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# Competition-recovery and overyielding of maize in intercropping depend on species temporal complementarity and nitrogen supply

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## ABSTRACT

**Context:** Maize (*Zea mays* L.)-based intercropping – growing maize with at least one species in the same field for a significant period – is a common practice in China. Intercropping may allow ecological intensification of maize production by achieving higher yields and higher resource-use efficiency than sole maize. Such advantages strongly depend on interactions between species and nitrogen availability. Unfortunately, there is a shortage of experiments combining both species choice and nitrogen management.

**Research question:** It remains unclear how growth characteristics of the companion species, and notably its temporal complementarity with maize, and nitrogen fertilizer affect the performance of maize-based intercropping. Therefore, this work aims to explore the importance of the recovery response in relation to the duration of co-growth and that of maize recovery in interaction with nitrogen availability on the yield advantage of maize-based intercropping.

**Methods:** A two-year field experiment was conducted in Gansu Province (China) to quantitatively determine the effect of different companion species and nitrogen fertilizer rates on yields, relative yields and land equivalent ratios (LER). Experimental treatments included two nitrogen input rates (120 and 240 kg N ha<sup>-1</sup>), and six companion species in a substitutive design: wheat (*Triticum aestivum* L.), linseed (*Linum usitatissimum* L.), cabbage (*Brassica oleracea* L.), garlic (*Allium sativum* L.), pea (*Pisum sativum* L.) and soybean (*Glycine max* L.).

**Results:** Yields of intercropped maize were higher at 240 kg N ha<sup>-1</sup> than at 120 kg N ha<sup>-1</sup>. Averaged over nitrogen inputs, the yield of maize intercropped with pea, cabbage, garlic, wheat, linseed and soybean was 71%, 72%, 78%, 53%, 50% and 58% of that of sole maize. LERs were greater than one for all species combinations, except for soybean/maize. LERs and overyielding of maize were higher at 120 kg N ha<sup>-1</sup> than at 240 kg N ha<sup>-1</sup>. Overyielding of maize was negatively correlated to species co-growth duration and positively correlated to temporal niche differentiation, with the highest overyielding of maize with garlic corresponding to the shortest co-growth period.

**Conclusions:** Overyielding was significantly increased with the duration of the recovery period of maize (after harvest of the companion species), while it was negatively correlated with the duration of the co-growth period. Our results suggest that the competition-recovery principle contributed greatly to yield advantage in maize-based intercropping.

**Implications:** Our results should be considered in designing maize-based intercropping by choosing species and dates of sowing and harvesting for maximizing yield benefits.

## 1. Introduction

Monoculture-based maize production leads to a range of negative

environmental impacts such as nutrient spillovers and soil degradation. Intercropping may allow ecological intensification of maize production by achieving higher resource-use efficiency than sole maize (Yu et al.,

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2015; Zhang et al., 2016; Hong et al., 2019). Intercropping is the cultivation of more than one species in the same field at the same time for a significant period of time, but without necessarily sowing or harvesting the two species at the same time (Willey, 1979). Intercropping may be an efficient means to deliver sustainable and productive agriculture (Lithourgidis et al., 2011; Li et al., 2020a; Tilman, 2020; Yang et al., 2021) by enhancing land productivity, and simultaneously enabling a reduction in external inputs such as fertilizer (Bedoussac et al., 2015; Li et al., 2020b).

When intercropped species are sown and/or harvested at different times, this is called relay intercropping (Li et al., 2013). The difference between the growing periods of intercropped species is a key determinant of relay intercropping advantages (Fridley, 2002; Yu et al., 2015; Li et al., 2020a). The species sown first benefits from reduced competition during its early growth, while it often, and at least initially, dominates a later-sown species during co-growth. The species that is harvested later may recover from competition and compensate for initial growth reduction after harvest of the early-maturing species (Li et al., 2001a, 2001b; Gou et al., 2016).

Above- and belowground interspecific interactions play an important role in determining the structure and dynamics of plant communities in both agricultural and natural ecosystems (Aerts, 1999; Callaway and Pugnaire, 1999). The balance between positive and negative interactions contributes to intercropping advantages. For example, crop root exudates may release limiting nutrients such as phosphorus or iron from soil (Li et al., 2014), while intercropped species can also access these soil nutrients.

Li et al. (2001a, 2001b) formulated the “competition-recovery production” principle in wheat/maize and wheat/soybean intercropping to describe the growth acceleration of maize and soybean, respectively, that occurs after wheat harvest. These studies showed that the biomass per plant of intercropped maize at final harvest was not significantly different from that of sole cropped maize plants. Conversely, at wheat harvest, the biomass of single maize plants in the intercrop was only 45–78% of that of the sole crop. Intercropped maize plants thus had a faster growth rate than maize plants in the pure stand, probably due to: (1) greater availability of light and belowground resources per plant after harvest of the companion species (Li et al., 2001a, 2001b; Gou et al., 2016), and (2) plastic plant growth responses to intercropping (Zhu et al., 2015). For instance, in intercrops of pigeon pea (*Cajanus cajan*) and sorghum (*Sorghum bicolor*), sorghum is the early-sown and early-maturing species. While nitrogen uptake by pigeon pea plants was reduced during the co-growth with sorghum, it exceeded that in the sole crop after harvest of sorghum (Madhavan and Shanmugasundaram, 1990). The competition-recovery phenomenon is also found in many other intercropping systems such as maize/pigeon pea (Dalal, 1974) or barley/maize (Zhang et al., 2015). Competition-recovery is associated with a greater root length growth in the intercrop than in the sole crop. Xia et al. (2013) demonstrated that the dynamics of root length and root distribution of maize was correlated with the corresponding shoot biomass when maize was intercropped with turnip, faba bean or chickpea.

The effects of interspecific interactions on productivity vary among crop species combinations (Sharaiha and Gliessman, 1992). In relay intercrops such as cotton/wheat, the complementarity in resource capture is related to differences between the component crops in the timing of interception of solar radiation (Zhang et al., 2008a, 2008b, 2008c) leading to high land equivalent ratio (LER). On the other hand, Li et al. (2017) demonstrated involvement of belowground resources in yield advantages in multi-species cropping systems.

There is thus a body of knowledge on growth responses in relay intercropping and the importance of the competition-recovery production principle in the yield advantage of late maturing species, such as maize. Maize can potentially be intercropped with many crop species, differing in intercropping advantage (Li et al., 2020b). Thus, it is necessary to determine how the traits of the companion species

influence the competition-recovery in maize-based intercropping. We hypothesized that: (1) the competition-recovery of maize will be greater if the recovery period is longer (i.e. if the companion species is harvested earlier because maize has a longer time to recover), (2) the recovery will be greater with more N-fertilizer input, because the growth of maize will not be constrained by soil nutrient resources running out at the end of the growing season (Gou et al., 2018).

Unfortunately, there is a shortage of field experiments that combine both species choice and nitrogen management to explore the importance of the recovery response in relation to the duration of co-growth and the duration of maize recovery. Therefore, we conducted a field experiment to investigate the occurrence of growth recovery in different maize-based intercropping systems. The objectives of the present study were to determine how different companion species and N-application rates affect: (1) yield advantage of intercropping, and (2) overyielding of maize and competition-recovery.

## 2. Materials and methods

### 2.1. Site description

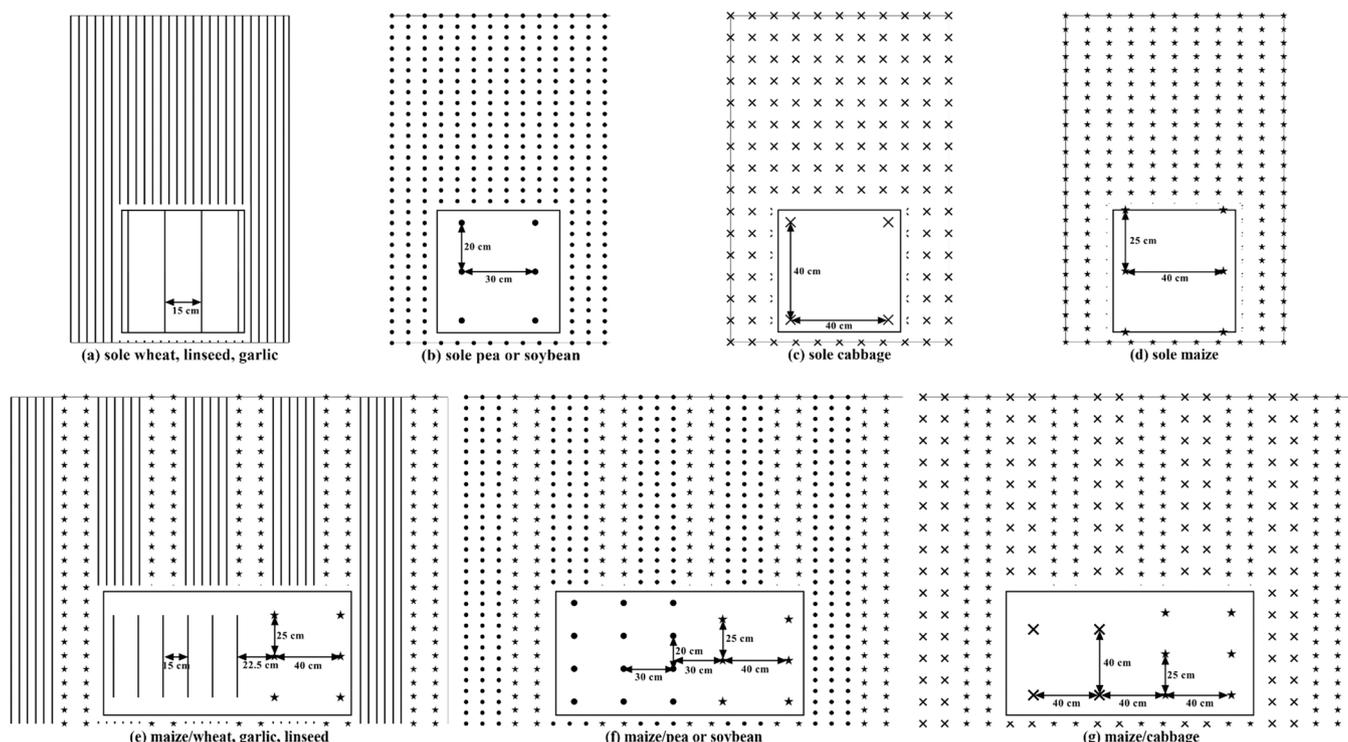
Field experiments were conducted in 2009 and 2010 at the Baiyun Experimental Station of the Gansu Academy of Agricultural Sciences in Wuwei in China (38°07' N, 102°59' E). The experimental site is located at an altitude of 1504 m where the average annual mean temperature is 7.7°C with cumulative temperatures above 10°C of 3149°Cd and 175 days of frost per year. The climate is arid with 150 mm of annual precipitation and a potential evaporation of 2021 mm. The soil type is an Orthic Anthrosol; in the topsoil (0–20 cm), pH in water is 8.0, total nitrogen concentration is 0.86 g kg<sup>-1</sup>, Olsen-P concentration is 23 mg kg<sup>-1</sup>, available K concentration is 122 mg kg<sup>-1</sup> and organic matter content is 16 g kg<sup>-1</sup> (Xia et al., 2013).

### 2.2. Experimental design

In both years, the experiment was laid out as a randomized block design with three replicates. Thirteen cropping systems were compared: (1) six intercropping systems of maize (*Zea mays* L.) with pea (*Pisum sativum* L.), cabbage (*Brassica oleracea* L.), garlic (*Allium sativum* L.), wheat (*Triticum aestivum* L.), linseed (*Linum usitatissimum* L.) or soybean (*Glycine max* L.), and (2) the seven corresponding sole crops (Figs. 1 and S1).

Each intercrop plot was 48 m<sup>2</sup> (8 × 6 m) while each sole crop plot was 24 m<sup>2</sup> (4 × 6 m). Row distances varied in accordance with common practice (Fig. 1): (1) 40 cm for maize and cabbage, (2) 30 cm for pea and soybean, and (3) 15 cm for wheat, linseed and garlic. Intercrop plots consisted of five strips of 1.6 m width. Each strip consisted of two rows of maize 40 cm apart followed by two rows of cabbage 40 cm apart, or three rows of pea or soybean 30 cm apart, or six rows of wheat, linseed or garlic 15 cm apart. The row distance was 40 cm between maize and cabbage, 30 cm between maize and pea or soybean, and 22.5 cm between maize and wheat, linseed or garlic. Species density corresponds to the locally recommended density in the sole crop (10, 550, 300, 6.25, 25, 16 and 16 plants m<sup>-2</sup> for maize, wheat, linseed, cabbage, garlic, pea and soybean, respectively) and species densities in the row were the same in intercrops and sole crops.

Pea, cabbage, garlic, wheat and linseed were all sown on 22 March in 2009 and on 25 March in 2010 while soybean and maize were sown about three weeks later, on 12 April in 2009 and on 14 April in 2010 (Table 1). Emergence occurred one to three weeks after sowing (Table 1). Companion species had harvesting dates varying from late June-early July for pea, cabbage and garlic, to mid-July for wheat, to early August for linseed, to late September for soybean and to late September-early October for maize. Accordingly, the co-growth period between companion species and maize varied (Table 1) from 52 days (with pea in 2009) to 148 days (with soybean in 2009). The recovery



**Fig. 1.** Row configuration of maize and six companion species. Sole crops of wheat, linseed and garlic were sown at 15 cm row distance (black lines; a). Sole crops of pea or soybean were grown at 30 cm row distance (black points; b). Sole cabbage (black cross; c) and sole maize (five-pointed stars; d) were both sown at 40 cm row distance. The intercrops with wheat, linseed and garlic (e) comprised two maize rows at 40 cm distance alternating with 6 rows of the companion species at 15 cm distance and a distance between maize and companion species rows of 22.5 cm. The intercrop of maize with pea or soybean (f) comprised 2 rows of maize alternating with 3 rows of the companion species at 30 cm distance and a distance between maize and the companion species rows of 30 cm. The intercrop of maize with cabbage (g) comprised 2 rows of maize alternating with 2 rows of cabbage, with all rows at 40 cm distance.

**Table 1**

Details on sowing date, emergence date, time from sowing to emergence, harvest date, and resulting metrics on the duration of co-growth between companion species and maize, and the time available for maize recovery after co-growth.

Year and crops	Sowing date	Emergence date	Time from sowing to emergence (days)	Harvest date	Growth duration (days)	Grow-alone time of companion species	$P_{overlap}$	Duration of maize growing alone (days)	$P_{total}$	TND
2009										
Pea	22 Mar	08 Apr	17	24 Jun	77	25	52	100	177	0.71
Cabbage	22 Mar	02 Apr	11	30 Jun	89	31	58	94	183	0.68
Garlic	22 Mar	02 Apr	11	02 Jul	91	31	60	92	183	0.67
Wheat	22 Mar	02 Apr	11	12 Jul	101	31	70	82	183	0.62
Linseed	22 Mar	05 Apr	14	12 Aug	129	28	101	51	180	0.44
Soybean	12 Apr	02 May	20	28 Sep	149	1	148	4	153	0.03
Maize	12 Apr	03 May	21	02 Oct	152					
2010										
Pea	25 Mar	05 Apr	11	06 Jul	92	28	64	86	178	0.64
Cabbage	25 Mar	01 Apr	7	06 Jul	96	32	64	86	182	0.65
Garlic	25 Mar	03 Apr	9	06 Jul	94	30	64	86	180	0.64
Wheat	25 Mar	03 Apr	9	17 Jul	105	30	75	75	180	0.58
Linseed	25 Mar	07 Apr	13	05 Aug	120	26	94	56	176	0.47
Soybean	14 Apr	04 May	20	26 Sep	145	0	146	4	149	0.02
Maize	14 Apr	03 May	19	30 Sep	150					

$P_{overlap}$  and  $P_{total}$  represent the period of overlap of the growing periods of the intercropped species and the duration of the whole intercrop from sowing of the first crop till harvest of the last crop, respectively. TND represent temporal niche differentiation.

period of maize varied from only four days with soybean in both years to 100 days with pea in 2009 (Table 1).

### 2.3. Crop management

In both years, during the growing period, all plots were irrigated seven times, each time using  $0.09 \text{ m}^3 \text{ m}^{-2}$  (90 mm). Previous studies (Li et al., 2001a, 2001b) have shown that the nitrogen requirement of

earlier sown species can be completely met by base fertilization while the later sown species requires a top dressing of nitrogen fertilizer. Maize does benefit from a top dressing of nitrogen fertilizer in the intercrop, in part because the earlier sown species acquires nitrogen not only within their own strip but also in the maize strip (Li et al., 2005). In this study, a base fertilization of  $120 \text{ kg N ha}^{-1}$  and  $78.6 \text{ kg P ha}^{-1}$  was broadcast and incorporated into the top 20 cm of the soil before sowing in all treatments, on 21st March 2009 and 24th March 2010. In the

240 kg N ha<sup>-1</sup> treatments, a top dressing of nitrogen fertilizer was applied homogeneously to the plots prior to irrigation at maize elongation. This top dressing was applied to both the intercropping and the sole crop treatments, including the earlier sown crops to ensure maximum comparability between treatments. All nitrogen fertilizer was applied as urea (46% N). No potassium fertilizer was given because of the high potassium content of the soil. No pesticides were applied, and weeding was done manually at maize elongation (V6 stage).

#### 2.4. Crop sampling

At crop maturity, the central strip in each intercropped and sole cropped plot (6 m × 1.6 m) was hand-harvested. Then the grains were sun-dried and weighed to determine the yield after threshing by hand.

#### 2.5. Calculations

##### 2.5.1. Land equivalent ratio

The land equivalent ratio (LER) is defined as the relative land area required when growing sole crops to produce the component crop yields obtained in a unit area of intercrop. The LER is calculated as:

$$\text{LER} = \text{PLER}_m + \text{PLER}_c = \frac{Y_{im}}{Y_{sm}} + \frac{Y_{ic}}{Y_{sc}} \quad (1)$$

where  $\text{PLER}_m$  and  $\text{PLER}_c$  are the partial land equivalent ratio of maize and companion species, respectively.  $Y_{im}$  and  $Y_{ic}$  are the yields of maize and companion species when intercropped, and  $Y_{sm}$  and  $Y_{sc}$  are the yields of maize and companion species when sole cropped.  $\text{LER} > 1$  indicates a per area advantage to intercropping compared with sole cropping for the quantitative variable of production per unit area.

We also used the relative yield advantage ( $\Delta\text{RY}_m$ ) and of the companion species ( $\Delta\text{RY}_c$ ) to evaluate the contribution of the intercropped species to the LER of the intercropping system (Loreau and Hector, 2001):

$$\Delta\text{RY}_m = \text{PLER}_m - P_m \quad (2)$$

$$\Delta\text{RY}_c = \text{PLER}_c - P_c \quad (3)$$

where  $P_m$  and  $P_c$  are the proportions of maize and companion species in the intercrop.  $P_m$  and  $P_c$  are determined as  $P_m = W_m / (W_m + W_c)$  and  $P_c = W_c / (W_m + W_c)$ , where  $W_m$  and  $W_c$  are the widths of the maize and companion species strips in the intercropping system,  $W_m$  and  $W_c$  were calculated as:

$$W_m = (n_m - 1) \times r_m + 2 \times \frac{r_m}{r_m + r_c} \times r_b \quad (4)$$

$$W_c = (n_c - 1) \times r_c + 2 \times \frac{r_c}{r_m + r_c} \times r_b \quad (5)$$

where  $n_m$  and  $n_c$  are the number of rows of maize and the companion species in each strip,  $r_m$  and  $r_c$  are the row distance of maize and companion species, and  $r_b$  the distance between maize and companion species (Li et al., 2020a). Note that  $\text{LER} = 1 + \Delta\text{RY}_m + \Delta\text{RY}_c$ , because  $P_m + P_c = 1$ . Based on the above, in this study, the species proportions ( $P_m$  and  $P_c$ ) are: (1) 50% for both maize and cabbage, (2) 46% for maize and 54% for pea or soybean, and (3) 45% for maize and 55% for wheat, linseed or garlic. Positive values for relative yield advantage indicate a relative yield advantage for a species, i.e. the relative yield exceeds the proportion of the space a species is assigned in the intercrop according to the sowing configuration. In an intercrop with unequal species proportions,  $\Delta\text{RY}$  is suitable for assessing yield advantage in intercropping when species proportions are not 0.5, as is the case here.

##### 2.5.2. Overyielding

Overyielding (OY) for grain yield or biomass of intercropped species

relative to sole crops was defined by Li et al. (2016) to reveal a yield increase or decrease of a species when intercropped compared with its sole crop:

$$\text{OY}_m = \frac{Y_{im} - P_m Y_{sm}}{P_m Y_{sm}} \times 100 \quad (6)$$

$$\text{OY}_c = \frac{Y_{ic} - P_c Y_{sc}}{P_c Y_{sc}} \times 100 \quad (7)$$

Overyielding percentage represents the difference between observed yield and expected yield, expressed as a percentage of expected yield. Positive values for overyielding indicate a yield advantage for a species when intercropped, and negative values indicate yield disadvantage.

##### 2.5.3. Temporal niche differentiation (TND)

To express the proportion of the total growing period of an intercropping system in which species are growing alone we calculated the TND using the sowing and harvest dates of each species in the intercrop as follows (Yu et al., 2015):

$$\text{TND} = \frac{P_{\text{total}} - P_{\text{overlap}}}{P_{\text{total}}} \quad (8)$$

where  $P_{\text{overlap}}$  represents the period of overlap of the growing periods of the intercropped species, and  $P_{\text{total}}$  the duration of the whole intercrop from sowing of the first crop till harvest of the last crop. A TND of 0 means full overlap of the two species (the species are sown and harvested at the same time) while a TND of 1 means no overlap, which refers to double cropping (the second species is sown after the first species is harvested).

#### 2.6. Statistical analysis

Three-way ANOVA was carried out to determine the significance effects of year (Y; 2009 vs 2010), nitrogen rate (N; 120 kg N ha<sup>-1</sup> vs 240 kg N ha<sup>-1</sup>), cropping system (C; intercrop vs sole crop) and their interactions on yield of companion species.

Three-way ANOVA was carried out to determine the effects of year (Y; 2009 vs 2010), nitrogen rate (N; 120 kg N ha<sup>-1</sup> vs 240 kg N ha<sup>-1</sup>), companion species (CS) and their interactions on: (1) maize yield in intercrop, (2) LER, (3)  $\text{PLER}_m$ , (4) overyielding of maize, and (5) overyielding of companion species.

Mean values ( $n = 3$ ) were compared by pairwise least significant differences (LSD) at the 5% level. Simple linear regression was applied to examine the relationship between overyielding of maize and three explanatory variables: (1) species co-growth duration (d), (2) duration of maize growing alone (d), and (3) temporal niche differentiation (TND).

Analysis of variance was performed using SAS v.8.0 software (SAS Institute, Inc., Cary, NC, USA). Figures were generated by GraphPad Prism 8.0 (GraphPad Software, Inc., La Jolla, CA, USA).

### 3. Results

#### 3.1. Yields of companion species and maize

Analysis of variance showed significant main effects and two-way interaction effects of year, nitrogen fertilizer and cropping system on the yields of companion species, but the three-way interaction Y\*N\*C was not significant (Table 2). Year affected the yields of pea and soybean, but not the yield of the other species, while the effect of Nitrogen on yield interacted with year in pea, cabbage, garlic and linseed. A significant main effect of Nitrogen was found in all species except wheat and soybean, but the N effect interacted not only significantly with year in four out of the six species, as noted above, but it interacted also with cropping system in cabbage and wheat. Hence, species responded in complex ways to the interactive effects of nitrogen fertilizer, cropping

**Table 2**  
Yields of companion species in intercropping and sole cropping at two nitrogen application rates in 2009 and 2010 (t ha<sup>-1</sup>).

Year	Nitrogen (kg ha <sup>-1</sup> )	Pea		Cabbage		Garlic		Wheat		Linseed		Soybean	
		Sole	Intercrop	Sole	Intercrop	Sole	Intercrop	Sole	Intercrop	Sole	Intercrop	Sole	Intercrop
2009	120	0.7	0.9	114	89	16.0	15.0	4.9	6.8	2.6	2.4	2.3	1.1
	240	0.7	1.0	124	87	21.1	18.6	6.6	6.4	2.3	2.2	2.6	1.5
2010	120	1.4	1.8	105	90	16.4	17.1	5.7	6.6	2.2	2.6	1.6	1.2
	240	1.4	1.7	143	100	18.9	18.9	5.9	6.6	2.4	2.5	2.0	1.5
<i>P</i> values													
Year (Y)		< 0.0001		0.1302		0.6445		0.8632		0.2219		0.0005	
Nitrogen (N)		0.7267		0.0016		< 0.0001		0.2004		0.0616		0.0002	
Cropping System (C)		< 0.0001		< 0.0001		0.0334		0.0086		0.4255		< 0.0001	
Y×N		0.0162		0.0145		0.0020		0.2918		0.0505		0.8688	
Y×C		0.2454		0.7120		0.0042		0.8725		0.0062		0.0002	
N × C		0.3028		0.0146		0.0699		0.0469		0.3300		0.6052	
Y×N × C		0.4458		0.2750		0.5390		0.1111		0.3689		0.6052	

To facilitate comparison of intercrop yields and sole crop yields, the intercrop yields were expressed per unit area occupied by the species. Values are means of three replicates.

system (sole cropping or intercropping) and the influence of year.

Grain yields of intercropped maize were significantly ( $p < 0.001$ ) affected by year (Y), N rate (N) and companion species (CS), with the yield of intercropped maize higher in 2010 than in 2009 (on average 14.1 vs 10.9 t ha<sup>-1</sup>), higher at 240 kg N ha<sup>-1</sup> than at 120 kg N ha<sup>-1</sup> (on average 13.2 vs 11.8 t ha<sup>-1</sup>) and higher when intercropped with pea, cabbage, garlic than when intercropped with wheat, linseed and soybean (Table 3). Interactive effects Y × CS and Y × N × CS were also significant ( $p < 0.001$ ). Regardless of year and nitrogen, the highest

yield of intercropped maize was obtained with garlic and the lowest with linseed. Averaged over nitrogen rate and year, the yield of intercropped maize with pea, cabbage, garlic, wheat, linseed and soybean was 71%, 72%, 78%, 53%, 50% and 58% of that of sole maize. Because the effects of treatment interacted with those of year and N fertilizer, they are presented for each year and N input rate separately (Table 3).

**Table 3**  
Yields of maize in intercropping and sole cropping, land equivalent ratio, partial land equivalent, and overyielding proportions at two nitrogen application rates in 2009 and 2010.

Year	Nitrogen (kg ha <sup>-1</sup> )	Companion species	Intercropped maize yield (t ha <sup>-1</sup> ) (whole IC area basis)	Land equivalent ratio			Overyielding (%)	
				PLER <sub>m</sub>	PLER <sub>c</sub>	LER	OY <sub>m</sub>	OY <sub>c</sub>
2009	120	Pea	12.6b	0.81a	0.79a	1.60a	75.2ab	46.6a
		Cabbage	13.0ab	0.83a	0.39bc	1.22b	65.5b	-21.9bc
		Garlic	14.4a	0.92a	0.53b	1.45ab	103.8a	-3.7b
		Wheat	7.2cd	0.46b	0.79a	1.25b	1.9c	43.5a
		Linseed	5.7d	0.36b	0.53b	0.89c	-19.6c	-3.6b
	240	Soybean	7.9c	0.51b	0.27c	0.78c	9.9c	-49.2c
		Pea	12.1b	0.73b	0.75a	1.48a	59.5b	38.1a
		Cabbage	13.5a	0.82a	0.35c	1.17b	63.5b	-29.7cd
		Garlic	14.5a	0.88a	0.50b	1.37a	94.8a	-9.7bc
		Wheat	9.8c	0.59c	0.55b	1.14b	31.6c	-0.5b
2010	120	Linseed	9.8c	0.59c	0.53b	1.12b	31.6c	-4.5b
		Soybean	10.8bc	0.66bc	0.31c	0.97c	42.8c	-42.5d
		Pea	14.1a	0.69a	0.72a	1.42a	51.1a	33.7a
		Cabbage	14.2a	0.70a	0.43b	1.13cd	39.7a	-13.5cd
		Garlic	14.8a	0.73a	0.59a	1.32ab	62.6a	6.7bc
	240	Wheat	11.9b	0.59a	0.65a	1.24bc	30.3a	18.8ab
		Linseed	12.1b	0.60a	0.66a	1.26bc	32.4a	19.1ab
		Soybean	13.5ab	0.66a	0.41b	1.08d	44.5a	-24d
		Pea	16.9a	0.60a	0.68a	1.28a	30.7a	25a
		Cabbage	15.4bc	0.55abc	0.35c	0.90e	9.8b	-29.7c
240	Garlic	16.3ab	0.58abc	0.56b	1.14b	28.5a	1.8b	
	Wheat	13.6d	0.48cd	0.63ab	1.11bc	7.3b	13.8ab	
	Linseed	12.0e	0.43d	0.59ab	1.01cd	-5.2b	8.1b	
	Soybean	14.2cd	0.51bcd	0.40c	0.91de	10.0b	-25.5c	
	Pea	14.2cd	0.51bcd	0.40c	0.91de	10.0b	-25.5c	
<i>P</i> values								
Year (Y)			< 0.0001	< 0.0001	0.1703	0.0179	< 0.0001	0.1565
Nitrogen (N)			< 0.0001	0.0085	0.0132	0.0003	0.0085	0.0111
Companion species (CS)			< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Y×N			0.5182	< 0.0001	0.6511	0.0003	< 0.0001	0.6962
Y×CS			< 0.0001	< 0.0001	0.0523	< 0.0001	< 0.0001	0.0448
N × CS			0.2401	0.0283	0.2668	0.2056	0.0324	0.2705
Y×N × CS			< 0.0001	0.0055	0.2557	0.0452	0.0035	0.2588

The Yield of sole maize in 2009 was 15.7 t ha<sup>-1</sup> at 120 kg N ha<sup>-1</sup> and 16.5 t ha<sup>-1</sup> at 240 kg N ha<sup>-1</sup>. Sole maize yield in 2010 was 20.3 t ha<sup>-1</sup> at 120 kg N ha<sup>-1</sup> and 28.1 t ha<sup>-1</sup> at 240 kg N ha<sup>-1</sup>. Yields of intercropped maize are expressed per unit area of the whole system. PLER<sub>m</sub>, PLER<sub>c</sub> and LER represent partial land equivalent ratios of intercropped maize, and the companion species and the total land equivalent ratio of the intercropping system, respectively. OY<sub>m</sub> and OY<sub>c</sub> represent overyielding percentages of intercropped maize and the companion species, respectively. Yields of maize, PLER<sub>c</sub>, PLER<sub>m</sub>, LER and overyielding percentages with the same letter in the same column indicates absence of a significant difference at the 5% level at the same nitrogen rate in the same year.

### 3.2. Land equivalent ratio

There were significant main effects of year (Y), N rate (N), and companion species (CS) on land equivalent ratio (LER), as well as significant interactive effects of Y × N, Y × CS and Y × N × CS (Table 3). The LER values differed significantly among the different species combinations, with values ranging from 0.78 to 1.60 (Table 3). The LERs were slightly higher in 2009 than in 2010 (1.20 vs 1.15) while LERs were lower at higher nitrogen application (1.22 at 120 kg N ha<sup>-1</sup> vs 1.13 at 240 kg N ha<sup>-1</sup>). On average over levels of nitrogen and year, LERs for maize intercropped with pea and garlic were significantly higher than those obtained with other companion species. The highest LER values, ranging from 1.28 to 1.60, were found in maize/pea intercropping while maize/soybean intercropping had the lowest LER values (0.78–1.08). Among the 24 combinations of year, nitrogen rate and companion species combination, 19 combinations had an LER greater than one (Fig. 2; Table 3).

The partial land equivalent ratio of maize (PLER<sub>m</sub>) was significantly affected by Year (Y), nitrogen (N), companion species (CS) and their interactions (Table 3). Maize PLER was higher in 2009 than in 2010 (0.68 vs 0.59), and it was slightly higher at 120 kg N ha<sup>-1</sup> than at 240 kg N ha<sup>-1</sup> (0.65 vs 0.62). The PLER<sub>m</sub> was greater with pea, cabbage or garlic as companion species than with wheat, linseed and soybean. The highest PLER<sub>m</sub> was obtained with garlic and the lowest with linseed in both years (Table 3).

The partial land equivalent ratio of companion species (PLER<sub>c</sub>), was significantly affected by nitrogen rate (N) and companion species (CS) but not by year (Table 3). The average PLER<sub>c</sub> was higher at 120 kg N ha<sup>-1</sup> (0.56) than at 240 kg N ha<sup>-1</sup> (0.52). The highest PLER<sub>c</sub> was obtained for pea (0.74) and the lowest for soybean (0.35).

On average across the two years and the two nitrogen treatments, the relative yield advantage of maize was 0.18, while the average relative yield advantage of companion species was negligible (0.005). Twenty-two out of the 24 cases (91.6%) represented a relative yield advantage of maize (ΔRY<sub>m</sub> > 0; Fig. 2). Eleven out of 24 cases were located in the upper right quadrant with a relative yield advantage for both species, while another 11 cases were in the upper left quadrant with a relative

yield advantage for maize, but a relative yield loss for the companion species. Only one case was in the lower left quadrant corresponding to a relative yield loss for both species, and another single case was in lower right quadrant with a relative yield advantage for the companion species, but a relative yield loss for maize (Fig. 2).

### 3.3. Overyielding

All main effects (Y, N and CS) and their interactions significantly (p < 0.05) affected overyielding of maize (OY<sub>m</sub>; Table 3). The average overyielding of maize was higher in 2009 (46.7%) than in 2010 (46.7%), and higher at 120 kg N ha<sup>-1</sup> (41.4%) than at 240 kg N ha<sup>-1</sup> (33.7%). Overyielding was greater with pea, cabbage and garlic than with wheat, linseed and soybean. Highest overyielding of maize was obtained with garlic and the lowest with linseed (72.4% vs 9.8%).

Overyielding of companion species (OY<sub>c</sub>) was significantly affected by nitrogen rate (N; p = 0.01) and companion species (CS; p < 0.0001) and the interaction Y × CS (p < 0.05) (Table 3). On average, companion species did not experience overyielding, but OY<sub>c</sub> was positive (4.4%) at 120 kg N ha<sup>-1</sup> and negative (−4.6%) at 240 kg N ha<sup>-1</sup>. OY<sub>c</sub> values were on average positive for pea, wheat and linseed but negative for cabbage, garlic and soybean. However, the CS effect was different between both years.

### 3.4. Relationship between the overyielding of maize and species growth duration

The overyielding of maize had: (1) a significant negative correlation (p = 0.0008) with the species co-growth duration (Fig. 3a), (2) no correlation with the duration of maize growing alone after the earlier species' harvest (p = 0.8840), and (3) a significant positive correlation (p = 0.0044) with the temporal niche differentiation between maize and the companion species (Fig. 3).

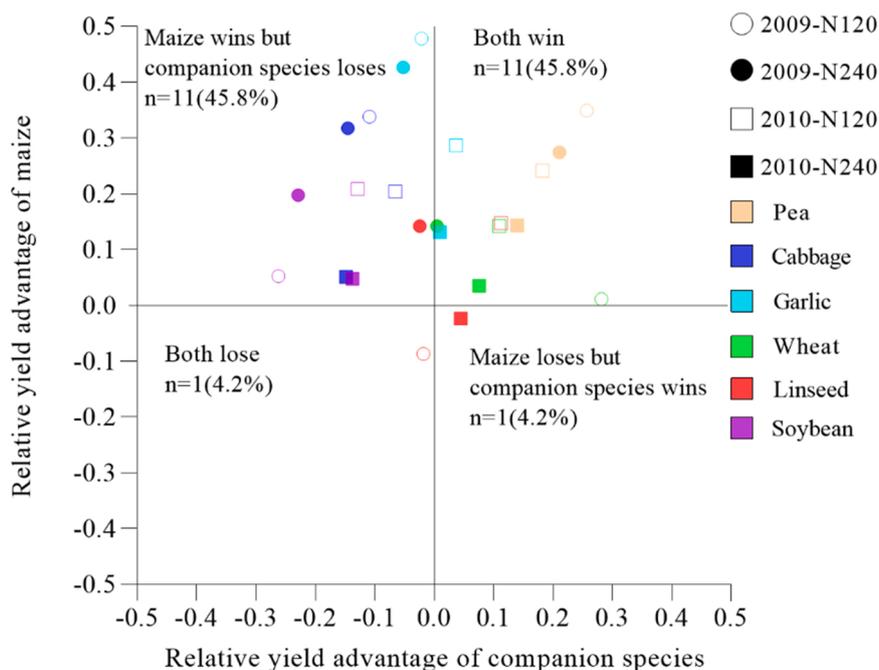
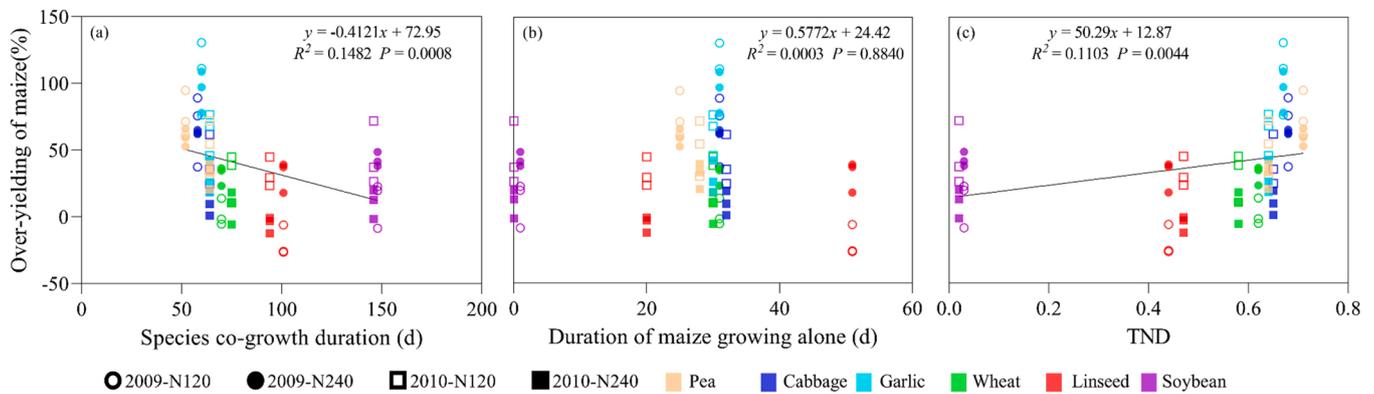


Fig. 2. Relative yield advantage of maize (ΔRY<sub>m</sub>; y-axis) versus relative yield advantage of the companion species (ΔRY<sub>c</sub>; x-axis) as affected by nitrogen application rate and year. Circles represent data in 2009 and squares represent data in 2010. Open symbols are for N120, while closed symbols are for N240. Colors indicate combinations of six different crop species with maize in an intercrop.



**Fig. 3.** The relationship between overyielding of maize and species co-growth duration (a), duration of maize growing alone (b), and temporal niche differentiation (c). Circles represent data in 2009 and squares represent data in 2010. Open symbols are for N120, while closed symbols are for N240. Colors indicate combinations of six different crop species with maize in an intercrop. Thick black lines in panels a and c represent significant linear relationships.

## 4. Discussion

### 4.1. Intercropping advantage

Relative yields are widely used to quantify species mixture efficiency and are helpful in illustrating the pattern of competitive outcomes in intercropping experiments (Justes et al., 2021; Williams and McCarthy, 2001). Trade-offs between the two intercropped species can be illustrated by plotting partial LER values (relative yields) or relative yield gains ( $\Delta RY$ ) of a species as a function of those of the associated species (Bedoussac et al., 2015; Bedoussac and Justes, 2011). Here, because the species proportions varied between different intercrops in accordance with the row distances used for different species, we plotted the relative yield advantage of maize ( $\Delta RY_m$ ) versus that of the companion species ( $\Delta RY_c$ ). Eleven out of 24 situations (species \* year in intercropping) corresponded to a situation where both maize and the companion species benefited from being cultivated in mixtures. Eleven out of 24 situations (species \* year in intercropping) corresponded to a situation in which maize grew better in the intercrop than in the sole crop but the yield of the companion species was suppressed. These results were consistent with those of Li et al. (2020a), who showed that maize was often a dominant species in maize-based intercropping systems. Many studies showed that maize/soybean intercropping had a significant yield advantage ( $LER > 1$ ; Yang et al., 2014, 2017), but this was not the case in our study. Different LER obtained in maize/soybean intercropping systems is among other factors related to the duration of co-growth (Xu et al., 2020). High LERs are more easily obtained in maize/soybean relay strip intercropping systems with only a short overlap period between the two crop species. Furthermore, in those studies with a LER above 1, soybean was sown in wider rows to avoid intense interspecific competition with maize, resulting in a yield advantage for relay intercropping. However, in our study, nearly simultaneous sowing and harvesting of the two species led to a longer interspecific competition for resources between maize and soybean, even a lack of recovery of maize growth and complementarity. These results were consistent with results of Li et al. (2020c), meanwhile, our previous study (Zhao et al., 2015) also indicated that the closer the proximity of intercropped species, the stronger interspecific competition was. In the present study, a narrow strip width of soybean led to an intense interspecific competition, which resulted in a less favorable performance of the two species.

While relative yield is meaningful for evaluating intercropping advantage, these indices must always be placed in perspective by considering the absolute yields of the crops (Bedoussac et al., 2015; Li et al., 2020a). In our study, the yield achieved in intercropping was significantly higher at high than at low nitrogen application rate, while the advantage of intercropping, characterized by LER values greater than one, was greater at a low than at high nitrogen application rate. It

has been suggested that intercropping is more suitable in low-N input situations (Fujita et al., 1992; Jensen, 1996; Bulson et al., 1997), but it has also been noted that an intercropping yield advantage in an absolute sense increased at higher rates of nitrogen input (Li et al., 2020b). Additionally, at a given nitrogen rate, the intercropping yield advantage depends on species combination and temporal niche differentiation (Dong et al., 2018). In the present study, the yield of maize depended on the companion species, its growing period relative to maize, and the nitrogen application rate. The overyielding of maize was relatively greater when the co-growth period was relatively shorter, suggesting that time niche differentiation plays an important role for maize recovery growth. An early harvest of the companion species and a short co-growth period between maize and the companion species allowed a longer period of recovery and a greater yield benefit from intercropping.

Yield increase in intercropping is often referred to as overyielding (Van der werf et al., 2021), which is not only due to intercrop species time niche differentiation (Yu et al., 2015), but also to area occupied by each species which determines resource competition between intercropped species (Van der werf et al., 2021). However, the definition of the area occupied by each species in intercropping can be problematic, even in strip intercropping, since there are various ways to define it (e.g., based on strip width, row distances, and relative density; Zhang et al., 2007; Yu et al., 2015; Li et al., 2020a; Van der werf et al., 2021). For example, in our study, the area proportion of maize in six intercropping system was 50% calculated according to relative density, but when calculated according to row distances, it was 45% when intercropped with wheat, linseed and garlic, 46% when intercropped with pea and soybean, and 50% when intercropped with cabbage. In our study, the trend of overyielding of maize did not change according to different ways of calculation of area proportion occupied by each species which was greater with garlic than with pea and cabbage and greater than with soybean, wheat and linseed. The similarity of the results of the current and previous study suggests that the difference in overyielding of maize with different companion species was due to combination of intercropped species and not to details of configuration.

### 4.2. Relationship between overyielding of maize and species co-growth duration

As indicated by Bedoussac and Justes (2011), the LER cannot identify intraspecific and interspecific interactions. In this paper, we assessed whether different growth durations would affect the recovery growth of maize and its yield in intercropping with companion species. We hypothesized that differences in co-growth duration will affect the degree of competition and complementary between species. Dong et al. (2018) showed that temporal niche differentiation contributes to yield advantage of intercropping in Northwest China. Engbersen et al. (2021)

further confirmed this in a field experiment conducted in Spain. Long co-growth duration leads to a decrease in the maize yield, because of more interspecific competition with the companion species and shorter recovery growth for maize (Yu et al., 2015; Feng et al., 2021). This suggests that the effect of intercropping on maize is due to the interplay of two time-related factors: (1) the intensity of competition during the co-growth period which depends on the companion species dry matter production, its resource acquisition (light, water, nutrients) and the duration of this co-growth period, and (2) the duration of the recovery growth of maize, and the resources and conditions remaining (both soil resources and late season radiation and temperature) after companion crop harvest. We found that maize production was greater when it had a relatively longer recovery growth period, due to a shorter co-growth period. Indeed, this alleviates a strong competition between intercropped species, in turn, providing a good opportunity for maize to acquire resources during grain filling.

The index for temporal niche differentiation (TND) (Yu et al., 2015) is an interesting metric to integrate the effects of the lengths of both the co-growth and recovery periods. In our experiment, the TND had a significant effect on yield of the intercropped maize. High TND, corresponding with short growth durations of companion species such as pea, cabbage and garlic, was associated with greater overyielding of maize. The opposite was observed at low TND, corresponding with long growth durations of companion species (wheat, linseed, and soybean). It provides evidence for the positive correlation between TND and overyielding of intercropped maize, and for a negative correlation between co-growth duration and overyielding of maize (Fig. 3). Indeed, short duration of co-growth led to less competition on maize and greater recovery for maize to use the available resources (Li et al., 2020a; DeMalach et al., 2016). The maize was at V6 stage when pea, cabbage or garlic were harvested, leaving about 90–100 days for maize growing alone. At wheat harvest, maize was at V12 stage, the duration of maize growing alone remaining was about 70–80 days. At linseed harvest, maize was at the R2 stage, and the duration of maize growing alone just remained about 40 days. At the time of harvest of soybean, the maize was at R5 stage, just 4 days being left for maize growing alone. Overyielding of maize with pea, cabbage and garlic was 54.1%, 44.6% and 72.5%, respectively, and with wheat, linseed and soybean was 17.7%, 9.8% and 26.8%, respectively. These results support our hypothesis that a longer recovery period for maize contributes to its greater overyielding and to the advantage of maize-based intercropping systems.

From the perspective of the companion species, the shorter the co-growth duration, the higher the partial LER of the companion species. Indeed, a short co-growth duration means that the companion species reached maturity during the early development of maize, corresponding to a limited competition intensity towards the companion (Ma et al., 2020).

#### 4.3. Recovery of intercropped maize is closely associated with appropriate rate of nitrogen application

Li et al. (2011) found that nitrogen application significantly increased nitrogen acquisition and recovery of intercropped maize. Liu et al. (2020) showed that maize developed a changed root distribution pattern in the soil after wheat was harvested according to different soil nitrogen levels. In our study, the grain yields of intercropped maize were greater at high nitrogen application rate, but the trend towards overyielding was stronger at low than high nitrogen fertilization. This indicates that intercropped maize had a more efficient nitrogen utilization by exploiting nitrogen in companion species strip at low nitrogen than that of at high nitrogen leading to a relative higher intercropping advantage in low nitrogen condition. This suggests that the growth recovery of intercropped maize was related not only to temporal niche differentiation, but also to appropriate nitrogen input in these intercropping systems. Maize received indirectly nitrogen compensation, because when companion species were harvested it acquired nitrogen

from the area where companion species were growing. This supports our hypothesis that the recovery of intercropped maize would be greater with more nitrogen fertilizer input.

Our study is a good example of the “competition-recovery production” principle proposed in our previous studies (Li et al., 2001a; b). At maize harvest, compared with sole maize, differences of maize yield performance suggested that maize followed a different recovery growth process depending on the companion species. However, the recovery production of maize not only depended on the recovery growth period, but also on species combination. The present study included maize/legume, maize/cereal and maize/vegetable intercropping systems. These different combinations led to different recovery production. As for maize/legume intercropping systems, a high intercropping advantage will be obtained at low nitrogen input due to N<sub>2</sub> fixation by the legumes (Li et al., 2020b). However, in our study, two maize/legume intercropping systems showed inconsistent outcomes in terms of intercropping advantage. In the maize/pea intercropping system, the overyielding percentage of maize was greater at low nitrogen input than at high nitrogen input in both years but in the maize/soybean intercropping system, the overyielding percentage was greater at low N in 2010 but at high N in 2009. The longer recovery growth for maize intercropped with pea can play a role here. At low nitrogen rate, the maize intercropped with pea had a more efficient nitrogen use because of higher N<sub>2</sub> fixation of pea (Fan et al., 2006; Hu et al., 2018), meanwhile, shorter co-growth period decreased duration of interspecific competition, Thus, a relative higher overyielding for maize intercropped with pea. However, the longer co-growth period leads to more intense interspecific competition for resources, especially for light, between tall maize and the lower soybean crop at late growth stages, which limits efficient N utilization, finally, overyielding of maize intercropped with soybean was on average not different between nitrogen application rates. Thus, our results give only partial support to the hypothesis that species complementarities between maize and legumes are stronger if nitrogen input is low. In addition, although partial land equivalent ratio (PLER) for maize intercropped with soybean was comparable with that for maize intercropped with other companion species, the PLER for soybean was much lower than that of other companion species (Table 2). This is likely due to the intense shading of soybean by the taller maize plants at the late growth stages (Cheng et al., 2022), eventually leading to less yield advantage of maize/soybean intercropping in our present study.

As discussed above, there is a balance between the two species, with the growth of intercropped maize reduced by competitive companion species during the co-growth period, and recovery during the subsequent maize growth after companion species harvesting. Therefore, in maize-based intercropping systems, it is important to choose a suitable companion species to maintain a balance. The choice not only depends on temporal niche differentiation, but also on the intensity of interspecific interactions between intercropped species during co-growth and the intensity of recovery growth of the later-maturing species growing alone.

## 5. Conclusions

The present study demonstrates that the duration of the co-growth period is one of the main factors explaining the yield achieved by maize in maize-based intercropping systems. Maize will exhibit greater benefits if it has a relative longer recovery time after harvesting of companion species, due to a greater temporal complementarity. On the other hand, although increasing nitrogen supply can improve the yield of the mixtures, the relative yield advantage over sole crops was greater at low nitrogen availability. This shows that intercropping with maize is an option to increase the land-use efficiency and enhance the benefits from species complementarities with the right companion species. However, the advantage of intercropping is not only affected by temporal niche differentiation. In further investigations, we should pay

more attention to the spatial or nutrient niche differentiation between intercropped species and how nitrogen rates will be fit for maize-based intercropping.

### CRedit authorship contribution statement

**Jianhua Zhao:** Conceptualization, Methodology, Project administration, Investigation, Formal analysis, Writing – original draft, Visualization. **Laurent Bedoussac:** Methodology, Formal analysis, Data curation, Writing – review & editing, Visualization. **Jianhao Sun:** Experimental work. **Wei Chen:** Experimental work. **Weiqli Li:** Experimental work. **Xingguo Bao:** Experimental work. **Wopke van der Werf:** Methodology, Formal analysis, Data curation, Writing – review & editing. **Long Li:** Conceptualization, Supervision, Funding acquisition, Methodology, Writing – review & editing.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data availability

Data will be made available on request.

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### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.fcr.2023.108820](https://doi.org/10.1016/j.fcr.2023.108820).

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