal to 1 in panels on the left and NE equal to 0 in panels on the right; the horizontal bars represent 95% confidence intervals

sole legumes than in the intercropped legume, while the maximum biomass reached in sole legumes was higher than in intercropped legumes (Fig. 9b).

Cereals had a greater increase in yield with increasing P uptake than legumes, but no difference in the Yield-P uptake relationship between sole crops and intercrops was found through model selection (Fig. 10, Table S4, S7). Both the initial slope and maximum yield were higher in the cereals than in the legumes (Fig. 10, Table S8).

The analysis shows that cereals produce more yield for the same P uptake than legumes, however, the conversion efficiency of P uptake to yield was not different for the two species when grown in sole crops or intercrops (Fig. 10, Table S7). The curvilinear responses of biomass and yield to P uptake indicate that aboveground biomass increase and grain yield are not so much constrained by P uptake (the focus of the synthesized studies) than by capture of other resources, e.g. light, water or N. Cereals had greater conversion efficiency of acquired P to biomass production and yield than legumes (Figs. 9, 10; Fig. S1, Table S6, S8).

Discussion

Results of this meta-analysis show that intercropping cereals and legumes substantially increases the uptake of P, both in a relative sense ($LER_P = 1.24 \pm 0.24$) and in an absolute sense ($NE_P = 3.67 \pm 1.00$ kg P/ha).

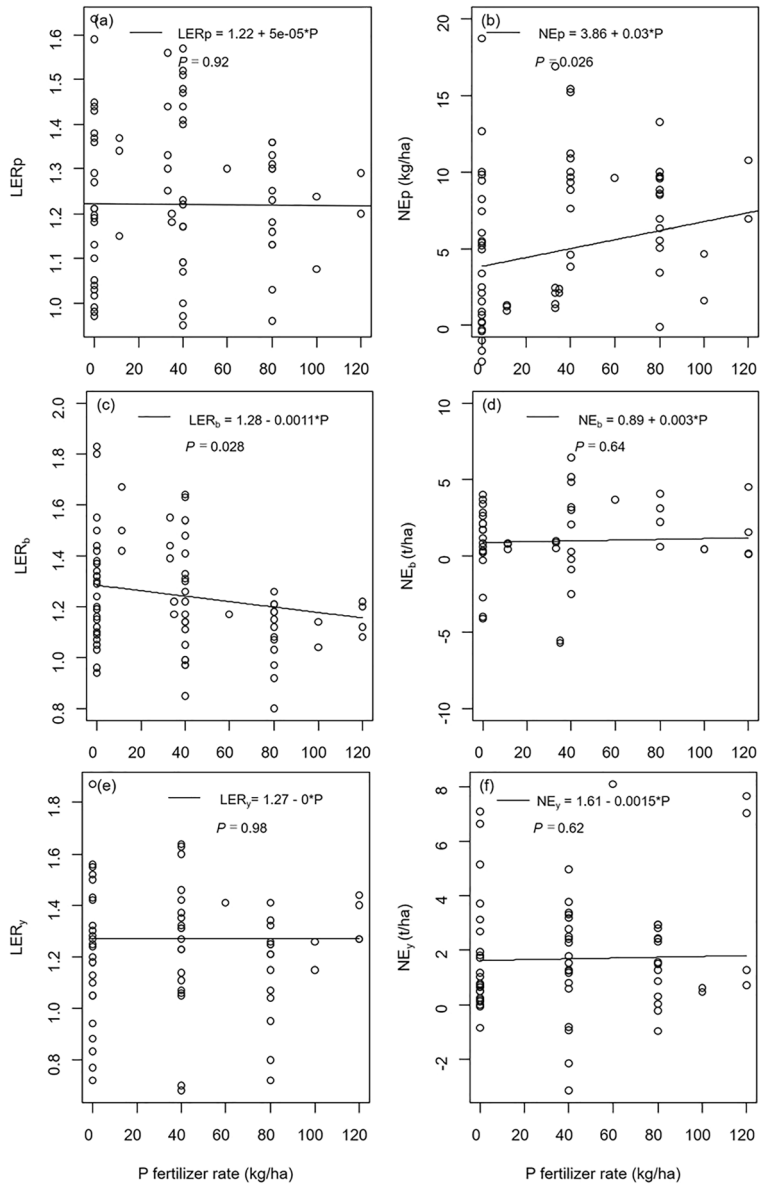

Fig. 6 Scatter plots of LER for P uptake (**a**), biomass (**c**) and yield (**e**) and NE for P uptake (**b**), biomass (**d**) and yield (**f**) against P fertilizer rate. The relationships were estimated by mixed models

Likewise, the land equivalent ratios for biomass and yield ($LER_B = 1.27 \pm 0.04$; $LER_Y = 1.27 \pm 0.06$) and the net effects for biomass and yield ($NE_B = 1.00 \pm 0.55$ t/ha; $NE_Y = 1.66 \pm 0.14$ t/ha) indicate substantial improvements in resource use efficiency due to intercropping. Thus, the increased P use efficiency is associated with a higher land use efficiency (LER > 1) and improved plant performance as indicated by positive net effects. Conversion efficiency of P uptake to biomass was lower in intercrops than in sole crops (Fig. 9) but the conversion efficiency of P uptake to yield was the same in intercrops and sole crops. Overall, the use efficiency of P was increased by 21% in intercropping, given LER_Y of 1.27 (1–1/1.27)*100 = 21% while the P input was the same in the sole crops and intercrop in all studies in the dataset (see below). Furthermore, we found that: 1) systems with maize supported a significantly higher LER for biomass production than systems without maize; 2) systems with faba bean had substantially higher P uptake efficiency and land use efficiency (LER_P, LER_B and LER_Y) than systems with soybean, supporting the notion that differences in P mobilizing ability between species translate to significant differences in intercrop performance; 3) absolute P uptake

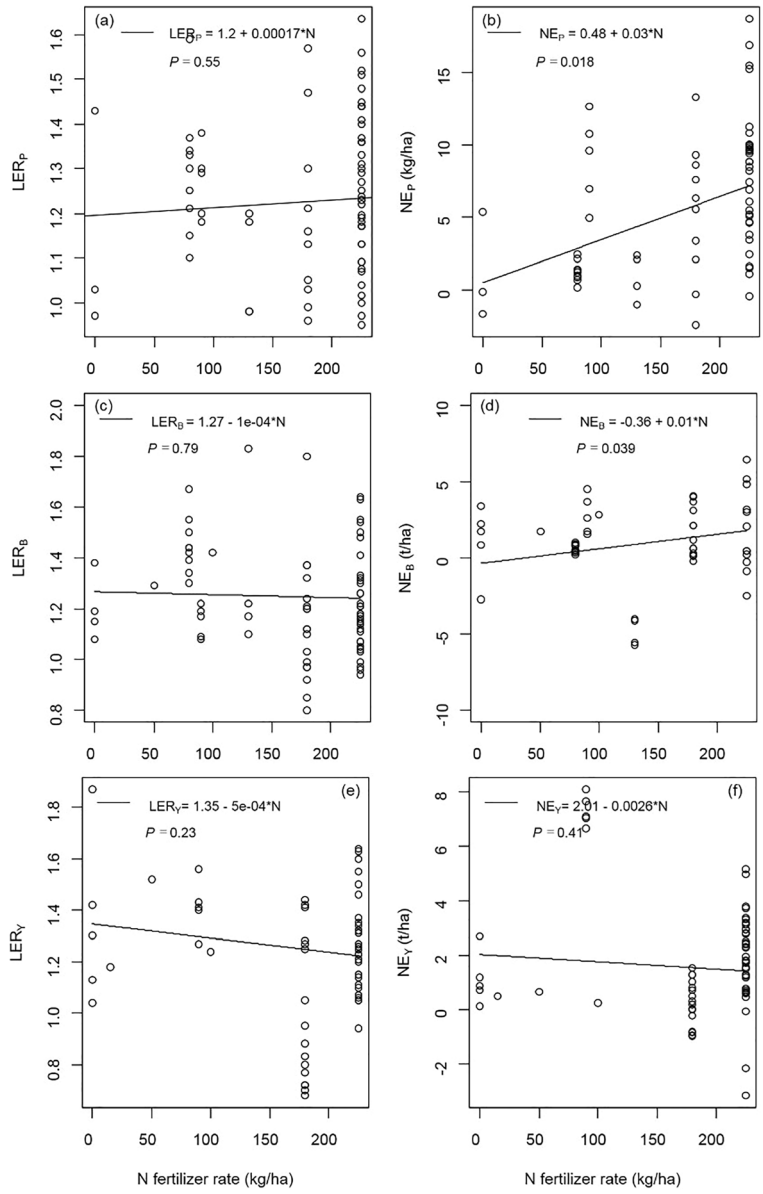

Fig. 7 Scatter plots and estimated regression lines relating to LER for P uptake (**a**), biomass (**c**) and yield (**e**) and NE for P uptake (**b**), biomass (**d**) and yield (**f**) to N fertilizer rate. The relationships were estimated by mixed models

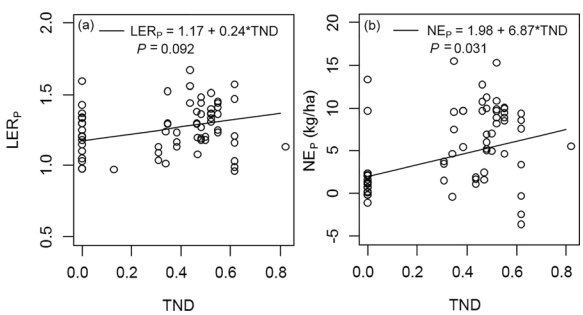

Fig. 8 Scatter plots and estimated regression lines relating to LER_P (**a**) and NE_P (**b**) to TND, fitted by mixed effects models

(NE_P) was positively correlated with N/P fertilizer input and TND, 4) the LER of biomass production decreased with P input.

P conversion efficiency in cereal-legume intercrops

Our analysis shows that the conversion efficiency of P uptake to biomass is significantly lower for species in mixtures than in sole crops, indicating growth limitations in intercrops due to other factors than P. These limitations could be related to competition for other resources, such as light or water. The study does not

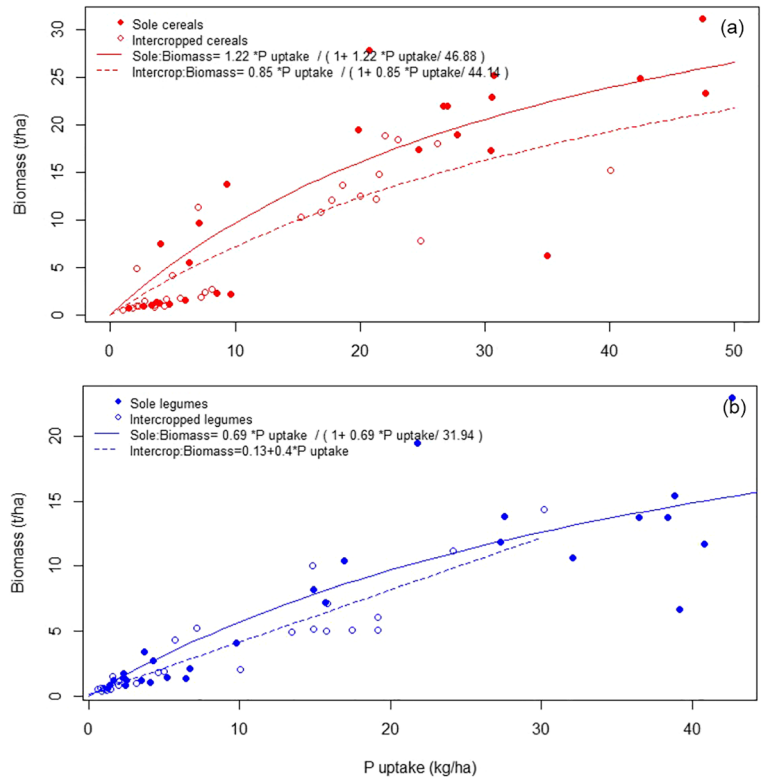

Fig. 9 Relationship between P uptake and biomass of cereals and legumes in intercrops and pure stands shows lower conversion efficiency of P uptake in intercrops as compared the pure stands for both cereals and legumes. The closed symbols represent observations in sole crops while open symbols (red for cereals and blue for legumes) represent observations in intercrops. Note the difference in the x and y-scales between the two panels, reflecting the overall greater P-uptake and biomass accumulation for cereals as compared to legumes

identify what is this other resource, but light or water are plausible candidates because in well-fertilized crops, yields are determined by light and water (Monteith 1977; Connor et al. 2011). In addition, soil management could influence the P uptake of legume-based intercropping systems, such as biochar amendments (Liu et al. 2017). Nevertheless, the conversion efficiency to yield was the same in intercropping and sole cropping, indicating that the allocation of biomass to yield is improved in intercropping as compared to pure stands. This confirms reports in the literature (Li et al. 2003, 2020b). Increased harvest index (proportion of biomass allocated to yield) is especially prevalent in relay intercrops in which component species do not fully compete during grain filling (Li et al. 2001; Xiang et al. 2012).

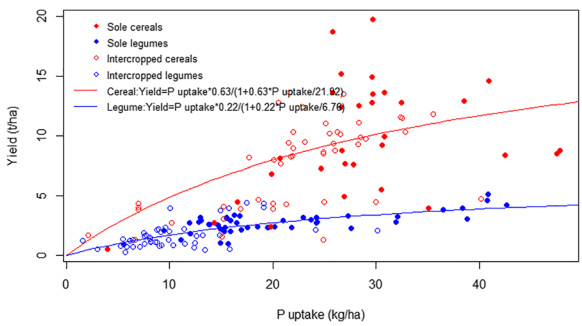

Fig. 10 Relationship between P uptake and yield of cereals and legumes in intercrops and pure stands shows no differences in P conversion efficiency to yield between intercrops and sole crops. Closed symbols represent observations in sole crops while open symbols (red for cereals and blue for legumes) represent observations in intercrops

Importance of P mobilization

We hypothesized that LER_P and NE_P would be different in intercrops with strongly P mobilizing species and species without this ability if P mobilization is an important driver for improved acquisition of P in intercropping. The data set had sufficient records to investigate the legume species effect for three legume species: soybean (*Glycine max*), faba bean (*Vicia faba*) and chickpea (*Cicer arietinum*), whereby the latter two are strongly P-mobilizing, whereas soybean has this capacity to a smaller extent. Insufficient data were found for other legume species, such as common bean (*Phaseolus vulgaris*), cowpea (*Vigna unguiculata*), pea (*Pisum sativum*), or peanut (*Arachis hypogaea*). The LER_P was largest for the P mobilizing species (faba

bean and chickpea) but it was also substantially greater than one for the non P-mobilizing species, soybean. This can be interpreted as evidence that P mobilization is important for increased P uptake in intercropping, but other mechanisms than P mobilization contribute also to improved P uptake in intercropping. This could, for instance, involve differences between species in rooting pattern or time of highest P demand (Hinsinger et al. 2011). The NE_P was greater than zero for all three species of legume, and no significant differences in net effect were detected between species, neither for P uptake, nor for biomass or yield. On the other hand, LER_B and LER_Y showed differences between species, with faba bean being highest, soybean lowest, and chickpea intermediate. The differences in LER_P, LER_B and LER_Y between species with or without P mobilizing ability, suggests that complementarity for P uptake can be a driver for yield increase, particularly under studies done at low P, as the differences in LER between P-mobilizing and P-non mobilizing species were not found for NE. Overall, we conclude that the analysis provides some evidence that P mobilization supports improved P uptake, growth and yield in intercropping, but it suggests that other mechanisms for complementarity also contribute, and the contribution of P mobilization is more important at low than at high production levels.

Effect of nutrient input

Cereal/legume intercrops had a higher land use efficiency (LER_B) than sole crops in low input agricultural systems, but this relative benefit decreased with increasing rate of P fertilizer (Fig. 6b). Likewise, it has been found that the comparative land use advantage of intercrops compared to sole crops, as measured by LER_Y, decreases with higher N fertilizer application when cereals and legumes are sown simultaneously (Yu et al. 2015; Li et al. 2020a, b). We found significant positive relationships between the net effects on P uptake and rate of N or P fertilizer input (Figs. 6b and 7b), indicating that intercropped species could take up more P as compared to sole crops with increasing P and N supply. This result clearly indicates that while relative advantages of intercropping may be large at low levels of input, the absolute advantage, measured in kg output per ha, may be larger with greater inputs. This observation is in line with findings reported by Li et al. (2020a, b), and provides the basis for considering intercropping as a possible component for an ecological intensification of agriculture, exploiting ecological phenomena, such as diversity effects, to amplify the use efficiency of agricultural inputs (Tilman 2020).

Does improved P uptake intercrops cause yield increase?

The similarity in the LERs for P uptake, biomass and yield raises the question whether improved P uptake in intercropping is a cause of yield increase or a consequence, or perhaps both. Evers et al. (2018) point to the importance of feedback loops in plant growth which makes it difficult to identify cause and effect in observational studies. For example, if a plant has access to more water, it may photosynthesize more, develop greater canopy, intercept more light and assimilate more carbon, then grow more and longer roots and acquire more P and N. Alternatively, a plant with better P mobilizing traits may acquire more P in a low-P environment than a species without such traits and as a result produce more or larger leaves and roots, leading to overall better growth. Finding the root cause in such interlocking feedback cycles of causality requires manipulative experiments, such as root barrier studies in which certain mechanisms are prevented from acting (Li et al. 2007; Faucon et al. 2017). Any complementarity that exists in an intercropping combination can enhance another complementarity by improving plant performance as the plant functions as an integrated whole. It is therefore totally expected that, if plant growth is enhanced in intercropping due to competitive relaxation for one or more resources (Li et al. 2020a), resource acquisition will be enhanced for multiple resources as a result of such feedback, with little chance to identify which resource complementarities were the original drivers and which were the consequence. As a matter of fact, the complementarity that is a driver at one phase of crop growth may be a consequence during another phase. We therefore cannot conclude from this analysis that complementarity for P uptake drives yield gains in intercropping. We can merely conclude that across the data available, the advantages of intercropping in terms of improved uptake of P mirror those for biomass and yield, as described in this and in other studies.

There are several methods to quantify P use efficiency in crop systems, such as the direct method (using isotope dilution or tracing), the difference method (comparing yield and/or P uptake with and without fertilizer),

the partial factor productivity method (yield per unit P applied), the physiological efficiency method (yield increment as a function of increment of P uptake) and the balance method (P uptake divided by P applied) (Syers et al. 2008). The above methods need to be adapted for use in intercropping because intercropping produces two crop outputs that need to be put on the same scale. This requires assumptions. Quantification of recovery requires levels of P input within the same trial. The majority of studies on P uptake and P use efficiency in intercropping do however not include P levels (but see Mei et al. 2012). Hence, quantification of comparative recovery of P in intercropping and pure stands is constrained, at least in a meta-analysis context.

Here, we used LER and NE to express the yields of component crops on a common scale. LER and LER_P are based on ratios of use efficiencies of land for producing yield and realizing P uptake, respectively. These relative metrics represent the ratio of the areas under sole cropping to the area under intercropping that give equal amounts of yield or P uptake. These metrics are sums of ratios of partial factor productivities (PFP) for land in intercrops and sole crops to realize yield or P uptake. We defined PfER as a metric to assess the relative fertilizer requirement of a given crop output produced in intercropping when using sole crops. PfER is the ratio of P applied to sole crops or intercrops for the same yield. Likewise, this ratio presents a sum of partial factor productivities in intercropping and sole crops, in this case PFPs for yield vs P input. The NE and NE_P simply sum the yield or P uptake of component crops in the mixture to aggregate the information across crop species. This metric loses the information which crop species is responsible for yield or P uptake, which is a limitation, though NE and NE_P could be calculated per species (which we did not do here). NE and NE_P give better insight in the absolute yield or P uptake in an intercropping system than LER or LER_P. Net effects metrics are therefore more useful to show absolute effects of intercropping at various levels of input at the field scale. However, because the species specific information is aggregated, this metric has a limitation to explore crop systems design at the multi-field level. For the latter purpose, relative metrics like LER, LER_P and PfER are more suitable. The topic of metrics for assessing use efficiency of inputs in intercropping warrants further discussion and conceptualization, and further discussion of the topic is needed to reach a consensus in the field on how efficiency may be quantified and how comparisons between intercropping systems and pure stands may be made. The current paper exemplifies a particular choice of metrics that we believe is useful, but we recognize that other choices would be possible and await further exploration.

In previous studies, researchers have used the water equivalent ratio (Mao et al. 2012; Tan et al. 2020) and nitrogen equivalent ratio (Xu et al. 2020; Li et al. 2020a, b) to express the intercropping advantage in terms of the required amount of a resource (water or nitrogen) for given yields of two species in an intercrop compared to pure stands. The water equivalent ratio (first used by Mao et al. 2012) represents the relative amount of water used in an intercrop and in sole crops to produce the same yields as produced in intercropping while the N fertilizer equivalent ratio (first used by Xu et al. 2020) represents the relative amount of N fertilizer used in sole crops to produce the same yields as produced in intercropping. With a water equivalent ratio or N fertilizer equivalent ratio greater than one, an intercropping system is more water or N use efficient than sole crops. From this meta-analysis we could determine the P fertilizer equivalent ratio:

$$\mathrm{PfER} = \frac{\mathrm{Pfert}_1 \times Y_1/M_1 + \mathrm{Pfert}_2 \times Y_2/M_2}{\mathrm{Pfert}_{\mathrm{IC}}} = \frac{\mathrm{Y}_1}{\mathrm{M}_1} \times \frac{\mathrm{Pfert}_1}{\mathrm{Pfert}_{\mathrm{IC}}} + \frac{\mathrm{Y}_2}{\mathrm{M}_2} \times \frac{\mathrm{Pfert}_2}{\mathrm{Pfert}_{\mathrm{IC}}} \quad (7)$$

where $\mathrm{Pfert}_{\mathrm{IC}}$ is P-fertilizer dose given to the intercrop (kg P per unit of total area of the intercrop) and Pfert_1 and Pfert_2 are the P-fertilizer doses given to the sole crops (kg P per unit area of the sole crop). In all of the 17 studies in the database, the P fertilizer amount in the sole crops was equal to that in the intercrop. Therefore, in this special case, the P fertilizer equivalent ratio (PfER) is equal to the land use efficiency, i.e. the LER_Y. The land equivalent ratio of 1.27 ± 0.06 found in the current study indicates that P fertilizer is used 21% more efficiently in intercrops than in sole crops (1 unit fertilizer in intercropping versus 1.27 units in sole crops for the same yields, i.e. a reduction of 21% in intercropping compared to sole crops). This finding is important given the finite nature of the global P resource (Cordell et al. 2009).

Power of the statistical analysis

The power of a data analysis depends on the differences one aims to detect, the variability in the data,

and the size of the data set (Bolker 2008). When statistical power is defined as the probability to reject a null hypothesis, it will increase with the true difference that exists, decrease with the variability in the data, and increase again with the amount of data. Here, we did not define which size of effect we wanted to detect; our aim was to characterize effect sizes (LER and NE for P uptake, biomass and yield), their mean and variation, and their dependency on species traits and management factors such as N input, P input and differences in growing period between species. Thus, the definition of power is not strictly applicable. However, it is applicable when one defines power as the ability to detect patterns in the data. As our literature search specifically targeted papers with information on P acquisition in intercropping, we found only 17 sources meeting the requirement. Thus, our dataset was fairly small compared to datasets used in other meta-analyses on intercropping in the literature (Yu et al. 2015; Martin-Guay et al. 2018; Xu et al. 2020; Li et al. 2020a, b), which limits the ability to detect patterns. Some of our analyses (notably for metrics related to biomass and yield) did not require the P uptake information and many more publications would have qualified if we had not used the inclusion criterion that source publication should have data on P uptake; however, the discovery of relationships between improved P uptake in intercropping and higher biomass and yield would not be helped by relaxing the inclusion criteria, and we therefore refrained from extending the dataset with records that did not have information on P acquisition. Despite the limitations in the data, we were able to demonstrate in this study that the LER for P uptake was 1.24 ± 0.04 while the net effect for P uptake was 3.67 ± 1.00 kg P per ha. This is to our knowledge the first report of these metrics in the literature. We also found that the PfER, an indicator for P fertilizer use efficiency was 1.24 ± 0.04, an indication that P use efficiency if substantially improved in intercropping. The values of LER for P uptake were similar to those reported for biomass and yield in our paper and in other meta-analyses for yield in the literature (Yu et al. 2015; Martin-Guay et al. 2018; Xu et al. 2020; Li et al. 2020a, b), confirming that the effect sizes identified in this study are in line with those of meta-analyses on yield that were based on more data.

Conclusions

This meta-analysis shows that intercropping is an effective method to achieve substantial increases in P uptake efficiency in agriculture. The internal use efficiency of P for biomass production was decreased in intercropping but the internal use efficiency of P for yield was not affected by intercropping, such that overall use efficiency, as the product of uptake efficiency and internal use efficiency was substantially increased by intercropping. The land equivalent ratio for P uptake did not change with P supply, but the net effect of intercropping on P uptake increased with P and N supply, indicating that intercropping supported improvements in P-use efficiency across levels of P input, but more so in an absolute sense at higher input levels. The use efficiency of applied P fertilizer was improved by intercropping, primarily by concentrating production on less land with the same P content in yield in sole crops and intercrops. The results confirm the notion that intercropping provides opportunities for enhancing resource use efficiency in agriculture.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11104-020-04768-x.

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