

## Article

# Above- and Below-Ground Interactions and Interspecific Relationships in Wheat/Maize Systems

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**Abstract:** Above- and below-ground interactions play a crucial role in achieving higher yields in intercropping systems. Nonetheless, it remains unclear how these interactions impact intercropping crop growth and regulate interspecific relationships. This study aimed to quantify the impact of above- and below-ground interactions on crop yield by determining the dynamics of dry matter accumulation, photosynthetically active radiation (PAR) transmittance, and leaf area index (LAI) in intercropped wheat and maize. Three below-ground intensities were set for an intercropping system: no root separation (CI: complete interaction below ground), 48  $\mu\text{m}$  nylon mesh separation (PI: partial interaction below ground), and 0.12 mm plastic sheet separation (NI: no interaction below ground). Two densities were set for maize: low (45,000 plants  $\text{hm}^{-2}$ ) and high (52,500 plants  $\text{hm}^{-2}$ ). At the same time, corresponding monoculture treatments were established. The grain yields in the CI and PI treatments were, on average, 23.7% and 13.7% higher than those in the NI treatment at high and low maize densities, respectively. Additionally, the grain yield for high density was 12.3% higher than that of low density in the CI treatment. The dry matter accumulation of intercropped wheat under the CI and PI treatments was, on average, 9.1%, 14.5%, and 9.0% higher than that in the NI treatment at the flowering, filling, and maturity stages, respectively. The dry matter accumulation of intercropped maize at the blister, milk, and physiological maturity stages increased by 41.4%, 32.1%, and 27.8%, respectively, under the CI treatment compared to the NI treatment. The PAR transmittance and LAI of maize at the V6 stage were significantly increased by increasing the intensity of below-ground interactions. This study showed that complete below-ground interaction contributed to a significant increase in the competitiveness of intercropped wheat with respect to maize ( $A_{\text{wm}}$ ) under the high-density maize treatment, especially at the filling stage of wheat. Moreover, the CI treatment enhanced the recovery effects of maize ( $R_{\text{m}}$ ) after wheat harvesting. Increasing the intensity of below-ground interactions can significantly enhance the  $A_{\text{wm}}$  and  $R_{\text{m}}$  in intercropping systems, favoring the accumulation of crop dry matter mass and light energy utilization to increase system yields.



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## 1. Introduction

Intercropping, which has been practiced in China for millennia, has the potential to achieve higher yields than monocropping, mainly due to increased efficiency in the utilization of water, light, nutrients, and other resources [1,2]. The implementation of rational intercropping patterns can facilitate the formation of a stratified canopy structure for crops, thereby enhancing the interception of light energy [3]. It also enhances ventilation and light transmission conditions, thereby maximizing the advantages of border rows [4]. In addition, root interpenetration has been shown to improve the competitive environment below ground in intercropping systems, which can significantly increase the productivity of land per unit area [5]. Wheat (*Triticum aestivum* L.)/maize (*Zea mays* L.) intercropping,

introduced in the 1970s in the oasis irrigation areas of northwest China, is still a common cropping pattern and has made a major contribution to poverty alleviation and food security [6]. Moreover, planting a combination of C3 and C4 crops can maximize area utilization and provide complementary benefits.

Wheat is sown in strips approximately six rows wide in the spring and harvested in midsummer in wheat/maize intercropping. The space between the wheat strips is utilized to sow two rows of maize in the late spring. Maize is typically harvested approximately 2 to 3 months after wheat, depending on local climatic conditions. In wheat/maize intercropping systems, early-planted wheat has a competitive advantage over late-planted maize [7]. Maize planted with wheat initially grows slower than sole-cropped maize; however, it continues to grow after wheat harvest, and the season ends with higher growth rates compared to sole-cropped maize. This phenomenon has been identified as the “recovery effect,” which manifests as an increase in above-ground dry matter accumulation [8].

The theoretical basis of crop intercropping systems is the interspecific interaction of plants [9]. Species interactions and diversity are important bases for maintaining community stability. These interactions play a critical role in controlling weeds, making efficient use of light, and restoring degraded environments [10,11]. When two crops are cultivated together, interspecific competition and interspecific facilitation coexist. It is possible to regulate which of these two phenomena ultimately manifests itself [12]. Interspecific competition encourages the utilization of different resources, as intercropping systems exploit specific resources based on spatial and temporal variations [13]. Furthermore, interspecific facilitation refers to the fact that resource utilization should be greater than the interspecific competition [14], and interspecific facilitation is produced by one crop promoting the growth of another crop.

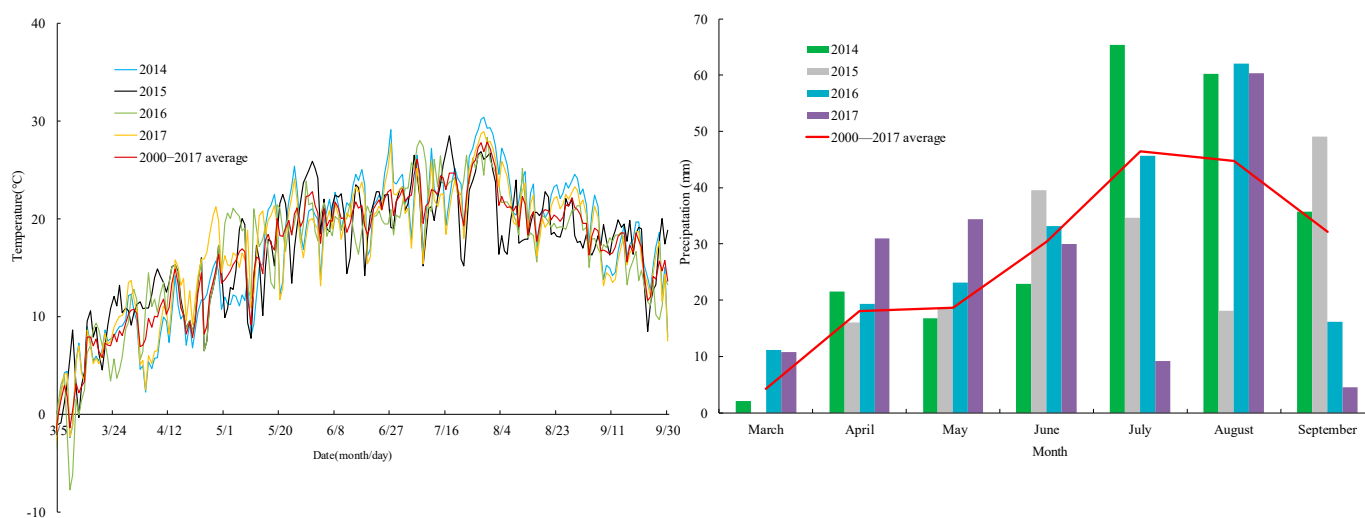
Spatially interspecific interactions can be divided into above-ground and below-ground interactions [15,16]. Numerous studies have shown that the benefits of intercropping result from interspecific interactions both above and below ground. In a maize/soybean intercropping dominance study, the contributions of above- and below-ground interactions were greater than the contribution of a single factor to intercropping dominance, and the role below ground was greater than that above ground [17]. The above- and below-ground ecological niches of each component are separated and expanded in time and space, allowing the crop canopy to fully utilize light energy and the below-ground root system to expand its spatial distribution and utilize water, nutrients, and other resources in a complementary manner [1,18]. Our previous studies have indicated that above- and below-ground interactions could significantly increase the advantages of intercropping wheat and maize and that increasing maize density could further increase the contribution of below-ground interactions to the advantages of intercropping [19]. It has been reported that above-ground interspecific interactions have a negative impact on the utilization of low light by intercropped peanuts [20], whereas below-ground interactions have a positive impact in this area. Nevertheless, the impact of above- and below-ground interactions on interspecific relationships in intercropped populations has not yet been documented.

Root partitioning is a vital technical methodology used to investigate interspecific associations above and below ground in intercropped crops. The principle is that the root system remains unseparated, such that both above- and below-ground actions exist and can be carried out. When separated by a nylon mesh, underground overlapping root interactions are eliminated, but the exchange of water and nutrients still occurs, as well as above- and below-ground interactions. Plastic sheet separation eliminates all below-ground interactions, leaving only the above-ground ones. In this study, we used the root partitioning method to quantify the effects of above- and below-ground interactions in wheat and maize intercropping systems. The objectives of the present study were to: (1) understand the effects of above- and below-ground interactions on intercropping crop dynamics for dry matter accumulation; (2) analyze PAR transmittance and leaf area index responses to above- and below-ground interaction intensity; and (3) understand the effects of above- and below-ground interactions on interspecific competitive and recovery effects.

## 2. Materials and Methods

### 2.1. Site Description

The field experiment was conducted from 2014 to 2017 at the Gansu Agriculture University Oasis Experiment Station (37°34' N; 102°94' E). The climate of this region is temperate continental. This station is located in a part of the Hexi corridor of northwestern China, with an altitude of 1506 m, and the thermal day above 10 °C constitutes about 155 days. The annual cumulative temperatures of  $\geq 0$  °C and  $\geq 10$  °C are 3513 °C and 2985 °C, respectively. The area is suitable for the development of intercropping, with abundant light resources and excess heat. The precipitation and mean air temperature during the four studied years of the wheat and maize growing seasons are presented in Figure 1. The soil at the site is classified as Aridisol. In the top 30 cm of the soil (depth), the total N, available P, available K, and organic matter were 0.93, 29.1, 152.8, and 19.2 g kg<sup>-1</sup>, respectively.



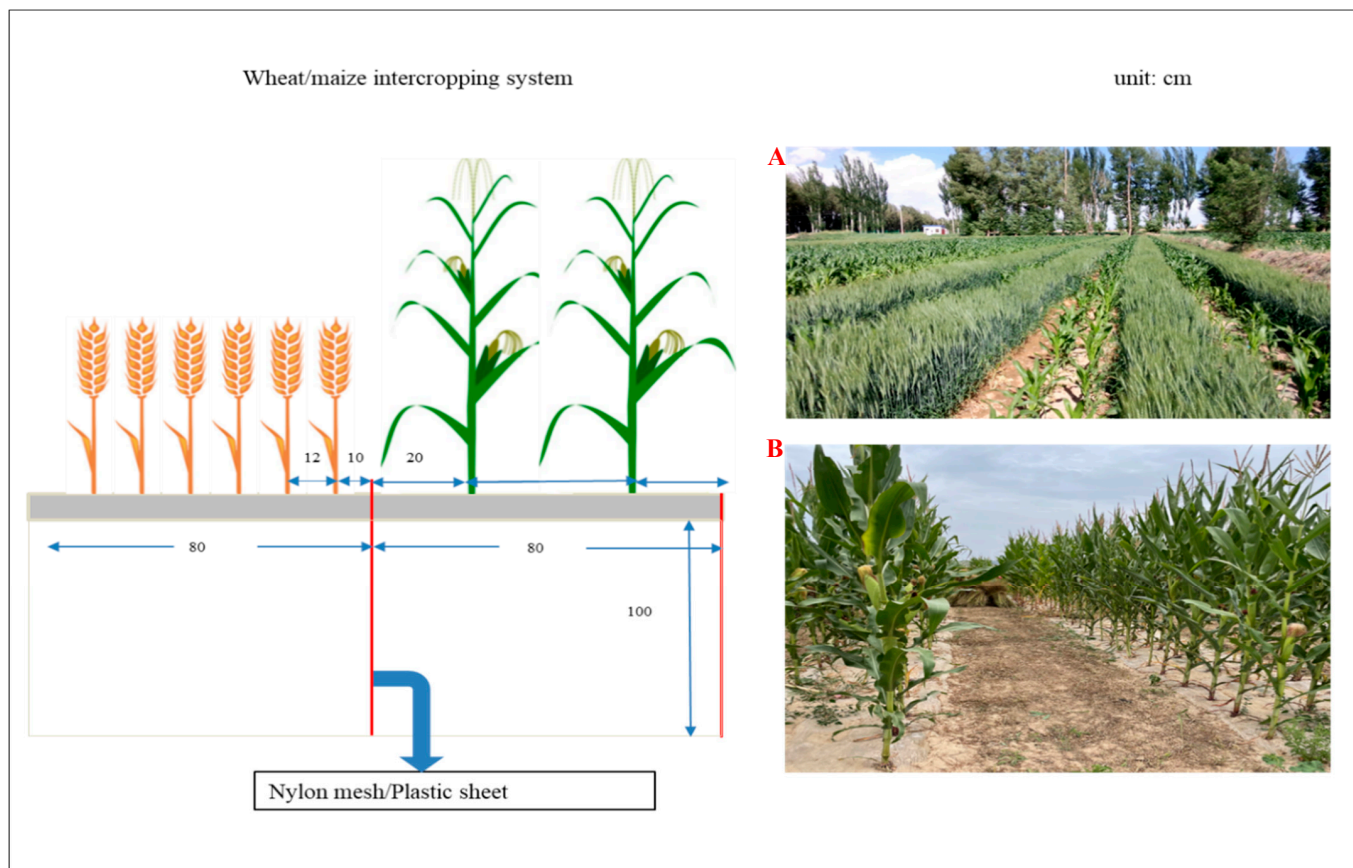
**Figure 1.** Precipitation (P) and air temperature (T) during crop-growing seasons in 2014, 2015, 2016, and 2017 in comparison to the average from 2000 to 2017 at the Wuwei Experimental Station.

### 2.2. Experimental Design

A randomized block experiment design was adopted, and three below-ground intensities were set for a wheat/maize intercropping system: no root separation (CI: Complete interaction below ground), 48  $\mu$ m nylon mesh separation (PI: Partial interaction below ground), and 0.12 mm plastic sheet separation (NI: No interaction below ground). Furthermore, based on the common maize planting density in the local area, two above-ground interaction intensities were set for maize: low (45,000 plants hm<sup>-2</sup>) and high (52,500 plants hm<sup>-2</sup>). At the same time, corresponding monoculture treatments were established—monoculture wheat (W) and monoculture maize (M1 and M2)—at two density levels. The densities of monoculture maize were 105,000 plants hm<sup>-2</sup> and 90,000 plants hm<sup>-2</sup>. The total number of treatments was nine, and each treatment was replicated three times. The field layout is shown in Figure 2. The field layout consisted of six rows of wheat (row spacing 12 cm) and two rows of maize (row spacing 40 cm) arranged in alternating strips. Each plot was 4.8 m wide and 8 m long and contained three sets of wheat–maize strips. Prior to planting, a trench 8 m long, 0.1 m wide, and 1 m deep was dug by hand at the location of each partition in each replication and treatment (including the no-blocking treatment). Nylon netting and plastic sheets were inserted vertically between the wheat and maize strips, followed by re-filling with the original soil.

The sowing dates and growth stages of spring wheat (cultivar Yong-Liang no. 4) and maize (cultivar Xian-Yu 335) are presented in Table 1. The application rates of urea nitrogen fertilizer were 225 kg N and 450 kg N hm<sup>-2</sup> for monocrop wheat and monocrop maize, respectively, and the application rates of P<sub>2</sub>O<sub>5</sub> were 150 and 225 kg P hm<sup>-2</sup>, respectively.

The amount of fertilizer applied to the intercrops was the same as that of the monocrops on an area basis. N and P were applied to wheat at sowing, while maize was fertilized using a split application method, with 135 kg hm<sup>-2</sup> of N and 67.5 kg hm<sup>-2</sup> of P at sowing, 270 kg hm<sup>-2</sup> of N and 135 kg hm<sup>-2</sup> of P at the V6 and VT stages (Table 1), and 45 kg hm<sup>-2</sup> of N and 22.5 kg hm<sup>-2</sup> at the P at R2 stages. Weeding was carried out by hand every week throughout the growing season. All maize strips were covered with clear plastic film at sowing to reduce soil moisture evaporation and ensure the emergence of maize. The plastic film was removed by hand after maize harvesting. The study region was a typical arid area with oasis irrigation, and crop production relied on supplemental irrigation. The irrigation system was consistent with the previous study [19].



**Figure 2.** Layout of intercrops and the partition of roots in the wheat/maize intercropping system: wheat/maize intercropping with an 80 cm strip of wheat (six rows) alternated with an 80 cm strip of maize (two rows). In the wheat/maize intercropping, three above- and below-ground interaction treatments were included: (i) CI: Complete below-ground interaction; (ii) PI: Partial below-ground interaction; (iii) NI: No below-ground interaction. Nylon meshes and plastic sheets were placed vertically to a depth of 100 cm. (A) shows the early co-growth period of wheat and maize, and (B) shows the recovery growth period of maize after the wheat harvest.

**Table 1.** Phenological stages of maize and wheat plants at the Wuwei Experimental Station, China, for 2014, 2015, 2016, and 2017.

Crop		Phenological Stages								
Wheat	Maize	Sowing	— Sowing	Jointing V3	Heading V6	Flowering V12	Filling VT	Maturity R2	R3	R6
		20 March 2014	21 April 2014	27 May 2014	11 June 2014	27 June 2014	12 July 2014	27 July 2014	27 August 2014	25 September 2014
Date		22 March 2015	25 April 2015	23 May 2015	4 June 2015	21 June 2015	10 July 2015	27 July 2015	5 September 2015	25 September 2015
		21 March 2016	18 April 2016	20 May 2016	6 June 2016	22 June 2016	7 July 2016	21 July 2016	26 August 2016	20 September 2016
		20 March 2017	17 April 2017	23 May 2017	8 June 2017	23 June 2017	8 July 2017	19 July 2017	29 August 2017	19 September 2017

Note: The designations V3, V6, V12, VT, R2, R3, and R6 indicate the third, sixth, twelfth, tasseling, blister, milk, and maturity stages of leaf development, respectively.

### 2.3. Measurements and Methods for Calculating Indices

#### 2.3.1. Grain Yield and LER

Wheat and maize were harvested by hand at full maturity in each plot under both monoculture and intercropping patterns. The grain was air-dried, cleaned, and weighed for grain yield.

The land equivalent ratio (LER) was used to calculate the land use advantage provided by intercropping.

$$\text{LER} = \text{LER}_w + \text{LER}_m = Y_{iw}/Y_w + Y_{im}/Y_m$$

where  $Y_{iw}$  and  $Y_{im}$  are the yields of intercropped wheat and maize, and  $Y_w$  and  $Y_m$  are the yields in monocultures of wheat and maize. An advantage in land use can be seen for intercropping practices when the LER exceeds 1.0.

#### 2.3.2. Dry Matter Accumulation and Leaf Area Index (LAI)

The plant samples were taken at the stages of jointing, tasseling, flowering, filling, and maturity for wheat, corresponding to the stages of V3, V6, V12, VT, R2, R3, and R6 of maize from 2014 to 2017. In each intercropping plot, one pair of wheat and maize strips was employed to monitor the accumulation of above-ground biomass, while the remaining two pairs of wheat and maize strips were utilized to monitor grain yield at maturity. In the monoculture plots, one-half of the plots were utilized for the monitoring of above-ground biomass accumulation, while the other half was employed for the monitoring of grain yield at maturity. At each sampling time, 15 wheat plants and 5 maize plants with consistent growth were taken. The samples were dried in an oven at 105 °C for 30 min to deactivate the enzymes. Following this, they were dried at a constant temperature of 80 °C until a consistent weight was reached. The biomass was weighed on an electronic balance. The biomass per hectare is calculated by dividing the amount of dry matter sampled by the number of plants sampled and then multiplying the result by the seeding density. The leaves were scanned using a flatbed scanner (CanoScan LiDE 200, Canon Inc., Tokyo, Japan), and then the total leaf area was measured. The LAI equals the total leaf area divided by the land area occupied.

#### 2.3.3. Interspecific Interaction Indices

The competitiveness of intercropped wheat to maize ( $A_{wm}$ ) is expressed as

$$A_{wm} = \left( \frac{Y_{iw}}{Y_{sw} \times F_w} \right) - \left( \frac{Y_{im}}{Y_{sm} \times F_m} \right)$$

where  $F_w$  and  $F_m$  are the proportions of sowing area for intercropped wheat and intercropped maize in the intercropping system (in this research,  $F_w = F_m = 0.5$ );  $Y_{iw}$  and  $Y_{im}$  are the grain yields of the intercropped wheat and intercropped maize, respectively; and  $Y_{sw}$  and  $Y_{sm}$  are the grain yields of sole wheat and sole maize, respectively. If  $A_{wm}$  is positive, this indicates that intercropped wheat is dominant, while if  $A_{wm}$  is negative, this indicates that intercropped maize is dominant [21,22].

The recovery effect of the intercropped maize ( $R_m$ ), which is defined as the differences in the above-ground biomass growth rate between the intercropped maize and the corresponding monoculture maize, is calculated as follows:

$$R_m = \frac{\text{BGR}_{im}}{\text{BGR}_{sm}}$$

where  $\text{BGR}_{im}$  and  $\text{BGR}_{sm}$  are the biomass growth rates of maize in intercropping and monoculture, respectively.

The biomass growth rate is defined as

$$\text{BGR} = \frac{W_2 - W_1}{T_2 - T_1}$$

where  $W_2$  and  $W_1$  are the biomass accumulation of maize sampled at wheat harvest and maize harvest, respectively, and  $T_1$  and  $T_2$  represent the two different sampling dates.

### 2.3.4. Photosynthetically Active Radiation Transmittance

The photosynthetically active radiation (PAR) was measured at the tasseling stage, flowering stage, and maturity stage of wheat, corresponding to the V6, V12, and R2 stages of maize (2016 and 2017), as all these stages come under the co-growth period of wheat/maize intercropping. For this purpose, the intensity of PAR fluxes above the wheat canopy was measured at 10 s intervals using a LI-191SA quantum sensor (LI-191SA, LI-COR Inc., Lincoln, NE, USA) and a LI-1400 datalogger, which was repeated three times for each plot. All quantum sensors were placed on the horizontal arm of an observation stand that was 5 cm higher than the crop canopy. All measurements were taken on a clear day between 11:30 and 12:30 to minimize the external effects of atmospheric conditions. PAR transmittance was determined according to previously published methods [23,24].

$$\text{PARTransmittance}(\%) = \frac{\text{PAR}_W}{\text{PAR}_M} \times 100\%$$

where  $\text{PAR}_W$  and  $\text{PAR}_M$  are the PAR at the top of wheat and maize top, respectively.

### 2.4. Statistical Analysis

The data were analyzed using statistical analysis software (SPSS software, 19.0, SPSS Institute Inc.<sup>®</sup>, Chicago, IL, USA). The data exhibited a normal distribution. The treatment effects were investigated using the LSD multiple-range test at a 0.05 probability level, and Duncan's method was used for post hoc multiple comparisons and significant difference tests. A two-way analysis of variance (ANOVA) was performed to determine the main effects of the interactions. Due to significant year-by-treatment interactions for most of the variables assessed, the treatment effect was evaluated separately for each year.

## 3. Result

### 3.1. Yield and LER

There was a significant difference between the intercropping and monoculture systems for grain yield, while the year was not significant (Table 2). When averaged over 4 years, the total grain yields were 14.3% and 5.1% higher in intercrops than in maize monoculture in the CI and PI treatments, respectively. Similarly, the total grain yields were 142.5%, 122.9%, and 96.0% higher in the CI, PI, and NI treatments, respectively, than in wheat monoculture.

**Table 2.** Effect of different interaction intensities and maize density on wheat grain yield, maize grain yield, total grain yield, and LER in sole- and intercropping systems as a 4-year average.

Treatment	Wheat	Maize	Total	LER
W	6210 a		6210 e	
M1		12,381 b	12,381 cd	
M2		13,972 a	13,972 bc	
CI1	4760 b	9592 de	14,186 b	1.54 ab
CI2	4777 b	11,112 c	15,936 a	1.57 a
PI1	4358 bc	8901 def	13,275 bcd	1.42 b
PI2	4193 bc	10,192 cd	14,413 ab	1.41 b
NI1	3819 c	8085 f	11,895 d	1.27 c
NI2	3758 c	8680 ef	12,449 cd	1.23 c
Significance				
Below-ground interaction (I)	**	**	**	**
Density (D)	NS	*	**	NS
I × D	NS	**	*	**

Note: Different letters represent the significant differences between different treatments. \* means  $p < 0.05$ ; \*\* means  $p < 0.01$ ; NS means no significant difference. W and M: sole wheat and sole maize, respectively. CI: Complete below-ground interaction. PI: Partial below-ground interaction. NI: No below-ground interaction. "1" and "2": Low- and high-density maize planting, respectively.

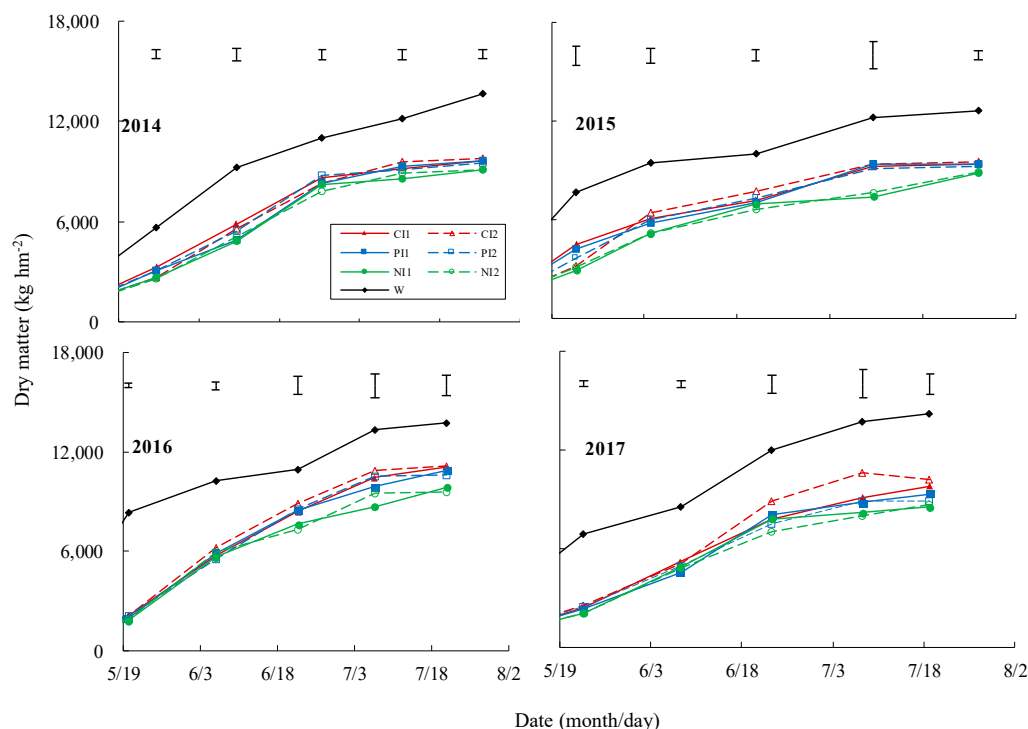
The effect of intercropping on grain yield varied with the below-ground interaction intensity and maize planting density (Table 2). A significant interaction was observed between the interaction intensity below ground and the maize planting density, while no significant differences were identified between years. When averaged over 4 years, there was no significant difference between the CI and PI treatments in grain yield. However, the average grain yield for the CI and PI treatments was 23.7% and 13.7% higher than that of the NI treatment at high and low density, respectively. Higher densities significantly increased grain yields in the complete below-ground intercropped treatments, where high densities were significantly higher by 12.3% compared to low densities. Therefore, the complete below-ground interaction treatment markedly enhanced yield gain in the intercropping system, with greater efficacy at high densities.

The LER of the intercrops varied from 1.23 to 1.57 on average over 4 years (Table 2). The LERs for all intercropped treatments were higher than unity, indicating that wheat/maize intercropping improved land use efficiency in this experiment. The LERs were significantly different between the different below-ground interaction treatments but not between the different maize density treatments. The value of LER in the CI treatment was 9.9% and 24.4% higher than that in the PI and NI treatments.

### 3.2. Dynamics of Above-Ground Dry Matter Accumulation

#### 3.2.1. Wheat

The above-ground dry matter accumulation of wheat from the seeding stage to maturity was influenced by different planting patterns (Figure 3). Monocrop wheat had higher above-ground dry matter accumulation than intercropped wheat at all the above stages. The above-ground dry matter accumulation of monocrop wheat was significantly higher by 163.1, 71.4, 39.3, 39.9, and 41.1% (respectively) than that of intercropped wheat at the seeding, booting, flowering, filling, and maturity stages when averaged over 4 years.

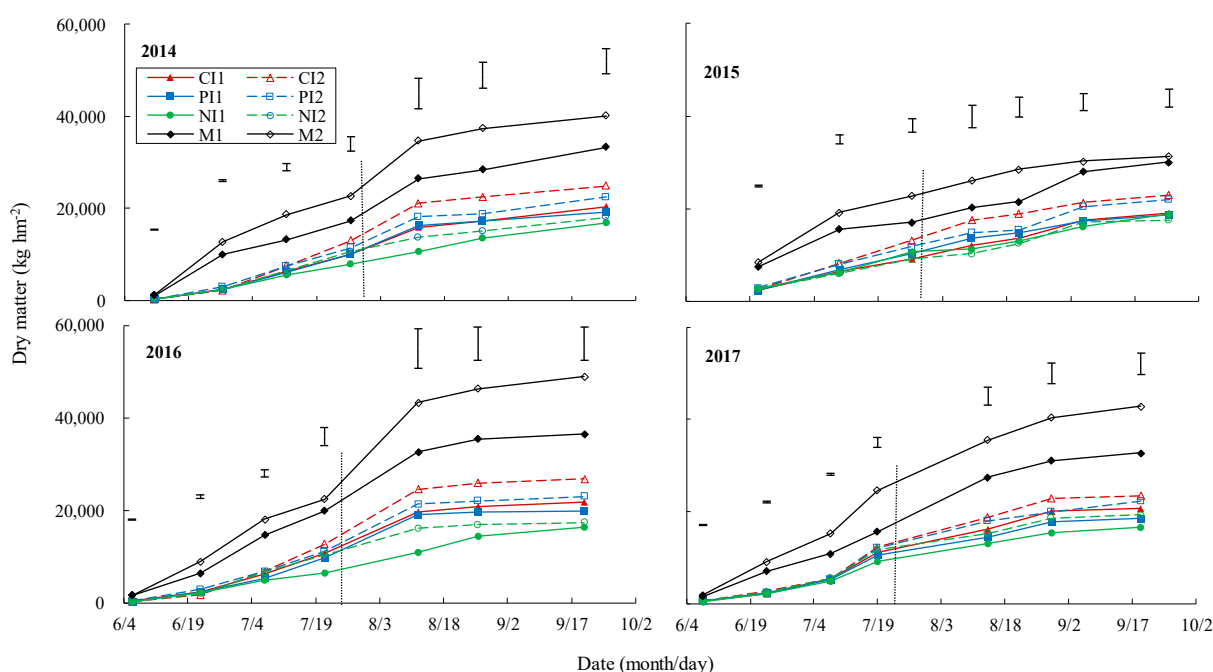


**Figure 3.** Dynamics of above-ground dry matter accumulation of sole- and intercropped wheat at jointing, earing, flowering, and filling maturity stages in 2014, 2015, 2016, and 2017. CI: Complete below-ground interaction. PI: Partial below-ground interaction. NI: No below-ground interaction. “1” and “2”: Low- and high-density maize planting, respectively. “1” and “2”: Low- and high-density maize planting, respectively. W: Sole wheat. The vertical bars represent the least significant difference (LSD) at  $p < 0.05$  among treatments within a measurement date.

The above-ground dry matter accumulation of wheat increased with the interaction intensity below ground in the intercropping system at the flowering and filling stages but was not significantly affected by maize plant density (Figure 3). The above-ground dry matter accumulation of intercropped wheat was not significantly different between the CI and PI treatments; they were 9.1%, 14.5%, and 9.0% greater than that in the NI treatment at the flowering, filling, and maturity stages when averaged over 4 years.

### 3.2.2. Maize

Monocrop maize exhibited higher above-ground dry matter accumulation compared to intercropped maize, which displayed distinct above- and below-ground interactions before wheat harvest (corresponding to the maize silking stage) (Figure 4). The dry matter accumulation of maize in the intercropping system increased by an average of 14.5% over 4 years compared to monocrop maize. From the maize silking stage to harvest, intercropped maize with different above- and below-ground interactions had rapid growth processing. The PI and NI treatments reached the same (or less) dry matter accumulation as monocrop maize, and the CI treatment had greater dry matter accumulation by 22.8% than monocrop maize when averaged across 4 years for the same base areas.



**Figure 4.** Dynamics of above-ground dry matter accumulation of sole- and intercropped maize at V3, V6, V12, VT, R2, R3, and R6 in 2014, 2015, 2016, and 2017. The vertical dotted lines indicate the stage of the wheat harvest. CI: Complete below-ground interaction. PI: Partial below-ground interaction. NI: No below-ground interaction. “1” and “2”: Low- and high-density maize planting, respectively. M: sole maize. The vertical bars represent the least significant difference (LSD) at  $p < 0.05$  among treatments within a measurement date.

In the intercropping system, the completely below-ground interaction treatment significantly increased the dry matter accumulation of maize after wheat harvesting (Figure 4). Across a 4-year average, maize under the CI treatment increased in above-ground dry matter weight by 41.4% at the blister stage (R2), 32.1% at the milk stage (R3), and 27.8% at physiological maturity (R6), respectively, in comparison to the NI treatment. With an increase in maize planting density, the high-density maize had a greater dry matter accumulation weight by 21.1% at the blister stage, 15.5% at the milk stage, and 15.9% at physiological maturity, respectively, than the low-density maize treatment, when averaged over 4 years. The results suggest that complete below-ground interaction, in combina-



tion with a high maize planting density, promotes significant rapid growth in maize after wheat harvesting.

### 3.3. Photosynthetically Active Radiation Transmittance

At all sampling stages (V6, V12, and R1), the photosynthetically active radiation transmittance (PAR transmittance) value revealed that the different above- and below-ground interaction treatments in the intercropping system significantly affected the PAR transmittance of wheat (Table 3). As the reproductive period progressed, the PAR transmittance of wheat in the intercropping system decreased. At V6, over the two-year period, no significant difference in PAR transmittance was found between the CI and PI treatments at varying below-ground interaction intensities within the intercropping system. However, they exhibited an average of 30.9% higher PAR transmittance than the NI treatment. With the increase in maize planting density, the PAR transmittance of high-density maize was found to be 18% higher than that of low-density maize in the PI treatment. At V12 and R1, a significant inter-annual variation in the wheat's PAR transmittance was observed. The PI treatment increased PAR transmittance significantly by 24.4% and 31.7% compared to the CI and NI treatments at V12 in 2017 and by 66.7% and 73.5% compared to the CI and NI treatments at R1 in 2016. Thus, the complete below-ground interaction treatment in intercropping led to a noteworthy increase in PAR transmittance for wheat at the maize V6 stage.

**Table 3.** Effect of different treatments on the photosynthetically active radiation transmittance (PAR transmittance) (%) of the intercropping system at V6, V12, and R1 of maize during cropping seasons from 2016 to 2017.

Year	Treatment	PAR Transmittance (%)		
		V6	V12	R1
2016	CI1	82 a	67 a	35 b
	CI2	76 ab	61 a	16 d
	PI1	82 a	69 a	49 a
	PI2	71 bc	53 a	36 b
	NI1	63 c	53 a	22 cd
	NI2	48 d	56 a	27 bc
2017	CI1	60 a	64 bc	34 c
	CI2	37 c	63 bc	39 bc
	PI1	55 a	77 ab	29 d
	PI2	45 b	81 a	42 b
	NI1	41 bc	59 c	44 ab
	NI2	42 bc	61 c	48 a
Significant				
Year		NS	**	**
Below-ground interaction (I)		**	**	**
Density (D)		**	NS	**
I × D		**	NS	**

Note: Different letters represent the significant differences between different planting patterns in different years. \*\* means  $p < 0.01$ ; NS means no significant difference. CI: Complete below-ground interaction. PI: Partial below-ground interaction. NI: No below-ground interaction. "1" and "2": Low- and high-density maize planting, respectively.

### 3.4. LAI

There were significant differences between the intercropping and monoculture systems in terms of LAI, although there were no significant differences observed among years (Tables 4 and 5). Compared to monoculture, the LAI of intercropped wheat was significantly lower (by 21.1%) at the jointing stage, while the LAI was higher than in monoculture from the earing to maturity stages, with an average increase of 14.5%. The LAI of intercropped

maize was, on average, 15.3% higher than that of monoculture during the whole growth period, and the highest LAI was reached in the high-density treatment.

**Table 4.** The LAI of wheat in monocultures and intercropping for different plant patterns as a 4-year average.

Treatment	Growth Period				
	Jointing Stage	Earing Stage	Filling Stage	Milk-Ripe Stage	Dough Stage
W	3.15 a	3.79 de	4.22 c	2.74 cd	0.80 c
CI1	2.79 b	4.63 b	5.53 a	3.67 a	1.34 a
CI2	2.86 b	4.72 a	5.16 a	3.55 a	1.35 a
PI1	2.55 c	4.16 c	4.81 b	3.30 b	1.11 b
PI2	2.58 c	4.29 c	4.65 b	3.22 b	1.09 b
NI1	2.44 cd	3.56 e	4.22 c	2.76 c	0.94 c
NI2	2.39 d	3.85 d	3.97 c	2.61 d	0.88 c
Significant					
Below-ground interaction (I)	**	**	**	**	**
Density (D)	NS	**	NS	*	NS
I × D	NS	*	**	NS	NS

Note: Different letters represent the significant differences between the different planting patterns for different years. \* means  $p < 0.05$ ; \*\* means  $p < 0.01$ ; NS means no significant difference. W: sole wheat. CI: Complete below-ground interaction. PI: Partial below-ground interaction. NI: No below-ground interaction. "1" and "2": Low- and high-density maize planting, respectively.

**Table 5.** The LAI of maize in monocultures and intercropping for different plant patterns as a 4-year average.

Treatment	Growth Period						
	V3	V6	V12	VT	R2	R3	R6
M1	1.13 d	1.44 d	2.62 d	3.34 d	4.39 d	4.49 e	3.85 d
M2	1.47 c	1.81 c	3.35 c	3.92 cd	5.22 c	5.09 d	4.54 c
CI1	1.39 c	2.04 b	3.41 c	4.35 c	5.12 c	6.01 bc	4.70 bc
CI2	1.95 a	2.63 a	4.52a	5.48 a	6.10 a	6.92 a	5.78 a
PI1	1.27 cd	1.51 d	3.11 cd	4.19 cd	4.70 d	5.83 c	4.37 c
PI2	1.72 b	2.24 b	4.01 b	4.99 b	5.71 b	6.42 b	5.10 b
NI1	1.19 d	1.26 e	2.80 d	3.54 cd	4.35 d	4.24 e	3.92 d
NI2	1.47 c	1.74 c	3.49 c	4.53 c	5.08 c	5.46 c	4.27 d
Significant							
Below-ground interaction (I)	*	**	*	**	**	**	**
Density (D)	**	**	**	**	**	**	**
I × D	**	**	**	**	**	**	**

Note: Different letters represent the significant differences between the different planting patterns for different years. \* means  $p < 0.05$ ; \*\* means  $p < 0.01$ . M: sole maize. CI: Complete below-ground interaction. PI: Partial below-ground interaction. NI: No below-ground interaction. "1" and "2": Low- and high-density maize planting, respectively.

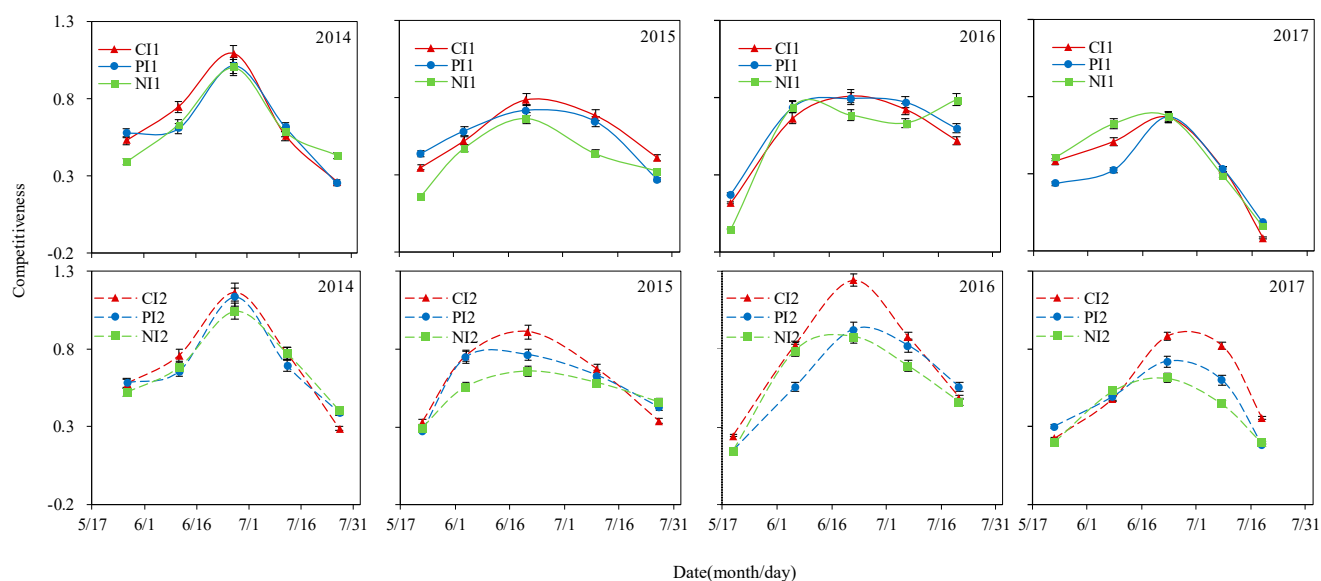
In the intercropping system, complete below-ground interaction significantly increased the LAI of intercropped wheat (Table 4). The CI treatment increased the LAI of wheat by 10.1, 10.6, 13.1, 10.9, and 22.5% compared to the PI treatment at the jointing, earing, filling, dough, and maturity stages, respectively. The CI treatment increased the LAI of wheat by an average of 31.3% over the PI treatment throughout the wheat-growing season. Similarly, the PI treatment increased the LAI of wheat by an average of 15.4% compared to the NI treatment during the whole wheat growth period.

In the intercropping systems, both complete below-ground interaction and maize high-density planting significantly increased the LAI of maize, and the interaction between them is significant (Table 5). On average, for the whole growth period under high density, the CI treatment significantly increased the LAI by 10.6% and 28.2% compared to the PI and

NI treatments, and the PI treatment significantly increased the LAI by 16% when compared with the NI treatment. At low densities of maize, except for the VT and R6 stages, the CI treatment increased the LAI by an average of 9.1% and 30.9% compared to the PI and NI treatments, and the PI treatment increased the LAI by an average of 19.9% compared to the NI treatment.

### 3.5. The Competitiveness and Recovery Effect

There was a significant year  $\times$  below-ground management interaction that affected the interspecific competition (Figure 5). As crop growth progressed,  $A_{wm}$  increased from early co-growth, reached a peak with an  $A_{wm}$  of 1.24 at the filling stage, and declined in the late co-growth stage. Across a 4-year average, the  $A_{wm}$  of intercropped wheat across the five co-growth stages was greater than 0. This indicated that intercropped wheat was the dominant species in the maize/wheat strip intercropping.



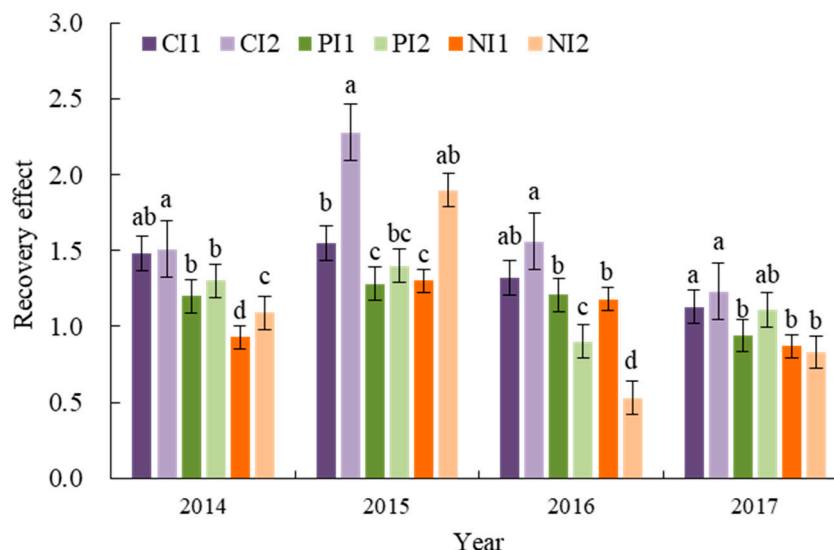
**Figure 5.** The dynamic interaction aggressivity of the wheat/maize intercropping system at the wheat jointing, earing, flowering, and filling maturity stages (corresponding maize V1, V3, V6, V12, and VT stages) in 2014, 2015, 2016, and 2017. CI: Complete below-ground interaction. PI: Partial below-ground interaction. NI: No below-ground interaction. “1” and “2”: Low- and high-density maize planting, respectively. The error bars indicate the standard errors of the means ( $n = 3$ ).

Below-ground interaction intensity and maize density significantly affected the aggressivity ( $A_{wm}$ ) of wheat relative to maize (Figure 5). At the jointing, flowering, and filling stages of wheat (corresponding to the V3, V12, and VT of maize), the  $A_{wm}$  was not significantly different under complete and partial below-ground interaction treatments, and it was significantly (32.6%, 14.9%, and 18.9%, respectively) higher than the no below-ground interaction treatment. Moreover, at the flowering and filling stages, the high-density compared to low-density maize treatments significantly increased the  $A_{wm}$  by 25.4, 11.1, 5.8, 36.8, 16.3, and 28.6% under the CI, PI, and NI treatments, respectively. Complete below-ground interactions contributed to a significant increase in  $A_{wm}$  under the high-density maize treatment, especially at the filling stage of wheat.

### 3.6. Recovery Growth Effect of Intercropped Maize

On average, over four years, the recovery effect of intercropped maize ( $R_m$ ) was significantly higher in the treatment with complete below-ground interaction by 28.5% and 43.7% compared to the treatments with partial below-ground interaction and no below-ground interaction, respectively (Figure 6). Except for 2015, the treatment with partial below-ground interaction had an average (22.6%) higher  $R_m$  than the treatment with no

below-ground interaction. The effect of maize density on  $R_m$  varied significantly from year to year. This study showed that the enhanced  $R_m$  was primarily attributed to below-ground interaction. It was also found that increasing the intensity of above-ground intercropping did not significantly affect  $R_m$ .



**Figure 6.** Recovery effect of maize in an intercropping system after wheat harvest in 2014, 2015, 2016, and 2017. CI: Complete below-ground interaction. PI: Partial below-ground interaction. NI: No below-ground interaction. “1” and “2”: Low- and high-density maize planting, respectively. The error bars indicate the standard errors of the means ( $n = 3$ ). The lowercase letters above the bars indicate significant differences ( $p < 0.05$ ).

#### 4. Discussions

##### 4.1. The Effect of Above- and Below-Ground Interactions on Intercropping Advantage

Crop root–shoot interactions play a vital role in the biological foundation of crop growth. This interaction facilitates nutrient acquisition and water uptake, which ultimately impact crop yield [25]. Therefore, understanding the regulatory mechanisms governing root–shoot communication can provide valuable insights for enhancing agricultural productivity. In intercropping systems, the separation of ecological niches between the above- and below-ground components is expanded in time and space, enabling the crop canopy to fully utilize light energy, and the spatial distribution of the below-ground root system is expanded for complementary utilization of water, nutrients, and other resources [26–28]. However, there are frequently discrepancies between component species with regard to the impact of above- and below-ground interspecific interactions on crop growth. Our study revealed that the LER for wheat/maize intercropping on grain yield was greater than 1 in all intercropped treatments, which showed that interspecific interaction has a positive contribution to crop yield. In this study, the completely above- and below-ground interactions increased the LER by 9.9% and 24.4% compared to the partial and no-interaction treatments, respectively. This suggests that above-ground interactions play a more significant role in the benefit of wheat/maize intercropping than below-ground interactions. Many studies have reported similar results [15,29]. However, some studies have shown that below-ground interaction contributes more than above-ground interaction to the advantages of the intercropping system in terms of shoot biomass and grain yield, for example, peanut/maize intercropping systems [20,30]. One of the different reasons may be that the co-growth period of wheat/maize intercropping is shorter than that of peanut/maize intercropping. Following the harvesting of wheat, maize has the opportunity to accumulate greater energy reserves, thereby increasing its yield and enhancing the overall productivity of the system [8]. Another reason may be that water use efficiency in wheat/maize intercropping is increased by above- and below-ground complete interaction [31]. Therefore,

the optimization of above- and below-ground interactions in intercropping represents a significant avenue for enhancing crop yields.

#### 4.2. *Effects of Above- and Below-Ground Interactions on Intercropping Light Utilization*

Studies have shown that plant photosynthesis is greatly influenced by the way in which the canopy of the crop is exposed to light [32,33]. Intercropping canopies are more effective than single crops [2,34]. The group light structure shifted from plane light exposure to three-dimensional exposure, which significantly increased the light exposure area and duration for the crop, enabling the hierarchical and three-dimensional utilization of light [35,36]. The multilayer intercropping structure led to an increase in light interception rate, a decrease in light leakage loss, an improvement in leaf area index, an extension of photosynthetic activity, and better utilization of light energy to some extent [37,38]. The primary factor responsible for the high productivity observed in the wheat/maize intercropping systems was the increased capture of radiation [39]. However, there are fewer studies on light energy utilization in intercropping from above-ground and below-ground interactions. Previous studies have demonstrated that the efficiency of light energy utilization in intercropping systems can be enhanced through the optimization of various factors, including crop combinations, row spacing, and bandwidth configurations [40,41]. The present study shows that the complete below-ground interaction and partial interaction treatments at the maize V6 stage had higher PAR transmittance levels compared to the no below-ground interaction treatment. The results indicate that water-nutrient exchanges within the subterranean root systems of wheat and maize are the primary contributors to the observed increase in PAR transmittance through differential growth and canopy development. The possible reason is that the intercropped maize root had a higher root length density [42].

#### 4.3. *Response of Interspecific Relationships and Crop Dry Matter Accumulation Dynamics to the Intensity of Above- and Below-Ground Interactions*

The accumulation of dry matter is an important basis for the yield of a population. Agronomic measures, including crop configuration, belt type, irrigation, and fertilization regimes, significantly impact the dynamics of dry matter accumulation in component crops within intercropping systems. Research suggests that above- and below-ground interactions promote root growth and water use efficiency in intercropping systems [30], which, in turn, increases yields. This study indicates that both complete and partial below-ground interaction have significantly greater effects on wheat dry matter accumulation compared to the no below-ground intercropping treatment during the late wheat growth period. Additionally, the increased intensity of above-ground intercropping did not have any significant effect on the dynamics of wheat dry matter accumulation. Different intensities of above-ground and below-ground interaction significantly influenced the accumulation of dry matter in maize during the late reproductive stage. Furthermore, an increase in maize density after wheat harvesting promoted the positive impact of complete above-ground and below-ground intercropping on the accumulation of dry matter in maize.

The basic ecological principles show that, when two crops are planted together, the interaction between crop species is bound to occur; this role enhances interspecific competition and also the results of the common role in determining an intercropping advantage (or not) [7,14]. The competition between intercropping systems can be categorized as above-ground competition and below-ground competition. Above-ground competition concerns the competition for light, heat, and gas, whereas below-ground competition concerns the competition for soil moisture, nutrients, and space [43]. Wheat is more competitive than maize, which puts maize at a resource disadvantage during the co-growth period [8]. After the wheat harvest, the growth space both above and below ground expands, leading to increased absorption and the utilization of light, heat, air, and water by intercropped maize. The intercropped maize growth rate increased in comparison to monoculture, resulting in a growth recovery effect [44]. Similarly, our findings indicate that the recovery effect

value of intercropped maize is almost always greater than 1, suggesting that intercropped maize exhibits a higher growth rate than sole maize. The late co-growth period (filling wheat) of maize and wheat showed enhancements in  $A_{wm}$  due to the synergistic impact of above-ground and complete below-ground interactions, as revealed by this study. In the present research, complete below-ground interaction significantly increased the maize recovery effect by 28.5% and 43.7%, respectively, compared to the partial interaction and no interaction treatments, but the effect of increasing maize density on the recovery effect varied between years. This indicates that synergistic above-ground and below-ground interactions during the co-growth period significantly increased wheat competitiveness relative to maize and that complete below-ground interaction was the key to promoting maize growth recovery.

## 5. Conclusions

Complete above- and below-ground interactions in intercropping systems significantly increased yield and LER, while increased above-ground interaction intensity had a yield-enhancing effect. During the co-growth period, complete above- and below-ground interactions significantly enhanced the competitiveness of intercropped wheat to maize ( $A_{wm}$ ). Moreover, intercropped wheat with complete above- and below-ground interactions had higher PAR transmittance and LAI. After the wheat harvest, complete above- and below-ground interactions significantly increased dry matter accumulation and LAI, which was the main reason for the enhanced recovery effect in maize. Increasing maize density significantly increased the positive effect of complete above- and below-ground interactions. Our findings indicate that the above- and below-ground interactions improved interspecific relationships, which then enhanced yield. More research on soil moisture, nutrients, and crop photosynthesis characteristics is required to further evaluate the effects of above- and below-ground interactions on the advantages of intercropped systems.

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