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The importance of aboveground and belowground interspecific interactions in determining crop growth and advantages of peanut/maize intercropping

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ABSTRACT

Intercropping of maize (*Zea mays* L.) and peanut (*Arachis hypogaea* L.) often results in greater yields than the respective sole crops. However, there is limited knowledge of aboveground and belowground interspecific interactions between maize and peanut in field. A two-year field experiment was conducted to investigate the effects of interspecific interactions on plant growth and grain yield for a peanut/maize intercropping system under different nitrogen (N) and phosphorus (P) levels. The method of root separation was employed to differentiate belowground from aboveground interspecific interactions. We observed that the global interspecific interaction effect on the shoot biomass of the intercropping system decreased with the coexistence period, and belowground interaction contributed more than aboveground interaction to advantages of the intercropping in terms of shoot biomass and grain yield. There was a positive effect from aboveground and belowground interspecific interactions on crop plant growth in the intercropping system, except that aboveground interaction had a negative effect on peanut during the late coexistence period. The advantage of intercropping on grain came mainly from increased maize yield (means 95%) due to aboveground interspecific competition for light and belowground interaction (61%–72% vs. 28%–39% in fertilizer treatments). There was a negative effect on grain yield from aboveground interaction for peanut, but belowground interspecific interaction positively affected peanut grain yield. The supply of N, P, or N + P increased grain yield of intercropped maize and the contribution from aboveground interspecific interaction. Our study suggests that the advantages of peanut/maize intercropping for yield mainly comes from aboveground interspecific competition for maize and belowground interspecific facilitation for peanut, and their respective yield can be enhanced by N and P. These findings are important for managing the intercropping system and optimizing the benefits from using this system.

1. Introduction

Intercropping is an agroecological practice where two or more crop species are grown simultaneously in the same field [1,2], and has been widely used by smallholders in developing countries [3]. It often allows higher productivity than traditional sole crops [4,5] mainly due to its more efficient use of resources, such as light [6–8], water [9,10], and nutrients [11–13]. When multiple crop species are intercropped, interspecific facilitation and competition usually occur simultaneously [14,15]. Facilitation between species enhances crop growth through many mechanisms, one being the improvement of the microenvironment to allow increased availability of soil resources [11]. Competition, however, can suppress the growth of one species due to non-proportional sharing of limited resources or allelopathy [16]. Therefore, making full use of facilitation and competition between intercropped species can enhance environmental resource use and reduce costs, which enhances the sustainability of agriculture [17]. Recent work on interspecific interactions between crops has mainly focused on crop productivity and intercropping advantages [15,18,19], with

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little emphasis as to how the positive and negative interspecific interactions develop during the crop growth process.

In intercropping system, the soil–air interface creates a spatial division between aboveground and belowground interspecific interactions. Many studies showed root barriers can be used to separate belowground interaction from aboveground interaction [9,20–22]. These studies demonstrate that belowground interaction is more important than aboveground interaction for determining the productivity of an intercropped system compared to sole crop plantings [12,22,23]. However, others argue that aboveground interaction has a greater effect on the advantages of intercropping than belowground interaction [6,7,18]. The effects on productivity of both aboveground and belowground interspecific interactions vary according to crop species combinations [15,24] and are further modified by the availability of environmental resources [25]. Therefore, it is important that we achieve a thorough understanding of the role of aboveground and belowground interactions in crops plant growth if we are to optimize the advantages of intercropping.

A peanut/maize intercropping system creates significant advantages in yield compared with sole cropping [26,27]. Previous studies indicate that the advantages mainly derive from enhancement of soil nutrients, soil enzyme activity, and composition of the soil microbial community [28], or improvement in iron (Fe) nutrition and symbiotic N_2 fixation of peanut [27,29], due to belowground interspecific facilitation. However, other studies have shown that the advantages of this intercropping system are closely related to aboveground interspecific interactions because peanut/maize intercropping can enhance the photosynthetic performance of crops and increase the utilization efficiency of maize to strong light and peanut to weak light [30–32]. The combination of peanut and maize, as an example of a typical intercropping system of a taller species and a shorter species, has been shown to have more competition for light between the species toward the end of coexistence period, which suppresses the growth and grain yield of peanut [26,32] and thus limits the sustainability of applying the practice. Thus, it is not clear exactly which interspecific interaction, aboveground or belowground, contributes more to the intercropping advantages, and how each evolves with the growth of the species plant.

Nitrogen (N) fertilizer can increase cereal growth [33] and mediate interspecific interactions in intercropping [4]. Phosphorus (P) fertilizer can improve the net photosynthetic rate of intercropped peanut [26] and negatively affect the availability of soil Fe [34]. It is not known whether N supply can enhance the effect of aboveground competition in maize or whether P promotes the effect of belowground facilitation on peanut in peanut/maize intercropping. To further improve and optimize the productivity of intercropping, it is crucial to understand that the roles of aboveground and belowground interspecific interactions on crops growth and grain yields, especially under different fertilizer levels in fields. Thus, our aim is to quantify and compare the contributions of aboveground and belowground interspecific interactions on the plant growth and grain yield of intercropped peanut and maize, and to optimize interspecific interactions through N and P fertilizer treatments.

2. Materials and methods

2.1. Experimental site

Two consecutive field experiments were conducted in 2009 and 2010 at Quzhou Experimental Station of China Agricultural University (36°52′N, 115°02′E, and an altitude of 37 m above sea level), Hebei Province, China. The study area is located in the warm temperate zone, which has a semi-humid continental monsoon climate. Mean annual temperature at the site is approximately 11 °C and the annual cumulative temperature above 0 °C is approximately 3700 °C. The frost-free period is 180–200 days, and effective solar radiation is approximately 4920 MJ m^{-2} $year^{-1}$. Annual precipitation is approximately 600 mm and 80% occurs from June to August. In 2009 and 2010, the respective annual precipitation was 428 mm and 391 mm, and the respective mean temperature was 13.3 °C and 13.0 °C (Fig. 1). The soil type at this location is a calcareous alluvial soil, with a loamy and silty texture. Percentages of clay, silt, and sand in the topsoil are 14.7%, 74.0%, and 11.3%, respectively. At the start of experiment, some of the characteristics of the 0–20 cm soil layer, determined according to the standard method [35], were as follows: 1.35 g cm^{-3} soil bulk density, pH 8.2, 12.2 g kg^{-1} organic matter, 0.82 g kg^{-1} total N, 24.2 mg kg^{-1} available N, 7.52 mg kg^{-1} Olsen P, and DTPA-Fe, -Mn, -Zn, -Cu 4.73 mg kg^{-1}, 3.67 mg kg^{-1}, 0.52 mg kg^{-1}, and 0. 92 mg kg^{-1}, respectively.

2.2. Experimental design

We used cultivars that are commonly used by local farmers were the following: maize (*Zea mays* L.) cv. Zhengdan 958 and peanut (*Arachis hypogaea* L.) cv. Huayu 16. The field experimental design was a randomized block design with three replicates, with three crop systems and three fertilizer treatments in 2009 and four fertilizer treatments in 2010.

The crop systems were the following: sole peanut (SP) (Fig. 2A); sole maize (SM) (Fig. 2B); intercropping of peanut/maize (IC) consisting of three alternating strips of two rows of maize and four rows of peanut, without root barriers between adjacent maize (IM) and peanut (IP) rows (Fig. 2C); and peanut/maize intercropping with root barriers between adjacent maize (IMB) and peanut (IPB) rows (Fig. 2D), which is the same strip-based intercropping system. In sole cropping, rows were spaced 60 cm apart, and plants were spaced 25 cm apart for maize (Fig. 2A); for peanut row spacing was 30 cm, and plant spacing within the row was 20 cm (Fig. 2B). The plant density was 66,667 plants ha^{-1} for sole maize and 166,667 plants ha^{-1} for sole peanut. Each sole crop plot contained 20 rows of peanut or 10 rows of maize. In peanut/maize intercropping plots without root barriers (with potential belowground interspecific interactions) or with root barriers (no belowground interspecific interaction), the row spacing was 30 cm for peanut and 40 cm for maize, and plant spacing within the row was 20 cm for both peanut and maize. The distance between adjacent maize and peanut rows was 35 cm (Fig. 2C, D). The plant density was 50,000 plants ha^{-1} for maize and 100,000 plants ha^{-1} for peanut. Thus, the relative density of intercropped maize (M) and intercropped peanut (PT) were 0.75 and 0.6, respectively. The proportion of plant density occupied by maize (O_m) and peanut (O_P) in intercropping was calculated by the following respective equations $O_m = M/(M + PT) = 0.556(5/9)$ and $O_P = P/(M + PT) = 0.444(4/9)$. In peanut/maize intercropping plots with root barriers, plastic sheet barriers were inserted into the ground between adjacent maize and peanut rows to a depth of 60 cm using a narrow-groove method [36] (Fig. 2D). The barriers were installed prior to maize sowing and about 10 days after peanut emergence, in order to prevent belowground interspecific interactions between maize and peanut. The distances from the barrier to peanut and maize rows were 15 cm and 20 cm, respectively (Fig. 2D).

Fertilizer treatments are shown in Table 1. There were three fertilizer treatments using N0P0, N1P0 and N0P1 for each crop system in 2009, and four fertilizer treatments using N0P0, N1P0, N0P1, and N1P1 for each crop system in 2010. The field plots received 90 kg N ha^{-1} as urea prior to peanut sowing and 90 kg N ha^{-1} as urea as a furrow dressing for the maize at the sixth-leaf stage

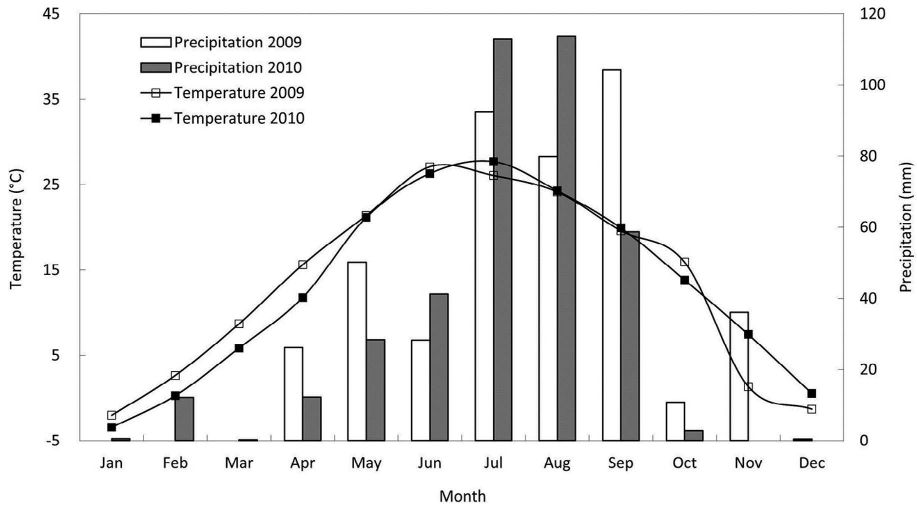

Fig. 1. Monthly mean temperature and precipitation in 2009 and 2010.

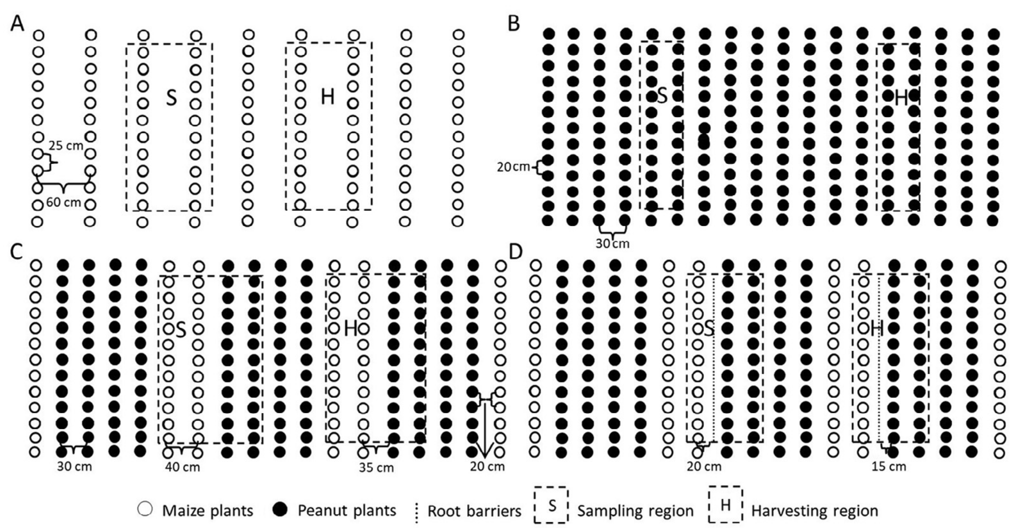

Fig. 2. Layout of the four cropping systems. (A) sole maize; (B) sole peanut; (C) maize/peanut intercropping without root barriers; (D) maize/peanut intercropping with root barriers.

Table 1
Fertilizer treatments in different crop systems.

Year	Fertilizer treatment	N (kg N ha^{-1})				P (kg P_2O_5 ha^{-1})			
		Sole peanut	Intercrop peanut	Sole maize	Intercrop maize	Sole peanut	Intercrop peanut	Sole maize	Intercrop maize
2009	N0P0	0	0	0	0	0	0	0	0
	N1P0	90	90	180	180	0	0	0	0
	N0P1	0	0	0	0	150	150	150	150
2010	N0P0	0	0	0	0	0	0	0	0
	N1P0	90	90	180	180	0	0	0	0
	N0P1	0	0	0	0	150	150	150	150
	N1P1	90	90	180	180	150	150	150	150

(V6, jointing stage) in N treatments, and 150 kg P_2O_5 ha^{-1} as diammonium phosphate prior to peanut sowing in P treatments. In both years, the field experiment was spray-irrigated to 60 mm for each plot after furrow dressing the maize with N fertilizer.

Each plot measured 48 m^2 (6 × 8 m) in area. Rows were oriented south-north. Peanut was sown on May 2, 2009 and harvested on September 15, 2009, and again sown on May 10, 2010 and harvested on September 12, 2010. Maize was sown on June 1, 2009 and harvested on September 15, 2009, and again sown on June 10, 2010 and harvested on October 6, 2010.

2.3. Sampling and analytical methods

2.3.1. Shoot biomass

Each experimental plot was divided into two sections. One section of each plot was used for measuring shoot biomass (peanut including pods) per plant (Fig. 2, the sampling region), while the other section was used for determining the yields for maize and peanut (Fig. 2, the harvest region).

Four peanut plants were sampled at 40, 63, 82, 99, and 117 days after germination in 2009, and 39, 60, 81, and 110 days after germination in 2010, and two maize plants were sampled at 25, 50, 65, 79, and 97 days after germination in 2009, and 23, 39, 62, 89, 114 days after germination in 2010. Tap water was used to wash the soil and dust off of the plants, and they were separated into vegetative and grain parts. Samples were oven-dried at 85 °C to constant weight.

2.3.2. Yield

Maize and peanut were manually harvested from a 2 m × 2 row sampling area in each plot at plant physiological maturity, but in the plot that had with root barriers, maize was manually harvested from a 4 m × 1 row sampling area (Fig. 2). Each plant type was separated into their grain and vegetative parts. The sampling method avoided border rows for each plot. Samples were sun dried to constant weight.

2.3.3. Fitting the growth model

Logistic growth curves were fitted to the shoot biomass data for all treatments except intercropped peanut with root barriers (the lack of sample data during the seedling period meant the growth curves could not be fitted) in order to characterize the growth [5]:

$$Y_t = K/\left(1 + e^{r(t_{50}-t)}\right) \tag{1}$$

where Y_t (g plant^{-1}) is per-plant shoot biomass at t days after seedling; K (g plant^{-1}) represents the maximum per plant biomass; r (day^{-1}) is the intrinsic growth rate; and t_{50} (day) is the time (days after germination) for maximum absolute growth rate. All three parameters (K, r, and t_{50}) were estimated using the nonlinear least square function "*nls*" in R [37]. Parameter values were determined by fitting the growth curves to the data per plot. Points in the figures show average values over replicates, and the curves in the figures represent the estimated logistic curves of the mean parameter values across replicates.

2.3.4. Calculation

In this article, the biological yield of maize or peanut is the total yield of plant material, not including root mass. The weighted mean total grain yield per hectare in sole crop systems (SC) was calculated according to [37]:

$$\text{Weighted mean SC yield} = U_{SCP} \times O_P + U_{SCM} \times O_M \tag{2}$$

where U_{SCP} and U_{SCM} are grain yields per hectare of peanut and maize as sole crops, respectively. O_P and O_M are the proportions of plant density occupied by peanut and maize in intercropping, which are 4/9 and 5/9, respectively.

Land equivalent ratio (LER) was used as an indicator of land/resource-use efficiency and the yield advantage of intercropping compared with sole crop. It was calculated according to Trenbath [1]:

$$\text{LER} = \text{PLERM} + \text{PLERP} = Y_{IM}/Y_{SM} + Y_{IP}/Y_{SP} \tag{3}$$

where PLERM and PLERP are partial land equivalent ratio for maize and peanut, respectively, Y_{SM} and Y_{IM} are grain yields per hectare of sole maize and intercropped maize, respectively, and Y_{SP} and Y_{IP} are grain yields per hectare of sole peanut and intercropped peanut, respectively. The partial land equivalent ratio values were calculated as the ratios between intercropped and sole crop yields. A LER > 1 indicates that the intercropping system uses environmental resources for growth more efficiently than sole crops grown in a similar area.

The effects of aboveground and belowground interspecific interaction on crops shoot biomass and grain yield per hectare were calculated using LER or PLER. When there is no root barrier in the intercrop, aboveground and belowground interspecific interactions simultaneously occur to crop shoot biomass and grain yield. We term this the *global interspecific interaction effect* (GIIE). When there is a root barrier, only aboveground interspecific interaction influences crop shoot biomass and grain yield. Assuming that the aboveground and belowground effects are additive, the contribution from belowground interspecific interaction equals the global interspecific interaction effect minus the aboveground interspecific interaction effect.

Thus, the global interspecific interaction effect (GIIE), aboveground interspecific interaction effect (AIIE), and belowground interspecific interaction effect (BIIE) were obtained as GIIE = LER – 1, AIIE = LER – $\text{LER}_{barrier}$ and BIIE = GIIE – AE for the intercropping system. For the intercrop component species, the calculations were as follows: Peanut-GIIE = PLERP – O_P, AIIE = PLERP – $\text{PLERP}_{barrier}$ and BIIE = GIIE – AIIE, Maize-GIIE = PLERM – O_M, AIIE = PLERM – $\text{PLERM}_{barrier}$ and BIIE = GIIE – AIIE. The contribution from the aboveground effect (CAE) and belowground effect (CBE) was obtained as CAE = AIIE/GIIE × 100% and CBE = BIIE/GIIE × 100%, respectively. Here, $\text{LER}_{barrier}$, $\text{PLERP}_{barrier}$, and $\text{PLERM}_{barrier}$ are the land equivalent ratio, partial land equivalent ratio for peanut, and partial land equivalent ratio for maize in intercropping system with root barriers, respectively.

2.4. Data analysis

The effects of intercropping and root barriers on shoot biomass in the intercropped species and grain yield in the cropping systems were analyzed using SPSS v24.0 (SPSS Inc., Chicago, IL, USA). Significant differences between the treatments were determined by LSD at $P < 0.05$.

3. Results

3.1. Effects of interspecific interaction on shoot biomass dynamics per peanut plant

There were significant differences in the growth of peanut plants between the sole and intercropped system, and responses were influenced by fertilizer treatments. Compared with the sole crop plots, the growth of intercropped peanut was significantly enhanced without the supply N and P, or with only the supply P, except at the maturity stage. The peanut shoot biomass in the intercropped system was reduced compared to sole crop when N or N + P were supplied about 60 days after seedling (DAS) (Fig. 3). When there were root barriers between the adjacent rows of maize and peanut to eliminate belowground interspecific interactions, the shoot biomass per plant of intercropped peanut was reduced, regardless of fertilizer treatment, especially at about 80 DAS (the pod swelling stage), as well as harvest time. The difference achieved statistical significance (Fig. 3). The supply of N promoted the growth of peanut in sole cropped system but did not influence peanut growth in the intercropped system. The supply of only P promoted the growth of intercropped peanut but suppressed peanut growth in the sole system (Fig. 3).

3.2. Effects of interspecific interaction on shoot biomass dynamics per maize plant

Intercropped maize growth was only slightly lower than that of the sole crop (Fig. 4). When there was a root barrier between adjacent maize and peanut rows to eliminate belowground interspeci-

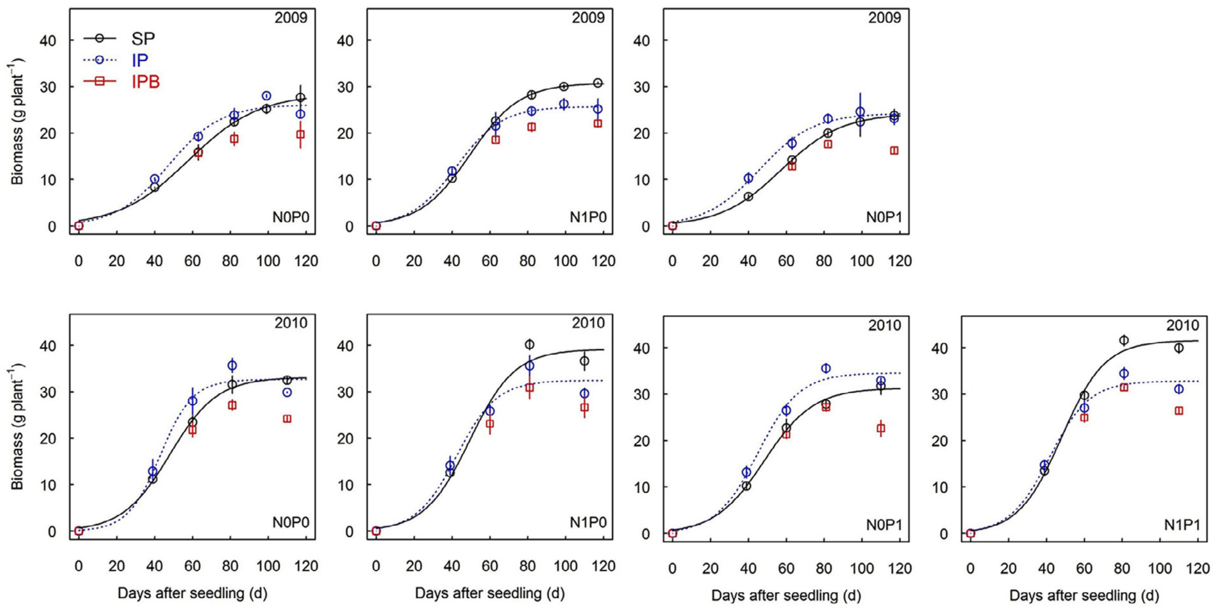

Fig. 3. Effects of peanut/maize intercropping on biomass per plant of peanut at different growth stages (2009 and 2010). SP represents sole peanut; IP and IPB represent intercropped peanut without and with root barriers, respectively. N0P0, 0 kg N ha^{-1} and 0 kg P_2O_5 ha^{-1}; N1P0, 90 kg N ha^{-1} for sole and intercropped peanut and 180 kg N ha^{-1} for sole and intercropped maize, 0 kg P_2O_5 ha^{-1}; N0P1, 0 kg N ha^{-1} and 150 kg P_2O_5 ha^{-1}; N1P1, 90 kg N ha^{-1} for sole and intercropped peanut and 180 kg N ha^{-1} for sole and intercropped maize, and 150 kg P_2O_5 ha^{-1}. The error bars are standard deviations from the means (n = 3).

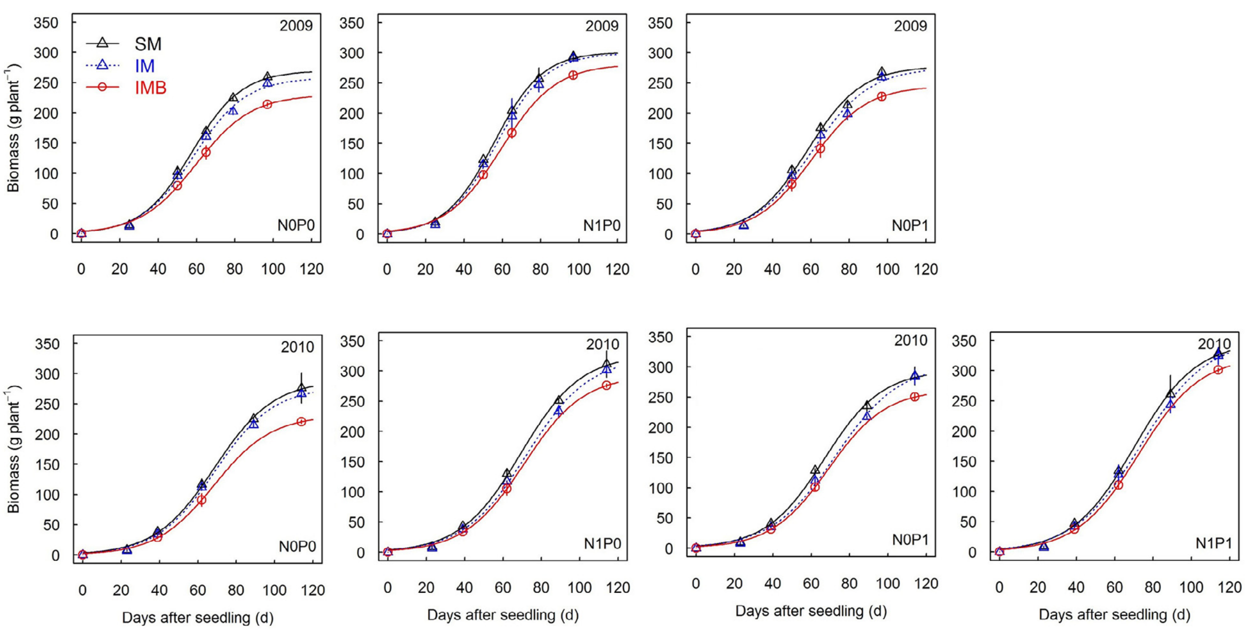

Fig. 4. Effects of peanut/maize intercropping on biomass per plant of maize at different growth stages (2009 and 2010). SM represents sole maize, while IM and IMB represent intercropped maize without and with root barriers, respectively. N0P0, 0 kg N ha^{-1} and 0 kg P_2O_5 ha^{-1}; N1P0, 90 kg N ha^{-1} for sole and intercropped peanut and 180 kg N ha^{-1} for sole and intercropped maize, 0 kg P_2O_5 ha^{-1}; N0P1, 0 kg N ha^{-1} and 150 kg P_2O_5 ha^{-1}; N1P1, 90 kg N ha^{-1} for sole and intercropped peanut and 180 kg N ha^{-1} for sole and intercropped maize, and 150 kg P_2O_5 ha^{-1}. The error bars are standard deviations from the means (n = 3).

fic interactions, maize of growth was significantly decreased in the intercrop treatments at the milk (about 80 DAS) and harvest stages (Fig. 4). Supply of N, P, or N + P significantly enhanced maize growth in sole and intercropped systems compared with the no fertilizer treatments.

3.3. Contribution of aboveground and belowground interspecific interaction effect on peanut shoot biomass

The global interspecific interaction effect (GIIE) on peanut shoot biomass was gradually reduced over the course of growth and development, except when only P was supplied in 2010 experiments. The GIIE on peanut biomass increased with the supply of P, except at early coexistence period in 2010, and decreased with the supply of N, compared with no supply of N and P (Table 2). Analysis of GIIE on shoot biomass indicated that both aboveground and belowground interspecific interaction improved peanut growth, except that the aboveground interspecific interaction reduced peanut shoot biomass at late coexistence period (Table 2). The contribution of the aboveground interspecific interaction effect (CAE) on peanut shoot biomass gradually decreased over the course of growth and development, but the contribution of

Table 2
Global interspecific interaction effect (GIIE) and contribution of aboveground and belowground interspecific interaction effects (CAE and CBE) on shoot biomass of intercropped species at different growth stages (mean, n = 3).

Crop	Year	Fertilizer level	Early coexistence period			Middle coexistence period			Late coexistence period		
			GIIE	CAE (%)	CBE (%)	GIIE	CAE (%)	CBE (%)	GIIE	CAE (%)	CBE (%)
Peanut	2009	N0P0	0.291	44	56	0.194	30	70	0.082	−14	114
		N1P0	0.133	38	62	0.081	11	89	0.047	−29	129
		N0P1	0.308	32	68	0.249	34	66	0.140	−24	124
	2010	N0P0	0.277	41	59	0.237	31	69	0.108	3	97
		N1P0	0.157	59	41	0.087	20	80	0.047	−14	114
		N0P1	0.261	47	53	0.321	44	56	0.179	−9	109
		N1P1	0.102	59	41	0.053	20	80	0.023	−198	298
Maize	2009	N0P0	0.147	18	82	0.156	26	74	0.163	39	61
		N1P0	0.148	29	71	0.161	37	63	0.187	62	38
		N0P1	0.124	21	79	0.143	34	66	0.171	48	52
	2010	N0P0	0.111	15	85	0.152	19	81	0.166	27	73
		N1P0	0.106	33	67	0.121	42	58	0.173	64	36
		N0P1	0.092	29	71	0.096	35	65	0.171	60	40
		N1P1	0.122	40	64	0.162	40	60	0.187	71	29

N0P0, 0 kg N ha^{-1} and 0 kg P_2O_5 ha^{-1}; N1P0, 90 kg N ha^{-1} for sole and intercropped peanut and 180 kg N ha^{-1} for sole and intercropped maize, 0 kg P_2O_5 ha^{-1}; N0P1, 0 kg N ha^{-1} and 150 kg P_2O_5 ha^{-1}; N1P1, 90 kg N ha^{-1} for sole and intercropped peanut and 180 kg N ha^{-1} for sole and intercropped maize, and 150 kg P_2O_5 ha^{-1}. Early coexistence period was around the podding stage of peanut and twelfth leaf stage of maize. The middle coexistence period was around the pod swelling stage for peanut and milk stage for maize. The late coexistence period was around the maturity stage for both peanut and maize.

the belowground interspecific interaction effect (CBE) was reversed. Supplying N reduced the CAE and increased the CBE on shoot biomass for peanut (Table 2).

3.4. Contribution of aboveground and belowground interspecific interaction effect on maize shoot biomass

The GIIE on shoot biomass of maize gradually increased over the course of growth and development. The supply of N or P increased the advantage of intercropping in term of maize shoot biomass in the late coexistence period (Table 2). Both aboveground and belowground interspecific interactions improved the growth of maize, and the CAE on maize shoot biomass gradually increased over the course of growth and development, while that of the CBE was reduced. The CAE on maize biomass was greater than that of the CBE in the late coexistence period, but this was only the case when fertilizers were supplied (Table 2). Supplying N, P, or N + P increased CAE and reduced CBE on maize biomass compared with when no fertilizer was supplied. In late coexistence period, the CAE on maize biomass with N + P supplied was greater than that of when only N or P was supplied (Table 2).

3.5. Contribution of aboveground and belowground interspecific interaction effect on intercropping system shoot biomass

The average GIIE on shoot biomass in intercropping system gradually decreased with the length of maize and peanut coexistence period. Both aboveground and belowground interspecific interactions had positive effects on shoot biomass of the intercropped system, and CBE had more significant contributions on advantages of intercropping in terms of final shoot biomass than did CAE. The advantage of intercropping according to shoot biomass of the intercropped species decreased when N was supplied and increased when P was supplied, except during the early coexistence period (Table 3). The CBE on shoot biomass of the intercropping system was higher than of the CAE and increased over the time of coexistence when no N was applied. N application increased the CAE on shoot biomass of intercropping system compared to no supply of N (Table 3).

3.6. Effects of aboveground and belowground interspecific interaction on crop grain yield

In the two-year field experiment, the average grain yield per hectare was significantly lower (26%) for intercropped maize than for sole maize, and 55% lower for intercropped peanut than for sole peanut. The combined intercropped yield was significantly higher (25%) than that of the weighed sole crop yield based on the IC proportions. The grain yields for intercropped maize, intercropped peanut, and the intercropping system as a whole were significantly reduced when there was a root barrier to eliminate the belowground interspecific interaction (Table 4). The average land equivalent ratio of the intercropping system was 1.20 ± 0.07 (Table 4). The partial land equivalent ratios (PLERs) for maize and peanut

Table 3
Global interspecific interaction effect (GIIE) and contribution of aboveground and belowground interspecific interaction effects (CAE and CBE) on shoot biomass in an intercropping system at different growth stages (mean, n = 3).

Year	Fertilizer level	Early coexistence period			Mid coexistence period			Late coexistence period		
		GIIE	CAE (%)	CBE (%)	GIIE	CAE (%)	CBE (%)	GIIE	CAE (%)	CBE (%)
2009	N0P0	0.439	37	63	0.366	37	63	0.243	18	82
	N1P0	0.316	40	60	0.242	39	61	0.234	46	54
	N0P1	0.432	28	72	0.393	34	66	0.310	24	76
2010	N0P0	0.383	34	66	0.388	26	74	0.274	17	83
	N1P0	0.243	54	46	0.228	40	60	0.216	56	44
	N0P1	0.373	32	68	0.417	43	57	0.350	25	75
	N1P1	0.223	49	51	0.215	33	67	0.210	44	56
Average value		0.344 ± 0.086	39 ± 9	60 ± 9	0.321 ± 0.086	36 ± 6	64 ± 6	0.262 ± 0.052	33 ± 16	67 ± 16

N0P0, 0 kg N ha^{-1} and 0 kg P_2O_5 ha^{-1}; N1P0, 90 kg N ha^{-1} for sole and intercropped peanut and 180 kg N ha^{-1} for sole and intercropped maize, 0 kg P_2O_5 ha^{-1}; N0P1, 0 kg N ha^{-1} and 150 kg P_2O_5 ha^{-1}; N1P1, 90 kg N ha^{-1} for sole and intercropped peanut and 180 kg N ha^{-1} for sole and intercropped maize, and 150 kg P_2O_5 ha^{-1}.

Table 4
Grain yield, partial land equivalent ratio (PLER), and land equivalent ratio (LER) on grain yield (mean ± SE, n = 3).

Year	Fertilizer level	Plant pattern	Maize		Peanut		System		Yield advantage[1] (t ha^{-1})
			Yield (t ha^{-1})	PLER	Yield t ha^{-1}	PLER	Yield (t ha^{-1})	LER	
2009	N0P0	SC	8.37 ± 0.42 b		4.86 ± 0.73 b		☆6.81 ± 0.22 ef		
		IC	6.20 ± 0.21 ef	0.742	2.35 ± 0.14 c	0.492	8.55 ± 0.30 b	1.23	1.74 ± 0.52 b
		ICB	5.12 ± 0.14 g	0.613	2.01 ± 0.07 cd	0.422	7.13 ± 0.14 de	1.03	0.32 ± 0.17 d
	N1P0	SC	9.45 ± 0.12 a		5.65 ± 0.81 a		☆7.76 ± 0.38 c		
		IC	7.91 ± 0.47 c	0.837	2.15 ± 0.31 c	0.391	10.1 ± 0.16 a	1.23	2.30 ± 0.20 a
		ICB	7.16 ± 0.23 d	0.758	1.71 ± 0.04 cd	0.306	8.86 ± 0.21 b	1.06	1.11 ± 0.19 c
	N0P1	SC	8.64 ± 0.20 b		4.22 ± 0.28 b		☆6.68 ± 0.11 f		
		IC	6.44 ± 0.01 e	0.746	2.15 ± 0.13 c	0.509	8.59 ± 0.12 b	1.25	1.91 ± 0.06 ab
		ICB	5.87 ± 0.24 f	0.680	1.40 ± 0.09 d	0.332	7.27 ± 0.32 d	1.01	0.60 ± 0.33 d
2010	N0P0	SC	10.9 ± 0.16 b		4.65 ± 0.25 c		☆8.13 ± 0.18 g		
		IC	7.56 ± 0.15 f	0.694	2.36 ± 0.19 de	0.509	9.92 ± 0.15 c	1.20	1.79 ± 0.32 ab
		ICB	6.45 ± 0.08 g	0.592	1.97 ± 0.22 f	0.424	8.42 ± 0.15 fg	1.02	0.29 ± 0.22 e
	N1P0	SC	11.8 ± 0.21 a		5.03 ± 0.35 b		☆8.81 ± 0.06 ef		
		IC	8.34 ± 0.44 d	0.704	2.01 ± 0.15 ef	0.400	10.3 ± 0.29 b	1.10	1.53 ± 0.30 b
		ICB	7.68 ± 0.18 ef	0.649	1.84 ± 0.10 f	0.367	9.52 ± 0.27 cd	1.02	0.71 ± 0.24 de
	N0P1	SC	11.2 ± 0.36 b		4.48 ± 0.30 c		☆8.24 ± 0.19 g		
		IC	8.10 ± 0.17 de	0.720	2.44 ± 0.10 d	0.546	10.5 ± 0.12 b	1.27	2.29 ± 0.08 a
		ICB	7.37 ± 0.15 f	0.656	1.69 ± 0.20 f	0.379	9.07 ± 0.34 e	1.04	0.83 ± 0.52 cd
	N1P1	SC	12.1 ± 0.63 a		5.50 ± 0.21 a		☆9.17 ± 0.28 de		
		IC	9.35 ± 0.24 c	0.773	2.01 ± 0.13 ef	0.366	11.4 ± 0.36 a	1.14	2.19 ± 0.10 a
		ICB	8.58 ± 0.27 d	0.709	1.87 ± 0.11 f	0.342	10.5 ± 0.37 b	1.05	1.28 ± 0.19 bc

N0P0, 0 kg N ha^{-1} and 0 kg P_2O_5 ha^{-1}; N1P0, 90 kg N ha^{-1} for sole and intercropped peanut and 180 kg N ha^{-1} for sole and intercropped maize, 0 kg P_2O_5 ha^{-1}; N0P1, 0 kg N ha^{-1} and 150 kg P_2O_5 ha^{-1}; N1P1, 90 kg N ha^{-1} for sole and intercropped peanut and 180 kg N ha^{-1} for sole and intercropped maize, and 150 kg P_2O_5 ha^{-1}. SC represents a sole crop system; IC and ICB represent intercrop without and with a root barrier, respectively. ☆SC weighted mean for sole crops. [1] Yield advantage is the difference between the actual combined intercrop yield and the weighted mean yield. Different lowercase letters within columns and years indicate differences that are significant at the 0.05 probability level.

grain were 0.74 ± 0.05 and 0.46 ± 0.07, which were higher than the proportion of plant density 0.556 (= 5/9) and 0.444 (= 4/9) in the intercropping system, respectively, but the PLERs for peanut were reduced when only N or N plus P were supplied. The land equivalent ratios (LERs) in grain for the intercropping system were higher than 1, and near 1 when root barriers were installed, regardless fertilizer treatment (Table 4).

Supplying N significantly increased maize and sole peanut yields but reduced intercropped peanut yields compared with no supply of N. At the same N level, supplying P increased maize yields compared with no supply of P. The LERs for the intercropped system were increased by supplying P but reduced by supplying N in 2010 (Table 4).

3.7. Contribution of aboveground and belowground interspecific interaction on crop grain yield

The aboveground and belowground interspecific interactions had positive effects on grain yields for maize and the intercropped system, and the contribution of belowground interspecific interaction was higher than that of aboveground interspecific interaction, except for intercropped maize receiving fertilizer treatments. The aboveground interspecific interaction had negative effects on grain yields for peanut, but belowground interspecific interaction had positive effects (Table 5).

The supply of N or N + P increased the contribution of aboveground interspecific interaction to grain yield for maize and intercropped system yields and decreased the effect of belowground interspecific interaction. Supplying only P increased the contribution of belowground interspecific interaction to peanut yield and decreased the contribution of aboveground interspecific interaction, and these results were reversed when N was supplied (Table 5).

4. Discussion

The interspecific interaction plays a crucial role in higher yields of intercropping systems [18,38]. However, there are often variations between component species in the effects of aboveground and belowground interspecific interactions on crop growth [15]. We observed that the global interspecific interaction effect on shoot biomass in a peanut/maize intercropping system decreased

Table 5
Contribution of above- and belowground interspecific interaction on grain yield for intercropped species and intercropping system at maturity stage (mean, n = 3).

Year	Fertilizer levels	Maize			Peanut			Intercropping system		
		GIIE	CAE (%)	CBE (%)	GIIE	CAE (%)	CBE (%)	GIIE	CAE (%)	CBE (%)
2009	N0P0	0.186	31	69	0.048	−46	146	0.234	15	85
	N1P0	0.281	72	28	−0.053	−259	159	0.228	28	72
	N0P1	0.190	65	35	0.065	−172	272	0.255	5	95
2010	N0P0	0.138	26	74	0.065	−31	131	0.203	8	92
	N1P0	0.148	63	37	−0.044	−173	73	0.104	19	81
	N0P1	0.164	61	39	0.102	−64	164	0.266	13	87
	N1P1	0.217	70	30	−0.078	−132	32	0.139	36	64

N0P0, 0 kg N ha^{-1} and 0 kg P_2O_5 ha^{-1}; N1P0, 90 kg N ha^{-1} for sole and intercropped peanut and 180 kg N ha^{-1} for sole and intercropped maize, 0 kg P_2O_5 ha^{-1}; N0P1, 0 kg N ha^{-1} and 150 kg P_2O_5 ha^{-1}; N1P1, 90 kg N ha^{-1} for sole and intercropped peanut and 180 kg N ha^{-1} for sole and intercropped maize, and 150 kg P_2O_5 ha^{-1}. GIIE represents global interspecific interaction effect; CAE and CBE represent the contribution of aboveground and belowground interspecific interaction effect, respectively.

with the course of coexistence period. We also observed that belowground interaction contributed more than aboveground interaction to advantages of the intercropping system in terms of shoot biomass and grain yield. There was a positive effect from aboveground and belowground interspecific interactions on crop plant growth in the intercropping system, except that aboveground interaction had a negative effect on peanut during late coexistence period. The roles of belowground interaction for peanut and aboveground interaction for maize increased over the growth period and were promoted by P and N supplementation, respectively.

4.1. Effects of belowground and aboveground interspecific interaction on advantages of the intercropping

In this study, the LERs for peanut/maize intercropping on grain yield and final shoot biomass were 1.20 and 1.27, respectively, which showed that interspecific interaction has positive contribution to crop productivity, as previously observed [26,27,32]. When root barriers were introduced to eliminate belowground interspecific interaction, it was observed that advantages of the intercropping on grain yields and final shoot biomass were reduced by 82% and 67%, respectively. This indicates that belowground interactions contribute more to advantage of the peanut/maize intercropping than do aboveground interactions. The same results were also observed in other intercropping system [9,12,21,22]. However, in a maize/soybean relay intercropping system, productivity is affected more by aboveground interactions than belowground interactions [7,18]. One of the different reasons may be that peanut/maize intercropping has a longer coexistence period than maize/soybean relay intercropping. Another reason may be that peanut/maize intercropping modifies the soil microenvironment [29,39], which improves Fe nutrition in peanut and promotes symbiotic N_2 fixation [27,40,41], and that maize acquires more soil inorganic N from the row of peanut [27]. In some taller/shorter crops intercropping systems, the yield of shorter crop often decreases due to shading from the taller crop [42]. Our study found the same result, and the advantage of intercropping peanut in terms of shoot biomass gradually lessened with the period of coexistence.

The availability of soil nutrients can mediate the effects of interspecific interactions in intercropping systems [4,25,43]. We found that supplying N increased the contributions of aboveground interspecific interaction to the final shoot biomass and grain yields of the intercropping system by 76%–229% and 87%–177%, respectively, as compared to plots that did not receive supplemental N. Supplying P increased GIIE on the final shoot biomass of the intercropping system compared to those that did not receive supplemental P (Table 3). Therefore, the intercropping system has significantly higher grain yields with supplementation of N plus P than with the other fertilizer treatments (Table 4). It is suggested that managing intercrop component interactions with N and P supply may be used to optimize the intercropping advantages in the system, as previously has been proposed [18,26,43,44].

4.2. Effects of belowground and aboveground interspecific interaction on maize

In most cereal/legume intercropping systems, the cereals have a greater competitive ability to uptake soil inorganic nitrogen and may benefit from the transfer of fixed nitrogen from the legumes [33,45–48]. In peanut/maize intercropping, we found that belowground interspecific interaction had a positive effect on shoot biomass and grain yield for maize (Tables 2, 5), due to the maize's acquisition of more nitrogen [41]. About 30 days after the seedling (sixth leaf stage), the maize became taller and had more competition for light, significantly increasing the net photosynthetic rate and the allocation of photosynthates to grains [30,32]. Consequently, the advantages of intercropping on maize shoot biomass increased and the contribution of aboveground interspecific interaction to shoot biomass increased as growth progressed (Table 2). This was specifically what occurred during the late coexistence period, when aboveground interspecific interaction dominated the growth of maize that was supplemented with N, P, or N + P conditions due to N or P promoting crop growth [43,44,49]. Therefore, the contribution of aboveground interaction to the advantage seen in final shoot biomass and grain yield was greater than the contribution from belowground interaction (Tables 2, 5). The same result was found in a study of maize and soybean relay intercropping [18]. In our study, we observed that advantages of the intercropping on grain yield mainly came from the intercropped maize, which contributed anywhere from 62% to 156% (Table 5). It is suggested that maize's aboveground interspecific competition for light played a key role in achieving the advantage of grain yield in intercropping system of peanut/maize.

4.3. Effects of belowground and aboveground interspecific interaction on peanut

Peanut/maize intercropping can effectively improve Fe nutrition of peanut by maize root secretion of phytosiderophores, change the biogeochemical and microbial properties of the rhizosphere [29,50,51], and promote the expression of Fe uptake genes (*AhFRO1* and *AhYSL1*) roots [50] and Fe transporter genes (AhNRAMP1 and AhDMT1) in roots and leaves of peanut [39,52], which enhanced peanut symbiotic N_2 fixation [27,39]. Thus, we observed that belowground interspecific interaction had a positive effect on intercropped peanut growth and its shoot biomass (Fig. 2; Table 2). However, the advantage for peanut shoot biomass decreased over the course of the coexistence period (Table 2), which is likely due to the reduction of the net photosynthetic rate in the peanut crop as a consequence of serious light competition from maize [30,32]. It had been also reported that aboveground light competition reduced the dry weight of the shorter crop in a taller/shorter crop intercropping system [15]. Moreover, this disadvantage was aggravated because the taller crops experienced increased growth with the availability of soil nutrients [33,43,53]. Therefore, when N or P was applied, maize probably competed even more strongly for light against the peanut crop, with the enhanced maize growth suppressing peanut growth and leading to the negative effect on the final shoot biomass and grain yield for this shorter crop. Thus, intercropped peanut was not found to have an intercropping advantage in terms of grain yield when N or N + P was supplied to the intercropped plots (Tables 2 and 5). Compared with no P supply, the growth of sole peanut plots was suppressed by only supplemental P, showing a lower growth than intercropped peanut (Table 2), which may be closely related to P fertilizer negatively effecting the availability of soil Fe [34]. Also, it was observed that the contribution of belowground interaction to peanut grain yield increased when only P was supplied (Table 5). These results imply that belowground interspecific facilitation has more significant contributions to peanut growth and grain yield than aboveground interspecific interaction and is promoted by P.

5. Conclusions

Our study of peanut/maize intercropping shows that belowground interspecific interactions stimulate peanut growth, while aboveground interspecific interactions seem to suppress peanut growth but promote maize growth during late coexistence phase. Both aboveground and belowground interspecific interactions had positive effects on advantages of the intercropping, but belowground interaction had more of a contribution than aboveground interaction. It is suggested that belowground interspecific facilitation for peanut and aboveground interspecific competition for maize play the key roles in controlling productivity of a peanut/-maize intercropping system. Adding N increased the contribution of aboveground interspecific interaction to maize grain yield; adding P improved the belowground interspecific interaction on peanut grain yield. Thus, to optimize the advantages of peanut/maize intercropping and improve crop yields, it is essential to optimize belowground interspecific interactions and manage aboveground interspecific competition for light using N and P fertilizer treatments.

CRediT authorship contribution statement

Nianyuan Jiao: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Resources, Validation, Writing - original draft, Writing - review & editing. **Jiangtao Wang**: Writing - review & editing. **Chao Ma**: Writing - review & editing. **Chaochun Zhang**: Writing - review & editing. **Dayong Guo**: Data curation, Writing - review & editing. **Fusuo Zhang**: Conceptualization, Funding acquisition, Resources, Supervision, Writing - review & editing. **Erik Steen Jensen**: Writing - original draft, Writing - review & editing.

Declaration of competing interest

Authors declare that there are no conflicts of interest.

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