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Interspecific Root Interactions Enhance Biomass and Nutrient Acquisition of Millet (*Setaria itlica*) and Mungbean (*Vigna radiata*) in Intercropping System

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Abstract

Intercropping systems have been widely practiced because of the advantages in productivity and resource efficiencies. However, limited knowledge is available on how below-ground interspecific interaction affects yields and nutrient acquisition of crops in the intercropping. Pot experiments were carried out to facilitate the complementary induced by root interactions from below-ground in millet and mungbean intercropping. The data regarding yield, biomass, nutrient uptake, parameters of root morphology traits and photosynthesis were recorded. The experiment included three treatments: no barrier treatment (NB) allowing complete root interaction, mesh barrier (MB) of partial root interaction and solid barrier (SB) without any exchanges of water and nutrients and root interaction. The yields of millet and mungbean were increased by 53.6% and 27.8% in the treatments with complete root interactions compared to that without root interactions. Nitrogen (N), phosphorus (P) and potassium (K) acquisitions of crops were 1.71, 1.97 and 1.47 times for millet, and 1.25, 1.21, and 1.19 times for mungbean in complete root interactions as high as in no root interactions, respectively. The length and surface area was increased by 52.9 and 40.6% for millet while 51.4 and 46.8% for mungbean in complete root interactions compared to that in no root interactions. The improvement of yield and nutrient acquisition may result from crop structural and functional plasticity induced from interspecific root interactions of below-ground. The results would contribute to a comprehensive understanding of the response of millet and mungbean to the root interaction on the basis of interspecific facilitation for millet/mungbean intercropping.

Keywords: Cereal; Legume; Nitrogen acquisition; Root morphology; Yield

Introduction

Intercropping has become popular and has been practiced globally because of its high land productivity and high resources use efficiency across the world. Significant over-yielding has been observed in various intercropping systems, especially with cereal and legume combinations (Bedoussac *et al.*, 2015), such as maize/bean, maize/cassava (Sangakkara *et al.*, 2012) intercropping in Asia, winter rye/Caucasian clover (Andrzejewska *et al.*, 2014), maize/red fescue (Manevski *et al.*, 2015) intercropping in Europe, maize/soybean (Tsujimoto *et al.*, 2015) intercropping in Africa.

Over yielding in cereal/legume intercropping has been well documented, the advantage often obtains from niche complimentary and direct interspecific facilitation. The advantage of the intercropping includes above-ground and below-ground interactions between intercropped species (Li *et al.*, 2007; Lv *et al.*, 2014). Above-ground interactions such as light interception and light use efficiency between two species were one of the important factors to intercropping advantages (Albaugh *et al.*, 2014; Yang *et al.*, 2014). Below-ground interspecific interactions includes high nutrient use efficiency, such as water (Xu *et al.*, 2008; Tsujimoto *et al.*, 2015), nitrogen (Isaac *et al.*, 2012; Anglade *et al.*, 2015), phosphorus (Li *et al.*, 2007; Bedoussac *et al.*, 2015; Latati *et al.*, 2016) and microelements (Dong *et al.*, 2008) in intercropping.

The improvement of nutrient acquisition by interspecific root interactions may play an important role on the complementary or facilitation for over yielding advantage for intercropped species. Nitrogen acquisition of wheat shoot and grain was enhanced by 90.6% and 98.4% in wheat/faba bean (Xiao *et al*., 2004). For legumes, N_2 fixation could be enhanced by being intercropped with cereals. A field experiment in Europe found that N_2 fixation rate of pea was increased by 88% in intercrops compared to 58% in sole crops, and the accumulated N of intercrops were enhanced (Bedoussac and Justes, 2010). And there is a higher percentage of N derived from atmosphere in intercropping compared to sole pea (Naudin *et al.*, 2010). In maize/faba bean intercropping, phosphorus is mobilized by

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faba bean, then the intercropped maize could benefit from the available phosphorus on P deficient soils, led to a high nutrient acquisition and a greater productivity compared to monoculture (Li *et al.,* 2007). Nutrient acquisition was enhanced in maize/soybean intercropping, N , P and K acquisitions of maize were increased by 17.5, 30.7 and 14.9% by above-ground effects while 21.3, 34.4 and 17.8% by below-ground effects derived from root interactions, respectively (Lv *et al.,* 2014).

The root morphology traits were also contributed to the yield and the complementary resources capture in the intercropping compared to the monoculture (Abdulkadir *et al.,* 2006; Junhua *et al.,* 2009). Jamont *et al*. (2013) reported 64% of faba bean root length was located in the upper part, while 70% was in the lower part for rapeseeds, which led to a higher N acquisition in the intercropping compared to that of monoculture. The positive influence mainly comes from belowground interspecific interactions (Thilakarathna *et al.,* 2016). However, there are limited knowledge on how does this intercropping complementarily facilitate nutrient N uptake and acquisition by below-ground root interactions via structural and functional plasticity while the legume is mixed in the systems.

Millet (*Setaria itlica*) intercropped with mungbean (*Vigna radiata* (Linn.) Wilczek.) has been proved to significantly increase land productivity and revenue of household farmers (Meena *et al.,* 2012). Over-yielding and better nutrient uptake was found in millet/mungbean intercropping compared to sole treatments (Ram and Meena 2014). While to date, the mechanism underlying the complementary of yield and nutrient acquisition derived from interspecific root interactions was still kept unknown.

Thus the objective of our present study was that (1) growth advantage of intercropped species may caused by dry matter accumulation and growth via high nutrient acquisition of intercropped species and; (2) the improvement of high nutrients acquisition probably cause by plasticity effects derived from below-ground, which including both structural and functional plasticity such as the leaves number and height of crops, the root architecture, and photosynthesis, etc.

Materials and Methods

Experiments Design

Pot experiments were conducted in 2015 at the Experimental Station of Liaoning Academy of Agricultural Sciences at Shenyang, northeast China. Millet (*Setaria itlica*) and mungbean (*Phaseolus radiatus*) intercropping was tested. The three treatments were (1) a solid root barrier (no root interactions) with no root or water contact or nutrient exchange between the two species; (2) a 30-µm pore size mesh barrier (partial root interactions) with no root contact but with exchange of water and nutrients; and (3) no barrier (full root interactions), with full root contact and exchange of water and nutrients. The pots were arranged in a complete randomized block design with three replicates of each treatment.

Each pot was 32 cm in height and 36 cm in diameter, contained 15 kg air-dried soil during 2015. The pots were divided into two compartments by barriers described above to separate the two intercropped plant species. The soil was sandy and was collected from Fuxin Long-term Observation and Experimental Station, Liaoning, China, where millet/mungbean intercropping is commonly practiced. The soil was sieved to pass through a 2-mm mesh. The soil had an organic matter content of 8.2 g kg^{-1}, total N P, K of 0.21, 0.87, 18.3 g kg^{-1} and available N, P, K of 71.0, 63.5, 166 mg kg^{-1}, and a pH of $CaCl_2$ solution was 6.78. The water content of the air-dried soil was 2.8%. Millet and mungbean were sown at 5 July in 2015, and harvested at 8 November. Each pot contained 4 millets and 2 mungbeans plants in equal halves of each pot.

Measurements of Photosynthesis and Dry Matter

Photosynthesis parameters namely net photosynthesis rate (*Pn)*, stomatal conductance (*Gs)*, intercellular carbon dioxide concentration (*Ci)*, and transpiration rate (*Tr)* were measured with LI-6400 (Li-Cor, Lincoln, NE) from 9:30 to 11:30 am on a sunny day at heading stage for millet and flowering stage for mungbean on 3rd August 2015. A fixed light intensity of 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was selected. The first fully expanded leaf from the top of the canopy was used for the measurements in both crops. Each leaf sample was analyzed three times to minimize instrumental error.

The stem, leaves, fruits and roots of the crops were separated at harvest to determine the final dry matter content of each crop component in the intercropping treatments. All the roots of both crops in each pot were separated from the soil by careful washing. The sampled plant parts were oven-dried at 75°C for 72 h to a constant weight.

Total N, P, and K of crop samples were measured according to the methods from Salmeron *et al.* （2010). Crop materials were ground into a fine powder and then were measured by adding 5 mL of 18.4 mol L^{-1} HNO_3, 1.5 g K_2SO_4, and 0.15 g of $CuSO_4$ to dry, and 0.5 g samples of millet and mungbean in digestion tubes. After a thorough mixing, the solution was put aside to stand overnight, boiled to clear solution the next day, and cooled before distillation. Boric acid was added to the distillate, titrated with sulfuric acid until the solution turned from green to pink, and the contents of total N, P, and K in these solutions were calculated.

Statistical Analysis

ANOVA analysis was done by using one-way analysis of variance tests in SAS (V8). The LSD (least significant difference) multiple comparisons were determined at $a \leqslant 0.05$.

Results

Yields and Dry Matter

Root interactions increased the growth and yields of both millet and mungbean in the intercropping in 2015 (Fig. 1A and B). Millet yield in no barrier (complete root interactions) was increased by 53.6% and 33.1% compared to that in solid barrier (no root interactions) and mesh barrier (mesh root interaction). The yield of mungbean was increased by 27.8% in complete root interactions treatment compared with no root interactions (Fig. 1A). While there was no significant difference of harvest index of both crops (Fig. 1B).

Shoot and root biomass of millet was significant increased by 34.6% and 78.9% in complete root interactions treatments compared to that in no root interactions treatments. However, the root biomass of mungbean was significant greater in no barrier than in solid barrier, but for shoot biomass, no significant difference was found (Fig. 2A and B). For the ratio of root and shoot (Fig. 2C), significant difference was found in mungbean between complete and no root interactions treatment, while for millet, there was no notable difference among the three root interactions separation treatments.

Above- and Below Ground Growth of Mixing Crops

The results showed that plant height and leaves number of millet was increased by 17.9% and 42.8% in root interactions treatment compared to that without root interactions, the value for mungbean was 5.71% and 28.6%, respectively (Table 1). And the root length, surface area and root volume of both crops were significantly enhanced by no barrier treatment compared to solid barrier, while the average root diameter was decreased for millet when allow root interaction, for mungbean root diameter, no significant difference was observed among the three root patterns. Total root length and surface area of crops were increased by 52.9 and 40.6% for millet while 51.4 and 46.8% for mungbean, respectively (Table 2).

Photosynthesis

The SPAD of millet was increased by 12.6–28.1% in complete root interactions compared to that without root interactions treatments during the growing seasons, while there was no significant difference of SPAD of mungbean among the three root interactions patterns (Table 2). Net photosynthesis rates (*Pn*) of millet was 1.35 times in complete root interactions as much as that in no root interactions treatments for the flowering growth stages, while there was no significant difference for both growth stages for mungbean (Table 3). Both intercellular carbon dioxide concentration (*Ci*) and transpiration rate (*Tr*) of millet were increased in partial root interactions compared to that without root interactions treatments at the flowering growing stages.

Table 1: Effect on the height and leaves numbers of crops

Species	Root separate patterns	Height (cm $plant^{-1}$)	Leaves of total plant (No. $plant^{-1}$)
Millet	SB	59.1±1.36 b	17.3±0.48 b
	MB	64.5±1.62 ab	17.8±0.63 ab
	NB	69.7±3.22 a	19.5±0.65 a
Mungbean	SB	49.0±3.50 a	17.5±1.19 a
	MB	50.5±5.13 a	17.0±1.68 a
	NB	51.8±4.42 a	20.3±1.80 a

SB refers to solid barrier, MB for mesh barrier and NB for no barrier
Same small letter indicates no significant difference between treatments in same year and crop at *P*<0.05

Table 2: SPAD of leaves in intercropping affected by inter specific root interactions

Crops	Growth stages	Solid barrier	Mesh barrier	No barrier
Millet	Branching	38.0±1.08 b	44.4±2.09 a	45.9±2.22 a
	Flowering	39.7±1.13 b	45.2±1.21 a	44.7±3.46 a
	Seed filling	24.9±0.97 b	29.7±0.97 ab	31.9±1.19 a
Mungbean	Jointing	37.8±1.96 a	38.1±1.73 a	39.6±2.08 a
	Flowering	39.9±0.82 a	38.0±3.11 a	39.7±2.25 a
	Seed filling	31.3±1.54 a	32.0±1.31 a	31.9±1.27 a

SB refers to solid barrier, MB for mesh barrier and NB for no barrier
Same small letter indicates no significant difference between treatments in the three root separation patterns at *P*<0.05

Table 3: Net photosynthesis rate (*Pn*), stamatal conductance (*Gs*), Intercellular CO_2 (*Ci*) and transpiration rate (*Tr*) of intercropped millet and mungbean in 2015

Crop species	Root separation	*Pn* µmol CO_2 m^{-2} s^{-1}	*Gs* mmol m^{-2} s^{-1}	*Ci* µmol mol^{-1}	*Tr* mmol $m^{-2}s^{-1}$
Millet	SB	16.2±1.75 b	0.22±0.02 a	112±13.1 b	3.86±0.71 a
	MB	21.8±0.91 a	0.38±0.07 a	209±14.3 a	6.79±0.49 a
	NB	21.8±1.25 a	0.31±0.04 a	179±13.2 ab	4.72±0.75 b
Mungbean	SB	12.6±1.48 a	0.09±0.02 a	79.2±7.1 a	2.08±0.24 b
	MB	14.3±0.75 a	0.16±0.03 a	122±12.9 a	3.51±0.34 a
	NB	16.2±1.27 a	0.16±0.08 a	142±13.3 a	3.17±0.04 ab

SB refers to solid barrier, MB for mesh barrier and NB for no barrier
Same small letter indicates no significant difference between treatments in the three root separation patters at *P*<0.05

N, P and K Acquisition

The results showed that N, P and K acquisition of both crops were significantly enhanced by no root interactions compared to that without root interactions treatments (Fig. 3). Nitrogen acquisition of above-ground and below-ground of crops were increased by 70.5%, 73.5% for millet and 25.2%, 77.1% for mungbean in complete root interactions treatments compared to that without root interactions (Fig. 3A and B). Above-ground P acquisitions of millet and mungbean were 1.97 and 1.21 times in complete root interactions as much as those in no root interactions, and 2.54 and 1.91 times for below-ground (Fig. 3C and D), respectively. Similar results was also found in K

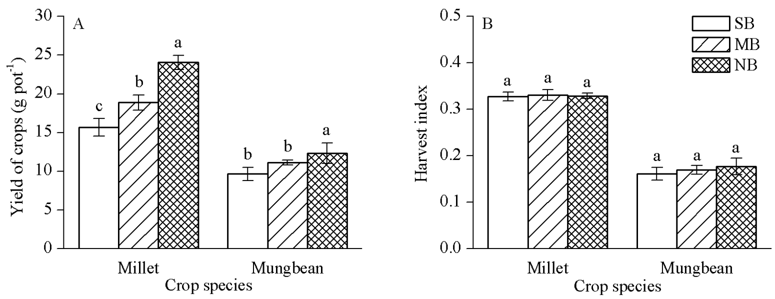

Fig. 1: Yield of millet and mungbean (A), Harvest index of millet and mungbean (B) with different root barrier patterns between two species in 2015 in greenhouse, Shenyang, China. SB indicates solid barrier, MB for mesh barrier and NB for no barrier. Bars with different letters indicate a significant difference (P<0.05) among three treatments of root interactions

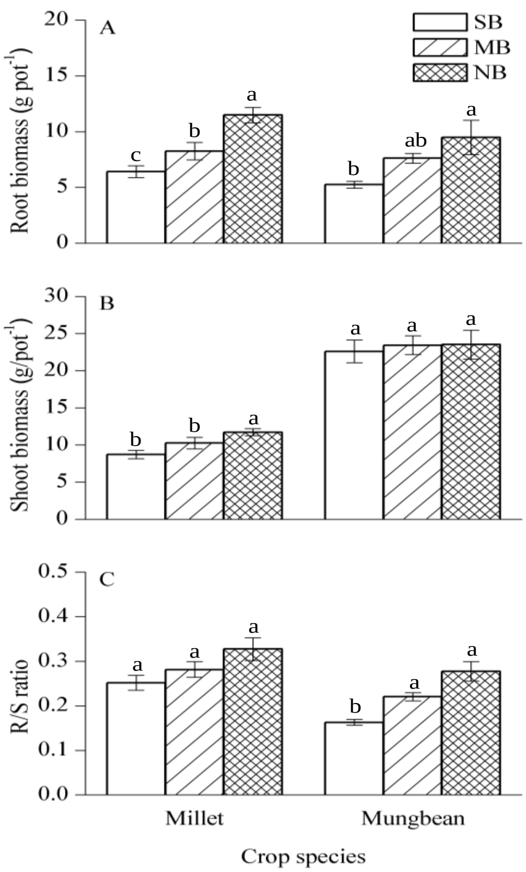

Fig. 2: Root biomass of millet and mungbean (A), shoot biomass of millet and mungbean (B), and root/shoot (R/S) Ratio of millet and mungbean (C) with different root barrier patterns between two species in 2015 in greenhouse, Shenyang, China. SB indicates solid barrier, MB for mesh barrier and NB for no barrier. Bars with different letters indicate a significant difference (P<0.05) among three treatments of root interactions

acquisitions of below-ground for both millet and mungbean, root interactions enhanced K acquisition compared to that without root interactions treatments (Fig. 3F).

Discussion

The below-ground interactions in a cereal and legume intercropping significant increase crop growth by the interspecific facilitation due to an enhancement of nutrient acquisition by structural and functional plasticity such as photosynthesis.

Interspecific Root Interactions Enhanced Nutrient Acquisition in Cereal/Legume Intercropping

Our results showed that crop yields and dry matter biomass were significantly enhanced by the high nutrient acquisition derived from the interspecific root interactions. The presence of white clover increased ryegrass yields and N uptake by 12–44% and 26–72% in ryegrass/white clover intercropping (Enriquez-Hidalgo *et al.*, 2016). N acquisition of wheat was increased and symbiotic N_2 fixation of fababean was enhanced by the root interactions from below-ground in wheat fababean intercropping (Xiao *et al.*, 2004). In rapeseed/fababean intercropping, intercropped rapeseeds accumulated 20% higher amount of N than that in monoculture, and percentage of biological N_2 fixation of fababean was increased by 9% than that in pure stand (Jamont *et al.*, 2013). N uptake of cereals in mixture was higher than that in the pure stand which was 95–140 kg N ha^{-1} versus 30–60 kg N ha^{-1} in white color-ryegrass mixture (Louarn *et al.*, 2015). And enhanced P acquisition was also found in a 4-year field study, maize over-yielding resulted from more uptake of phosphorus, which could be mobilized by faba bean, then the intercropped maize was benefit from the available phosphorus on P deficient soils, led to a high nutrient acquisition and a greater productivity compared to monoculture (Li *et al.*, 2007). Recently research showed that interspecific root interactions enhanced maize shoot biomass and maize shoot P uptake by 21.0% and 61.2% (Yan *et al.*, 2014). There are still some evidence demonstrated that some microelement such as Fe and Zn also contribute to the growth advantage of intercropped species in maize/peanut intercropping system (Zuo *et al.*, 2000; Inal *et al.*, 2007; Guo *et al.*, 2014; Shen *et al.*,

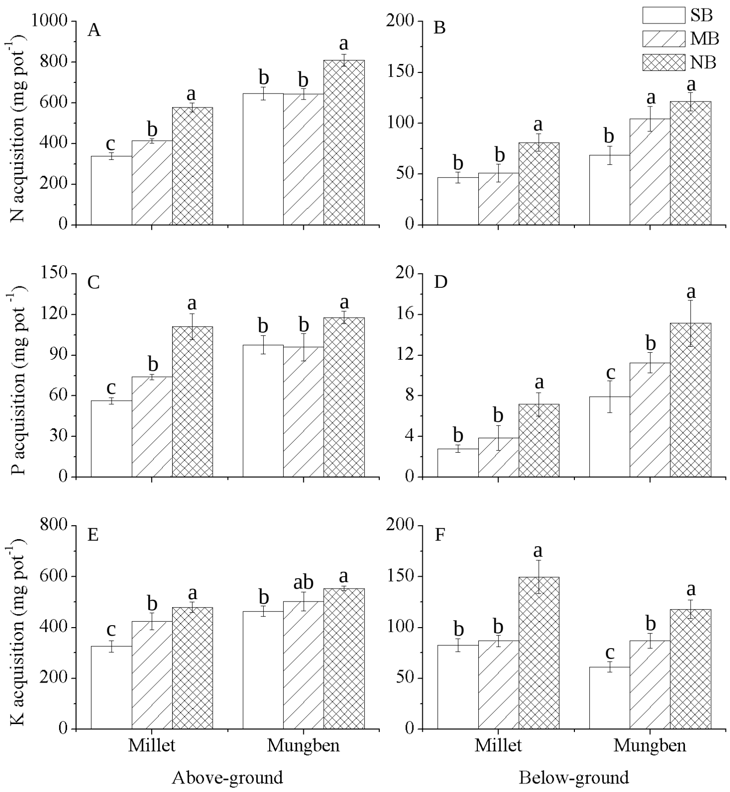

Fig. 3: N, P, and K acquisition of crops under solid barrier (SB), mesh barrier (MB), and no barrier (NB) in 2015, A for above-ground N acquisition, B for below-ground N acquisition, C for above-ground P acquisition, D for below-ground P acquisition, E for above-ground K acquisition, and F for below-ground K acquisition

2014). These studies indicate that the nutrient maybe an important part for the contribution to the facilitation from interspecific below-ground interaction. Further research should be conducted to test the importance and portion of nutrient contribution.

The present study also confirmed that the increase of yield, dry matter biomass and nutrients acquisition was involved with the structural and functional plasticity derived from interspecific root interactions. The effect of root interaction which occurred in the below-ground, combined with root morphology and altered photosynthesis parameters such as increasing *Pn* and *Ci*, may influence the growth and dry matter accumulation of crops, ultimately resulting in the enhanced growth and biomass and dry matter accumulation in the treatment with complete root interactions.

Root length and surface area was increased by 52.9% and 40.4% when allow complete root interactions compared to that without root interactions (Table 4). Cereals exhibited greater root morphological plasticity than legumes. Similar results was also found in maize/fababean intercropping, rhizosphere effects significantly enhanced maize root biomass and total root length by 25.4% and 67.9%, respectively, the alter of root morphology traits was derived from root interactions from below-ground (Yan *et al.,* 2014).

Table 4: Effects of root barrier on root parameters of millet and mungbean

Species	Treatment	Length (cm)	Surf Area (cm^2)	Avg Diam (mm)
Millet	SB	596±23.4 c	93.9±2.13 c	0.50±0.02 a
	MB	721±18.8 b	115±0.36 b	0.51±0.02 a
	NB	911±36.1 a	132±5.81 a	0.46±0.01 b
Mungbean	SB	535±22.2 b	87.9±7.30 b	0.52±0.02 a
	MB	697±30.0 a	116±6.52 a	0.53±0.02 a
	NB	810±12.9 a	129±4.68 a	0.51±0.03 a

SB refers to solid barrier, MB for mesh barrier and NB for no barrier
Same small letter indicates no significant difference between three root separation patterns treatments at $P<0.05$

Li *et al.* (2014) reported that most wheat roots had a diameter of less than 0.2 or 0.3 mm (the finest-rooted of the four species tested). In contrast, fababean had the coarsest roots (mostly in the 0.3–0.6 mm range). Hence, the response ratio was highest in wheat, graminaceous species (maize and wheat) exhibited higher morphological plasticity than leguminous species (faba bean and chickpea) (Li *et al.*, 2014). Root dry weight of oil sunflower was 1.83–2.51 times that of sole cropping, the root length and root surface area were 1.25–1.27 and 1.20–1.14 times as much as that in monoculture (Junhua *et al.,* 2009). It suggested that the alteration in root morphology traits might change the root-root interactions and reduce the competition of species in the intercropping systems (Shen *et al.*, 2014), thus the yield advantage was facilitated. Understanding the differences between cereals and legumes in root morphological responses to root interactions from below ground may provide a new insight into root-root interactions of plant species.

The leaves number of both millet and mungbean was higher in the complete root interactions treatments than those without root interactions. In a 2-year field experiment, plant height, stem girth, leaves/plant, fresh weight/plant, total green fodder were found to associated with crop dry matter yields in maize/cowpea intercropping (Kumar *et al.,* 2014). The SPAD and the rates of net photosynthesis were also enhanced under the root interactions condition. Recently study showed the importance of plasticity in the performance of intercropping, light capture was 23% higher in the intercropping with plasticity than that in the monoculture (Zhu *et al.,* 2015). Lv *et al.* (2014) showed that no notable differences was found on the photosynthetic parameters of maize among the intercrop and monoculture at the jointing stage in maize/soybean intercropping, while the *Pn*, *Tr*, *Gs*, and *Ci* of maize were significant higher in the treatments of no root separation than that root separation treatments (Lv *et al.,* 2014). Intercropping citrumelo plants with perennial grass was effective in Fe nutrition capture and dry matter weight which associated with SPAD index, preventing the development of leaf chlorosis and improving their growth compared to the control plants (Ammari and Rombola, 2010). The results indicated that the potential of structural and functional plasticity derived from root interactions by below-ground for enhancing nutrient acquisition in intercropping and the importance of plasticity in the performance of over yielding advantage of intercropping.

Conclusions

The below-ground interactions in a cereal and legume intercropping significant increase crop growth by the interspecific facilitation due to an enhancement of nutrient acquisition by structural and functional plasticity such as photosynthesis. Further research should be paid attention to the effect of interspecific root interactions on water and micro-nutrient acquisition between intercropped species in field study. The results provided a comprehensive mechanism of dry matter biomass and high resource use efficiency via structural and functional plasticity in intercropping, which might help optimize the productivity of intercropping by the selection of species or cultivars, the arrangement of space, to alleviate competition for resources by increasing interspecific facilitation.

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