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REGULAR ARTICLE

Interspecific root interactions increase maize yields in intercropping with different companion crops

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Abstract

Background: Intercropping is assumed to increase food production while reducing fertilizer needs and environmental impacts of crop production.

Aims: We aimed to (1) investigate the effects of intercropping on yields and nutrient uptake of maize, and (2) determine the relative contributions of above- and belowground interspecific interactions ($RC_{above/below}$) to these effects.

Methods: We conducted a 2-year, small-scale field experiment with maize grown either in monocropping or intercropped with faba bean, soy, blue lupin, or white mustard as companion crop. We included a treatment in which interspecific root interactions were restricted due to barriers in the soil. Maize and companion crops were analyzed for yields, and maize additionally for nutrient uptake. Maize partial land equivalent ratios (pLER), partial nitrogen and phosphorus equivalent ratios (pNER, pPER), and $RC_{above/below}$ were calculated.

Results: Intercropping resulted in a similar productivity of maize as in monocropping on an area basis. Maize pLER, pNER, and pPER were larger than 1.0 in several species combinations, indicating a positive effect of intercropping on maize yields and N and P uptake. Interspecific root interactions accounted for 62–85% of the maize yield increase in legume/maize intercropping, but for only 22% in mustard/maize intercropping.

Conclusion: Our results indicate that intercropping is beneficial for crop production since it increases maize yields and N and P uptake of maize plants, and it also provides yields of a companion crop. A substantial part of these positive effects can be attributed to interspecific root interactions.

KEYWORDS
mixed cropping, nitrogen uptake, phosphorus uptake, root partitioning, species interactions

1 | INTRODUCTION

Intensive agriculture has been increasingly questioned during the last years as it boosts global climate change, land degradation, biodiversity loss, and resource depletion which might result in severe food security and food sovereignty threats for a growing world population (Campbell et al., 2017). The major challenge of agriculture is, therefore, to increase food production while simultaneously reducing environmental burden, resource use, and social threats (Pe'er et al., 2020). Consequently, there is an urgent need to identify and understand agricultural practices that promote increased plant biomass and yield production, thereby lowering environmental problems. Recent research has shown that intercropping (IC) is one of the practices that increases yields and at the same time enhances the crop quality and reduces environmental problems (Duchene et al., 2017; Li et al., 2014).

IC refers to ancient agricultural practices that involve the simultaneous cultivation of at least two crop species or genotypes in close proximity. It is a common practice in peasant farming, and increasingly also in organic farming worldwide (Brooker et al., 2015; Li et al., 2014). IC is commonly assumed to increase above- and belowground biodiversity, soil and water conservation, as well as resilience against diseases, pests, and abiotic stresses (Ehrmann & Ritz, 2014; Malézieux et al., 2009).

IC has also been shown to result in an overall yield increase relative to monocropping which is referred to as overyielding. This is often measured by the land equivalent ratio (LER) (Duchene et al., 2017; Li et al., 2013). LER is defined as the relative land area needed for monocropping to produce the yields attained by IC. It is calculated as the sum of the partial land equivalent ratios (pLER) of the two crop species (Mead & Willey, 1980). If it exceeds 1.0, IC has a positive effect on the area of land needed to produce a given yield, and a larger area is needed in monocropping compared to IC for the same biomass production and yield. Meta-analyses and reviews summarizing between 58 and 939 observations of up to 126 IC studies found a mean LER of 1.17 to 1.30 (Bedoussac et al., 2015; Martin-Guay et al., 2018; Yu et al., 2016). Specifically, for soy/maize IC, a mean LER of 1.32 was reported (Xu et al., 2020). However, it is still a matter of debate under which conditions and with which companion crops IC results in overyielding since single LER ranged between 0.5 and > 4.0 in a global meta-analysis (Martin-Guay et al., 2018). Moreover, the underlying mechanisms and the contribution of root interactions to overyielding in IC are not fully understood yet.

Overyielding in IC is supposed to result from positive above- and belowground interspecific plant interactions (Li et al., 2014; Zhang et al., 2001). Positive aboveground interactions may be associated with the light and temperature environment being changed through IC which results in a more efficient light interception of the intercropped species (Lv et al., 2014; Zou et al., 2019). Positive belowground interactions are mostly attributed to a complementary resource use and interspecific facilitation processes resulting in a more efficient acquisition of macronutrients, such as nitrogen (N) and phosphorus (P), microelements, such as iron and zinc, and water by the intercropped species (Chen et al., 2018; Xue et al., 2016). These complementarity and facilitation processes have mostly been studied in legume/cereal IC systems, since legumes can increase N availability through symbiotic N_2 fixation and are also assumed to contribute substantially to plant P acquisition (Li et al., 2013; Xue et al., 2016).

Many IC studies reported that belowground interspecific interactions are more important for overyielding than aboveground interactions (Duchene et al., 2017; Li et al., 2014). However, only a few studies identified the relative contributions (RCs) of above- and belowground interspecific interactions to overyielding in IC, so far. To distinguish between above- and belowground effects, so-called separation or partitioning techniques have been used. They were first established by Donald (1958) who fully partitioned root (belowground) and shoot (aboveground) effects using barriers. Although the partitioning techniques have been used repeatedly since then, a quantification of the RCs of above- and belowground interspecific interactions to overyielding remains rare and inconsistent regarding calculation and findings (Chen et al., 2015; Zhang et al., 2001). Additional research is, therefore, needed to identify the RCs of above- and belowground interspecific interactions to overyielding.

This study aimed to (1) investigate the effects of IC (with four companion crops) on maize aboveground biomass (AGB), grain yields, and nutrient uptake as well as (2) determine the RCs of above- and belowground interspecific interactions to these effects. For this purpose, we conducted a small-scale field experiment for two consecutive years with maize-based IC having a root barrier treatment to (partly) restrict root interactions in the second year. We used maize (*Zea mays* L.) as the main crop as it is one of the most important crops for food production worldwide (Xu et al., 2020). As companion crops, we used three different legumes with contrasting root functional traits and differences in nutrient acquisition mechanisms (Hallama et al., 2019; Wen et al., 2019): faba bean (*Vicia faba* L.) forming taproots, soy [*Glycine max* (L.) Merr.] with a fibrous root system, and blue lupin (*Lupinus angustifolius* L.) forming also taproots but without mycorrhizal symbioses. In addition to these legumes, we used white mustard (*Sinapis alba* L.) as non-leguminous Brassicaceae species which is often cultivated as a cover crop. We decided for an experiment on a small scale because IC is mostly used by peasant farmers rather than on large fields. We hypothesized that (1) AGB production and grain yields of maize are enhanced in IC compared to monocropping, (2) N and P uptake of maize AGB as well as grain yields are higher in IC than in monocropping, (3) the effects of IC on maize AGB, maize grain yields, and maize N and P uptake are stronger in legume/maize than in mustard/maize IC, and (4) positive belowground interspecific interactions contribute more to these effects than aboveground interactions. As our study and the hypotheses focus on the IC effects on maize as the main crop, we decided to have only a maize monocropping control, whereas companion crops were not cultivated in monocropping.

2 | MATERIAL AND METHODS

2.1 | Experimental setup

The field experiment was conducted at the University of Bayreuth (Germany) from May to August in 2018 and 2019. The site is located in the southeast of Bayreuth (49°55′17′′ N, 11°35′17′′ E). The mean annual rainfall is 756 mm, and the mean annual temperature is 8.0°C (Lüers et al., 2014). The soil texture is loamy sand (10% clay, 23% silt, 67% sand). In the upper 15 cm, the following soil chemical properties were determined: pH 6.9, 23.9 g total C kg^{-1} soil, 2.2 g total N kg^{-1} soil, and 0.5 g plant available P kg^{-1} soil as the sum of water- and $NaHCO_3$-extractable P.

In the first year, five blocks subdivided into six plots (2.5 × 1.7 m) were cultivated in row IC (Supporting information 1), where maize (*Zea mays* L. cv. Damaun, ReinSaat KG, Austria) was intercropped

FIGURE 1 Photos of the field experiment in 2018 and 2019 showing the steaming process as part of the field preparation (A), the plot preparation in late April 2018 (B), plant interactions in the different species combinations in late June 2018 (C–G), plots before harvest in August 2018 (H), plot preparation with root barriers in late April 2019 (I), and plots before harvest in August 2019 (J)

with one of the following companion crops: faba bean (*Vicia faba* L. cv. Hangdown, ReinSaat KG, Austria), soy [*Gylcine max* (L.) Merr. cv. Green Shell, ReinSaat KG, Austria], blue lupin (*Lupinus angustifolius* L. cv. Sonet, Templiner Kräutergarten, Germany), or white mustard (*Sinapis alba* L., ReinSaat KG, Austria). As a control, maize was also cultivated in monocropping (Figure 1C). Each plot consisted of eight alternating rows of maize and companion crop with 12 plants per row having a distance of 20 cm between plants and rows (Figure 2A). As we used a replacement design, the distance between plants and rows was 20 cm in maize monocropping as well, thus, the monocropping plots had twice the number of maize plants as the IC plots (Figure 2A). Each species combination was replicated five times, summing up to a total of 25 plots (Supporting information 1). Before seeding, the soil was prepared by plowing, rotary tillage, and surface steaming. Surface steaming was done by inducing hot steam between the soil surface and a plastic sheet on top of the soil for 4 h (Figure 1A). This was mostly done to kill weed seeds and avoid the application of herbicides. All seeds except mustard were soaked in water for 24 h. Soy and lupin seeds were inoculated with commercial *Bradyrhizobium sp.* inoculants before seeding (lupin: *Bradyrhizobium sp. Lupinus*, Templiner Kräutergarten, Germany; soy:

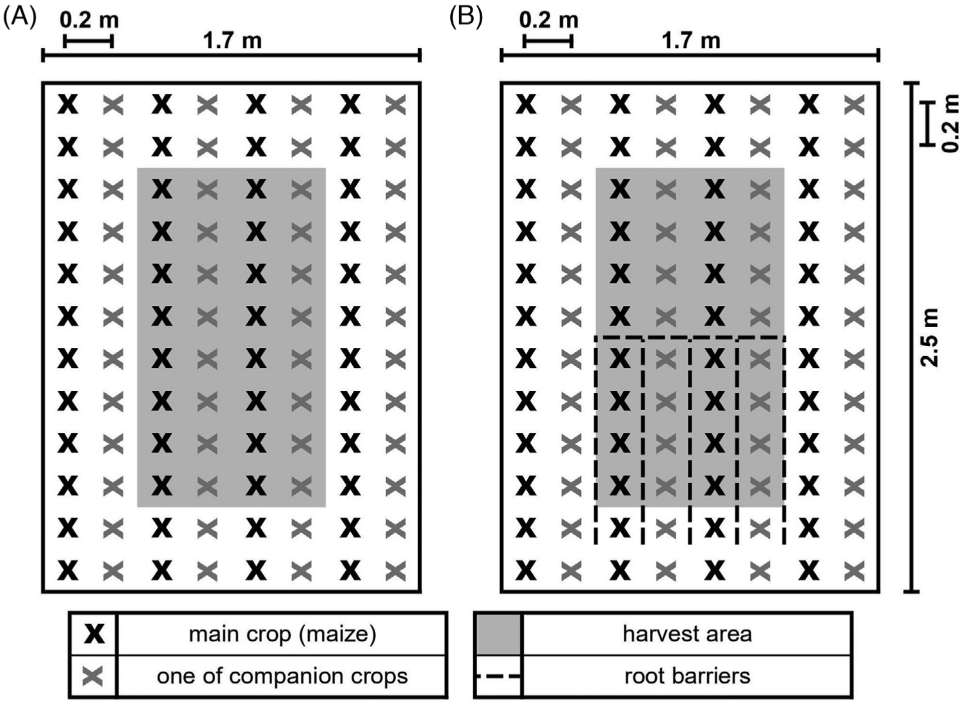

FIGURE 2 Experimental setup of the plots in 2018 without root barriers (A) and in 2019 with and without root barriers (B)

LegumeFix® Soya, Legume Technology Ltd, UK). First, faba bean was sown manually on April 18th 2018 because we expected it to grow more slowly and intended to harvest all plants at the same time. All other seeds were then sown manually 3 weeks later, on May 8th 2018. The five blocks were surrounded by a wire netting to prevent feeding damage (Figure 1C–G). As the summer 2018 was very dry, the plots were weekly watered by hand with a watering spray lance, whenever necessary to avoid competition for water between the plants. All plots were watered for the same period of time until water started to accumulate at the soil surface. After watering all plots once, the watering procedure was repeated twice to ensure that plants received enough water. At the end of the growing season, ten plants per species from the four innermost rows of each plot were harvested (Figure 2A). In the maize monocropping, 20 maize plants were harvested per plot.

In the second year, the same block design was used to cultivate maize (*Zea mays* L. cv. Golden Bantam, Bingenheimer Saatgut AG, Germany) in row IC with faba bean (*Vicia faba* L. cv. Hangdown, Bingenheimer Saatgut AG, Germany), soy [*Gylcine max* (L.) Merr. cv. Lica, Naturland, Germany], blue lupin (*Lupinus angustifolius* L. cv. Rumba, Templiner Kräutergarten, Germany), or white mustard (*Sinapis alba* L., Bingenheimer Saatgut AG, Germany) or in monocropping. In addition, in one half of each plot (*i.e.*, six plants in each row) root barriers according to Zhang et al. (2001) were installed to separate the plant rows to prevent interspecific root interactions between maize and companion crops (Figure 2B). For this purpose, impermeable plastic sheets made of plexiglass (3 mm thick) were inserted into the soil between the rows to a depth of 50 cm prior to sowing (Figure 1I). Root barriers were also installed in the maize monocropping plots to check whether the root barriers influenced the maize AGB. The lupin/maize IC was done without such a root barrier treatment due to time constraints during installation. All seeds were simultaneously sown by hand on May 8th and 9th, 2019. All seeds except for mustard were soaked in water for 24 h prior to sowing. As the summer 2019 was also very dry, the plots were regularly watered. At the end of the growing season, ten plants per species and plot were harvested (Figure 2B). Five of them were harvested in the plot part with root barriers (rb) and five in the part with no barriers (nb). All plants were analyzed for AGB production; maize plants were also analyzed for N and P uptake.

2.2 | Biomass analyses

Harvested companion crops were dried at 60°C and weighed. Harvested maize plants were divided into leaves, shoots, and grains, dried at 60°C and weighed. Dried leaves and shoots were cut with scissors, and subsamples of maize leaves, shoots, and grains were milled (MM400, Retsch, Haan, Germany). Subsamples were then analyzed for total N concentrations using an element analyzer (Vario Max, Elementar, Hanau, Germany). For total P concentrations, 100 mg of each subsample were dissolved in 1 mL of concentrated nitric acid at 170°C for 12 h (pressure digestion) before being analyzed with an inductively coupled plasma-optical emission spectroscopy (Vista-Pro radial, Varian Inc., Palo Alto, USA).

2.3 | Calculations

Maize AGB was calculated as the sum of the dry mass of leaves, shoots, and grains per single plant. For scaling up the AGB production to the square meter, maize AGB was multiplied by 12.5 (as 12.5 maize plants were cultivated per square meter in IC), or by 25 in the case of maize monocropping. Maize leaf, shoot, and grain N and P uptake was calculated by multiplying the dry mass of leaves, shoots, and grains with the corresponding N and P concentrations. Total maize N and P uptake per square meter was calculated as the sum of leaf, shoot, and grain N and P uptake.

The pLER of maize grain yield per square meter was calculated according to Mead and Willey (1980), as follows:

$$pLER = \frac{grain\ yield_{intercropping}\ \left(g\ m^{-2}\right)}{mean\ grain\ yield_{monocropping}\ \left(g\ m^{-2}\right)}. \tag{1}$$

Similarly, maize AGB N and P uptake was used to calculate partial N and P equivalent ratios (pNER and pPER; Equations 2 and 3) as a measure of the increase in N and P uptake of maize in IC compared to monocropping, as follows:

$$pNER = \frac{grain\ yield\ N_{intercropping}\ \left(g\ m^{-2}\right)}{mean\ grain\ yield\ N_{monocropping}\ \left(g\ m^{-2}\right)}, \tag{2}$$

$$pPER = \frac{grain\ yield\ P_{intercropping}\ \left(g\ m^{-2}\right)}{mean\ grain\ yield\ P_{monocropping}\ \left(g\ m^{-2}\right)}. \tag{3}$$

We further calculated the RC of above- (RC_{above}) and belowground (RC_{below}) interspecific interactions to maize yield increases in the different IC systems. For this purpose, we first calculated the relative yield increases (RYI) of single maize plants in IC compared to monocropping both with root barriers (rb; Equation 4) and with no root barriers (nb; Equation 5), as follows:

$$RYI1 = \frac{mean\ grain\ yield_{intercropping}\ (rb)}{mean\ grain\ yield_{monocropping}\ (rb)} - 1, \tag{4}$$

$$RYI2 = \frac{mean\ grain\ yield_{intercropping}\ (nb)}{mean\ grain\ yield_{monocropping}\ (nb)} - 1. \tag{5}$$

In the rb treatment, interspecific root interactions were largely excluded, thus, we assume that the RYI in this treatment is only derived from aboveground interspecific interactions. In the nb treatment , we assume that the RYI is derived from both aboveground and belowground interspecific interactions. The RCs were, therefore, calculated, as follows:

$$RC_{above} = \frac{RYI1}{RYI2} \times 100\%, \tag{6}$$

$$RC_{below} = 100\% - RC_{above}. \tag{7}$$

The calculation of RC also accounted for the small influence that the root barrier installation had on maize grain yields.

2.4 | Statistics

Data were tested separately for significant differences between species combinations, years, and barrier treatments. For this purpose, normality was checked with Shapiro–Wilk normality tests, and homogeneity of variances was tested with Levene's tests. Where normality and homogeneity assumptions were met, analyses of variance (ANOVA) followed by Tukey's post-hoc tests (Tukey HSD) were used to identify significant differences between species combinations, years, or barrier treatments. Where normality and homogeneity assumptions were not met, log-transformations of data were performed prior to ANOVA and Tukey HSD. All statistical analyses were performed in R (version 3.5.2; R Core Team, 2018) using the packages *agricolae* (version 1.3-2; de Mendiburu, 2020), *car* (version 3.0-7; Fox & Weisberg, 2019), *dplyr* (version 0.8.5; Wickham et al., 2020), and *ggplot2* (version 3.3.0; Wickham, 2016).

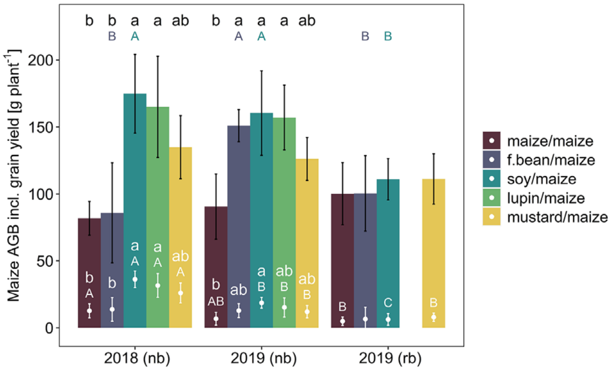

FIGURE 3 Aboveground biomass (AGB) per maize plant as the sum of grain yield and nongrain biomass, harvested in 2018 (no root barrier; nb) and 2019 (nb or with root barrier; rb). Columns show AGB means, white dots show grain yield means, and error bars indicate standard deviations ($n = 5$). A one-way ANOVA was conducted followed by Tukey post-hoc test. Lowercase letters indicate significant differences ($p < 0.05$) in the maize AGB (black lowercase letters) and grain yields (white lowercase letters) between the species combinations, tested separately for each year and barrier treatment. Capital letters indicate significant differences ($p < 0.05$) in the maize AGB (colored capital letters) and grain yields (white capital letters) between years and barrier treatments, tested separately for each species combination. Absence of letters indicates that there were no significant differences

3 | RESULTS

3.1 | Biomass and grain yields

On a single plant basis, maize AGB ranged between 81.8 ± 12.6 g plant^{-1} (maize monocropping, 2018) and 174.8 ± 29.4 g plant^{-1} (soy/maize IC, 2018) across all species combinations, years, and barrier treatments (Figure 3). Maize grain yields ranged between 4.9 ± 3.2 g plant^{-1} (maize monocropping, 2019, rb) and 36.2 ± 6.2 g plant^{-1} (soy/maize IC, 2018) across all species combinations, years, and barrier treatments (Figure 3). In 2018, maize AGB and grain yields were significantly higher in soy/maize and lupin/maize IC than in maize monocropping. In 2019, maize AGB was significantly higher in faba bean/maize, soy/maize, and lupin/maize IC than in

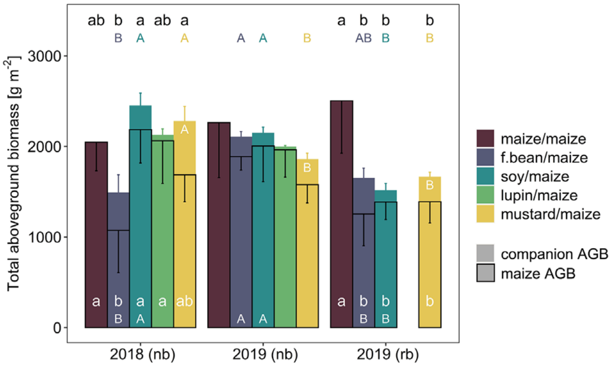

FIGURE 4 Total aboveground biomass (AGB) per area as the sum of maize AGB (black-rimmed) and companion AGB (rim-less on top), harvested in 2018 (no root barrier; nb) and 2019 (nb or with root barrier; rb). Columns show means and error bars indicate standard deviations ($n = 5$). A one-way ANOVA was conducted followed by Tukey post-hoc test. Lowercase letters indicate significant differences ($p < 0.05$) in the total AGB (sum of maize and companion AGB; black lowercase letters) and in the maize AGB (white lowercase letters) between the species combinations, tested separately for each year and barrier treatment. Capital letters indicate significant differences ($p < 0.05$) in the total AGB (colored capital letters), in the maize AGB (white capital letters; bottom of columns), and in the companion AGB (white capital letters; top of columns) between years and barrier treatments, tested separately for each species combination. Absence of letters indicates that there were no significant differences

maize monocropping (nb), whereas maize grain yields were significantly higher only in soy/maize IC compared to maize monocropping (nb). In 2019, maize AGB in faba bean/maize and soy/maize IC, and maize grain yields in soy/maize IC were significantly higher in the nb than in the rb treatment. Maize AGB and grain yields in maize monocropping did not differ significantly between nb and rb in 2019, showing that the installation of the root barriers did not negatively impact maize growth. In the rb treatment, maize AGB and grain yields showed no significant differences between the species combinations.

In contrast, on an area basis we observed a significantly lower maize AGB in faba bean/maize IC than in maize monocropping and in soy/maize and lupin/maize IC in 2018 (Figure 4). The total biomass (as the sum of maize and companion AGB) was significantly higher in soy/maize IC than in faba bean/maize IC in 2018. In the rb treatment in 2019, maize AGB and total biomass were significantly higher in maize monocropping than in all IC systems. In the nb treatment, we found no significant differences in maize AGB and total biomass between the species combinations in 2019. Maize AGB and total biomass in faba bean/maize IC were significantly higher in 2019 (nb) than in 2018. Maize AGB in faba bean/maize IC in 2019 was also significantly higher in the nb than in the rb treatment. Maize AGB and total biomass in soy/maize IC were significantly higher in the nb treatment (both years) than in the rb treatment. The companion crop AGB was not affected by year or barrier treatments, except for mustard, showing a significantly higher AGB in 2018 than in 2019.

The pLER of maize grain yields in IC were higher than 0.5 in all species combinations in both years, except for faba bean/maize IC in 2018 (Table 1). They were even larger than 1.0 in soy/maize and lupin/maize IC in both years (nb). The pLER was significantly higher in soy/maize and lupin/maize IC than in faba bean/maize IC in 2018. We found no significant difference between the species combinations in 2019 for both barrier treatments. The pLER of maize grain yields in soy/maize IC was significantly higher in the nb treatment (both years) than in the rb treatment.

Yield increases in mustard/maize IC resulted mostly (78%) from aboveground interspecific interactions (Table 2). In contrast, yield increases in soy/maize and faba bean/maize IC were caused mostly by belowground interspecific interactions, accounting for 85% of yield increases in soy/maize IC and for 62% in faba bean/maize IC.

3.2 | Nutrients (N and P)

On a single plant basis, N uptake of maize AGB and grains was significantly higher in soy/maize and lupin/maize IC than in maize monocropping in 2018 (Table 3, Supporting information 2). N uptake of maize AGB and grains was also significantly higher in faba bean/maize (AGB), soy/maize (grains), and lupin/maize IC (AGB) than in maize monocropping in 2019 (nb). On an area basis, however, we found no significant differences in N uptake of maize AGB and grains between monocropping and IC. N uptake of maize AGB and grains was significantly higher in soy/maize IC (AGB and grains) and in lupin/maize IC (grains) than in faba bean/maize IC in 2018. Maize N uptake in soy/maize and lupin/maize IC (AGB and grains), and in mustard/maize IC (grains) were significantly higher in 2018 than in 2019. Similarly, N concentrations of maize AGB in all species combinations were significantly higher in 2018 than in 2019, except for mustard/maize IC in 2019 (nb), but showed no significant differences between the species combinations (Supporting information 1). N concentrations of maize grain yields did not differ significantly between species combinations, years, and barrier treatments, except that they were significantly higher in mustard/maize IC than in maize monocropping in 2019 (nb).

On a single plant basis, P uptake of maize AGB and grains was significantly higher in soy/maize and lupin/maize IC than in maize monocropping in 2018 (Table 3, Supporting information 1). P uptake of maize AGB and grains was also significantly higher in soy/maize (AGB and grains) and lupin/maize IC (AGB) than in maize monocropping in 2019 (nb). On an area basis, however, we found no significant differences in P uptake of maize AGB and grains between monocropping and IC in both years (nb), except for faba bean/maize IC in 2018. In the rb treatment, P uptake of maize AGB was significantly higher in maize monocropping than in IC (Supporting information 1). P uptake of maize AGB and grains in soy/maize IC (both years; AGB and grains), and in faba bean/maize IC (2019; AGB) was significantly higher in the nb than in the rb treatment. P concentrations of maize AGB did not differ significantly between species combinations, years, and barrier treatments (Supporting information 1). P concentrations of maize grains did not differ significantly between species combinations, but were

TABLE 1 Partial land equivalent ratios (pLER) and partial nitrogen and phosphorus equivalent ratios (pNER and pPER) of maize grain yields, calculated for maize harvested in 2018 (no root barrier; nb) and 2019 (nb or with root barrier; rb)

		pLER	pNER	pPER
Faba bean/maize	2018 (nb)	0.54 ± 0.35^{b}	0.57 ± 0.37^{b}	0.57 ± 0.38^{b}
	2019 (nb)	0.95 ± 0.38	1.12 ± 0.41	0.99 ± 0.41
	2019 (rb)	0.67 ± 0.89	0.72 ± 0.97	0.66 ± 0.84
Soy/maize	2018 (nb)	1.43 ± 0.24^{aA}	1.32 ± 0.38^{aAB}	1.45 ± 0.24^{aAB}
	2019 (nb)	1.38 ± 0.30^{A}	1.56 ± 0.42^{A}	1.52 ± 0.38^{A}
	2019 (rb)	0.63 ± 0.44^{B}	0.66 ± 0.48^{B}	0.76 ± 0.58^{B}
Lupin/maize	2018 (nb)	1.25 ± 0.35^{a}	1.45 ± 0.34^{a}	1.30 ± 0.37^{a}
	2019 (nb)	1.13 ± 0.53	1.30 ± 0.53	1.19 ± 0.55
Mustard/maize	2018 (nb)	1.02 ± 0.29^{ab}	1.06 ± 0.33^{ab}	1.03 ± 0.32^{ab}
	2019 (nb)	0.89 ± 0.34	1.16 ± 0.39	0.92 ± 0.36
	2019 (rb)	0.80 ± 0.31	0.82 ± 0.37	0.84 ± 0.36

Note: Numbers show means ± standard deviations ($n = 5$). A one-way ANOVA was conducted followed by Tukey post-hoc test. Lowercase letters indicate significant differences ($p < 0.05$) between the species combinations, tested separately for each year and barrier treatment. Capital letters indicate significant differences ($p < 0.05$) between the years and barrier treatments, tested separately for each species combination. Absence of letters indicates that there were no significant differences.

TABLE 2 Mean relative contributions of above- (RC_{above}) and belowground (RC_{below}) interspecific interactions to yield increases of maize in 2019

Species combination	RC_{above} (%)	RC_{below} (%)
Faba bean/maize	38	62
Soy/maize	15	85
Mustard/maize	78	22

significantly higher in soy/maize, lupin/maize, and mustard/maize IC in 2018 than in 2019 (nb).

Similar to pLER, the pNER and pPER of maize grain yields in IC were higher than 0.5 across years and barrier treatments (Table 1). They were even larger than 1.0 in soy/maize and lupin/maize IC in both years (nb). The pNER was also larger than 1.0 in mustard/maize IC (both years) and in faba bean/maize IC (2019; nb). Both ratios were significantly higher in soy/maize and lupin/maize IC than in faba bean/maize IC in 2018. We found no significant differences between the species combinations in 2019 for both barrier treatments. In 2019, pNER and pPER of soy/maize IC were significantly higher in the nb than in the rb treatment.

4 | DISCUSSION

We found that IC had positive effects on biomass production and grain yields of maize on a plant basis, particularly when intercropped with legumes. On an area basis, IC with interspecific root interactions resulted in a similar productivity of maize as in monocropping, even though there were twice as many maize plants per area in monocropping than in IC.

4.1 | IC effects on single maize plants

On a single plant basis, we found that maize AGB and grain yields were significantly increased in IC compared to monocropping, especially when maize was intercropped with soy and lupin (Figure 3). Similarly, N and P uptake of maize AGB and grains were significantly increased in IC compared to monocropping, especially when maize was intercropped with soy and lupin (Table 3, Supporting Information 1). These findings indicate that resource competition between maize plants and companion crops in IC was less pronounced than competition between maize plants in maize monocropping. This could be due to a compensation effect (Horwith, 1985; Neamatollahi et al., 2013), that is, maize in IC had more resources available than maize in monocropping due to a lower maize plant density in IC than in monocropping and because companion crops produced less AGB than maize plants (Figure 4). It has been shown for maize monocropping with different planting densities that a lower grain yield per plant was fully compensated by a higher plant density (Testa et al., 2016). However, in the rb treatment, maize AGB, grain yields, and N and P uptake did not differ significantly between the species combinations on a single plant basis (Figure 3, Table 3, Supporting Information 1). This indicates that mainly interspecific root interactions caused the IC effects and that companion crops might use complementary and facilitative processes that provide maize in IC with additional nutrients (see Section 4.3).

The observation that there was no positive effect of faba bean/maize IC on maize AGB production, grain yields, and nutrient uptake of maize in 2018 (Figure 3, Table 3, Supporting Information 1) can be explained by the earlier sowing of faba beans in 2018, leading to a higher competition between the species for light, water, and nutrients when maize was sown later. This is in accordance with a global meta-analysis on legume/cereal IC showing that the species

TABLE 3 N and P concentrations per unit plant biomass (dry weight) as well as N and P uptake of maize grains per plant and per area, harvested in 2018 (no root barrier; nb) and 2019 (nb or with root barrier; rb)

		N (g kg^{-1})	P (g kg^{-1})	N (mg plant^{-1})	P (mg plant^{-1})	N (g m^{-2})	P (g m^{-2})
Maize/maize	2018 (nb)	21.5 ± 1.3	4.3 ± 0.4	278.6 ± 133.3^{bA}	56.6 ± 28.6^{b}	7.0 ± 3.3^{abA}	1.4 ± 0.7^{abA}
	2019 (nb)	$13.3 \pm 7.8^{(b)}$	2.7 ± 1.5	115.7 ± 91.8^{bAB}	23.5 ± 17.8^{b}	2.9 ± 2.3^{AB}	0.6 ± 0.4^{AB}
	2019 (rb)	14.6 ± 8.9	2.6 ± 1.6	90.6 ± 61.9^{B}	16.2 ± 11.3	2.3 ± 1.5^{B}	0.4 ± 0.3^{B}
F. bean/maize	2018 (nb)	22.7 ± 2.6	4.5 ± 0.4^{A}	315.5 ± 208.5^{b}	64.1 ± 43.1^{bA}	3.9 ± 2.6^{b}	0.8 ± 0.5^{b}
	2019 (nb)	$20.4 \pm 3.5^{(ab)}$	3.6 ± 1.0^{AB}	258.8 ± 93.9^{ab}	46.3 ± 19.3^{abAB}	3.2 ± 1.2	0.6 ± 0.2
	2019 (rb)	17.7 ± 11.7	2.7 ± 1.5^{B}	130.4 ± 175.1	21.4 ± 27.2^{B}	1.6 ± 2.2	0.3 ± 0.3
Soy/maize	2018 (nb)	20.9 ± 7.3	4.5 ± 0.1^{A}	736.5 ± 212.3^{aA}	164.3 ± 27.7^{aA}	9.2 ± 2.7^{aA}	2.1 ± 0.3^{aA}
	2019 (nb)	$19.1 \pm 2.0^{(ab)}$	3.8 ± 0.4^{B}	360.6 ± 96.4^{aB}	71.4 ± 18.0^{aB}	4.5 ± 1.2^{B}	0.9 ± 0.2^{B}
	2019 (rb)	20.3 ± 4.9	3.9 ± 0.5^{AB}	120.0 ± 86.5^{B}	24.5 ± 18.9^{C}	1.5 ± 1.1^{B}	0.3 ± 0.2^{C}
Lupin/maize	2018 (nb)	27.1 ± 9.7	4.6 ± 0.2^{A}	809.0 ± 187.4^{aA}	146.8 ± 42.1^{aA}	10.1 ± 2.3^{aA}	1.8 ± 0.5^{abA}
	2019 (nb)	$20.3 \pm 2.6^{(ab)}$	3.7 ± 0.5^{B}	301.9 ± 122.1^{abB}	55.9 ± 25.9^{abB}	3.8 ± 1.5^{B}	0.7 ± 0.3^{B}
Mustard/maize	2018 (nb)	22.6 ± 1.3	4.4 ± 0.3^{A}	590.9 ± 185.4^{abA}	116.0 ± 36.8^{abA}	7.4 ± 2.3^{abA}	1.5 ± 0.5^{abA}
	2019 (nb)	$23.1 \pm 3.7^{(a)}$	3.6 ± 0.4^{B}	267.6 ± 90.0^{abB}	43.4 ± 16.8^{abB}	3.3 ± 1.1^{B}	0.5 ± 0.2^{B}
	2019 (rb)	18.7 ± 3.0	3.4 ± 0.5^{B}	149.1 ± 67.9^{B}	27.3 ± 11.6^{B}	1.9 ± 0.8^{B}	0.3 ± 0.1^{B}

Note: Numbers show means ± standard deviations ($n = 5$). A one-way ANOVA was conducted followed by Tukey post-hoc test. Lowercase letters indicate significant differences ($p < 0.05$) between the species combinations, tested separately for each year and barrier treatment. Capital letters indicate significant differences ($p < 0.05$) between the years and barrier treatments, tested separately for each species combination. Brackets indicate that data were not normally distributed (log-transformation was not possible). Absence of letters indicates that there were no significant differences.

competitiveness and consequently the pLER were increased for earlier sown species, but decreased for later sown species (Yu et al., 2016).

4.2 | IC effects on an area basis

On an area basis, we found that maize in IC was similarly productive as in monocropping, even though there were twice as many maize plants per area in monocropping than in IC. Neither total biomass, maize AGB (Figure 4), maize grain yields nor maize N and P uptake (Table 3, Supporting Information 1) differed significantly between monocropping and IC in the nb treatments, except for maize AGB and maize AGB P uptake in faba bean/maize IC in 2018 (Figure 4, Supporting Information 1). This indicates again a lower competition in IC than in maize monocropping and, therefore, compensation effects, as discussed above. We also found that maize pLER was larger than 1.0 in soy/maize and lupin/maize IC in both years in the nb treatments (Table 1). Hence, LER of the whole IC system (which is the sum of the pLER of both species) is also larger than 1.0 in soy/maize and lupin/maize IC. Although companion crops have been shown to be less competitive than cereals resulting in low pLER values (Yu et al., 2016), LER of the whole IC system is likely also larger than 1.0 in mustard/maize IC (both years; nb) and in faba bean/maize IC (2019; nb) since maize pLER is already 0.9 to 1.0 (Table 1). We, therefore, assume a moderate overyielding of all species combinations (except for faba bean/maize IC in 2018) indicated by LER being larger than 1.0. The moderate overyielding is in the range reported in previous meta-analyses and reviews (Bedoussac et al., 2015; Yu et al., 2016). For example, soy enhanced AGB production and grain yields of maize in IC resulting in a global mean LER of 1.32 for soy/maize IC (Chen et al., 2019; Xu et al., 2020). Overyielding has also been found when maize was intercropped with soy, faba bean (Li et al., 2018; Xia et al., 2019), or lupins (Lelei and Onwonga, 2014). Similarly, overyielding has been found when maize was intercropped with turnip rape (*Brassica campestris* L.; Xia et al., 2013, 2019). In addition, another meta-analysis revealed that Brassicaceae, including mustard, increased maize AGB and grain yields when used as a cover crop (Hallama et al., 2019).

Moreover, we found that maize pNER and pPER in soy/maize and lupin/maize IC, and pNER in mustard/maize and faba bean/maize IC (the latter only in 2019) were larger than 1.0 in the nb treatments (Table 1). Moreover, we found that maize pPER in mustard/maize IC (both years; nb) and in faba bean/maize IC (2019; nb) were 0.9 to 1.0 (Table 1). Hence, NER and PER of the whole IC system (which is the sum of the pNER or pPER of both species, respectively) are very likely larger than 1.0 in all species combinations (nb), except for faba bean/maize IC in 2018. These findings indicate that N and P uptake in IC is probably higher than in monocropping. This is in accordance with previous studies showing that N and/or P uptake of maize were higher when intercropped with soy (Chen et al., 2019; Xia et al., 2019), lupin (Lelei & Onwonga, 2014), or turnip rape (Xia et al., 2013, 2019) than in monocropping. Our finding that total biomass, maize AGB, and maize AGB P uptake were significantly higher in maize monocropping than in IC in the rb treatment (Figure 4 and Supporting Information 1) further indicates that interspecific root interactions were important for IC effects on maize, as discussed above.

We further found that N uptake (Table 3, Supporting Information 1) of maize AGB and grains tended to be lower in 2019 than in 2018 in all species combinations, except for faba bean/maize IC. In contrast, P uptake (Table 3, Supporting Information 1) of maize AGB tended to be slightly higher in 2019 than in 2018. These findings indicate that the smaller AGB and yield increases in 2019 compared to 2018 might be due to a nutrient (mainly N) scarcity in the second year of the experiment. One reason for the decline in yield, and in N uptake could be the lack of nutrient inputs since only root biomass was left in our field experiment and no fertilizers were applied. A decline in maize AGB and N uptake over time along with decreases in soil N concentrations have also been found in a 3-year soy/maize IC study (Chen et al., 2017). Similarly, IC maize with groundnut, cowpea, soy, or nonleguminous species over 11 years resulted in maize grain yield decreases over time (Agyare et al., 2006).

4.3 | Above- and belowground interactions

We found that belowground interspecific interactions accounted for more than half of the maize yield increases in legume/maize IC. These findings are in accordance with previous studies that attributed overyielding in faba bean/maize IC mainly to belowground interspecific interactions and showed higher nutrient acquisition when roots of both species had physical contact (Li et al., 1999, 2007). Overyielding in soy/maize IC has also been shown to be associated more with belowground than with aboveground interactions (Lv et al., 2014). The high contribution of belowground interspecific interactions to maize yields in legume/maize IC may be explained by two major factors, that is, niche complementarity and interspecific facilitation, that both comprise several mechanisms. Complementarity refers to the complementary use of resources which decreases competition because nutrients are taken up in different parts of the soil, during different times or in different forms. In contrast, facilitation refers to beneficial interactions between the intercropped species that increase resource availability and improve environmental conditions for both species (Duchene et al., 2017; Xue et al., 2016). The fact that most mechanisms of complementary and facilitative nutrient acquisition are associated with a high N demand and/or the ability to symbiotically fix atmospheric N_2 might be the reason why the RC of belowground interspecific interactions to maize yields was much higher in legume/maize than in mustard/maize IC. Moreover, N availability for maize in mustard/maize IC was probably lower since mustard does not fix atmospheric N_2. However, it needs to be further investigated which of these potential mechanisms caused the increase in maize yields.

Furthermore, we found that aboveground interspecific interactions contributed considerably to maize yield increases in mustard/maize IC (Table 2). This indicates that a part of the yield increase of maize intercropped with mustard might be due to a lower competition for light in IC than in monocropping. A more efficient light use has been reported, for example, for several legume/maize IC systems compared to the respective monocrops (Kermah et al., 2017). In addition, also other aboveground interactions might positively influence plant growth. These include the effects of an increased overall biodiversity on pollinators, pests, and diseases, and the suppression of weeds through an early soil coverage (Brooker et al., 2015; Ehrmann & Ritz, 2014). Moreover, the microclimate regulation through increased soil shading and, therefore, reduced evapotranspiration and more balanced temperatures might contribute to overyielding in IC (Malézieux et al., 2009).

5 | CONCLUSIONS

We found that IC resulted in a similar productivity of maize as in monocropping on an area basis, and in an increase in maize AGB, grain yield, and N and P uptake on a plant basis, when interspecific root interactions were not restricted. Maize pLER, pNER, and pPER (and therefore also LER, NER, and PER of the whole IC system) were larger than 1.0 in several species combinations in the nb treatments, indicating a positive effect of IC on maize, especially in soy/maize and lupin/maize IC. This confirms our first hypothesis about maize AGB and grain yields and our second hypothesis about maize N and P uptake for the species combinations soy/maize and lupin/maize. The highest pLER, pNER, and pPER of maize were found for soy/maize and lupin/maize IC confirming our third hypothesis. We further found that interspecific root interactions contributed considerably to maize yield increases in legume/maize IC, whereas aboveground interspecific interactions were more important in mustard/maize IC. Our fourth hypothesis can, therefore, be confirmed for legume/maize IC, but needs to be rejected for mustard/maize IC. Taken together, our results indicate that IC is beneficial for maize production.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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