**Asymmetric facilitation in agroecosystem: Exploring concurrent positive and negative plant interactions**

**Running title: Asymmetric facilitation in rainfed farming**

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**Abstract**

Facilitation events were mostly reported in two modes of mutual promotion (+/+) and unilateral benefit (+/0) in cultivated plant populations, yet few investigations showed the third mode, i.e. +/-. We investigated the maize-faba bean intercropping system as the third mode which was little documented. Land equivalent ratio in intercropping system was significantly greater than in monocropping one, with faba bean as superior species (+), and maize as inferior species (-). For inferior species, interspecific competition restricted its substance remobilization and seed filling, and caused a relatively low pollen fertilization rate and high kernel abortion rate. This trend resulted from lower soil water availability in maize strip of intercropping system, and lower leaf chlorophyll content and photosynthetic rate in maize. Yield loss of inferior species provided mechanical explanation on the concurrent +/- facilitation. The findings enriched our understandings on asymmetric facilitation and the relationship between plant diversity and productivity in agroecosystems.

**Keywords**

Asymmetric facilitation; intercropping system; +/- mode; substance remobilization; seed filling; yield loss; agroecosystems.

**INTRODUCTION**

Existing studies have established the impacts of plant diversity on ecosystem service function, including the positive relationship between plant diversity and productivity (Cong *et al.* 2014; Lange *et al.* 2015; Prommer *et al.* 2020). This positive relationship is largely dependent on the interspecific facilitation, compensation and the relevant selection effects in plant community (Brooker *et al.* 2008, 2016; Isbell *et al.* 2017). When two plants grow together, interspecific competition between plants is inevitable (Hart *et al.* 2018). Most of the early ecological theories are based on negative plant–plant interactions (competition) between plants (Weaver & Grime 1980; Austin 1989). Yet, the important role of positive plant-plant interactions (facilitation) in shaping plant population development has been increasingly acknowledged over last decades (Callaway 1995; Brooker et al. 2008; Lin et al. 2012). The definition of facilitation has a process of evolution in classic ecology. (Callaway 1995) and (Bruno *et al.* 2003) believes that facilitation is "an interaction that is beneficial to at least one party and harmless to both". However, (Callaway 2007) more broadly defined the facilitation as "as long as the interaction is beneficial to one or the other". Taking together, the types of facilitation generally include mutual promotion (positive/positive, +/+) and unilateral benefit (positive/neutral, +/0), and antagonistic (+/-).

The pronounced examples of facilitation in agroecosystems have mostly come from intercropping (Brooker *et al.* 2015). Intercropping is a traditional planting pattern widely used all over the world (Li *et al.* 2014; Brooker *et al.* 2015), and intercrops usually produce higher yields per unit area than sole crops as measured by the land equivalent ratio (LER). The LER is defined as the relative area of land (under sole cropping to the intercropping) required to produce equal amounts of yield (Willey 1979; Cong *et al.* 2015; Li *et al.* 2020). The mechanism of yield increase in intercropping system is mainly focused on three aspects, including interspecific promotion, resource sharing, and niche complementarity respectively. Interspecific promotion generally refers to promoting the nodulation of legume crops (Li *et al.* 2016), improving the activation of insoluble nutrients (Li *et al.* 2007; Zhang *et al.* 2016), sharing resource and enhancing the fixed nitrogen transport from legumes to neighboring plants (Jensen *et al.* 2020). In this regard, niche complementarity is the tendency for coexisting species which occupy a similar position along one niche dimension to differ from another (Yu *et al.* 2015; Liu *et al.* 2018; Ma *et al.* 2019). In intercropping system, the early-sowing or early-maturing crop tends to have the opportunity to utilize greater amount of water resources for higher biomass, while the late-sowing or late-maturing one can improve biomass via the compensation effect after the early crop is harvested (Yin *et al.* 2020).

The competition process is not only controlled by heterogeneous gene expression in plants, but also affected by external environmental factors (Schofield *et al.* 2018). Within a short-term growing season, the temporal dynamics of resource capture and plant-plant interactions seem to be complicated (Hart *et al.* 2018). For example, the instantaneous assimilation rate obtained by logistic model fitting can represent the plants interactions at that time and the synchronous flow of resources in each competitor. Spatial dynamics of resource allocation frequently reflect the actual competition processes (Trinder *et al.* 2012). During the reproductive growth period of crops, root activity and nutrient uptake capacity would gradually decrease, and plants would remobilize more nutrients for the emerging "pool" (Kong *et al.* 2016), and accordingly affect yield formation (Thomas 2013). In this process, kernel number and its weight are critical traits controlling final yield and assimilates distribution in maize ears (Yan *et al.* 2018). Stressful environments, including low soil moisture and high evaporation frequently have a negative impact on kernel development, resulting in a decrease in final kernel weight, particularly in northwest China (Chen *et al.* 2013; Hisse *et al.* 2019). In northwest China, regional climate is briefly characterized by low rainfall and high evaporation. Plastic film mulching is widely used to improve soil water storage, and thus modify the plant water relation (Fengrui *et al.* 2000; Luo *et al.* 2018). However, little is known about whether the improved plant water relation can reshape the modes of facilitation.

Over last decades, most of facilitation events have been reported in two modes, i.e. mutual promotion (positive/positive, +/+) and unilateral benefit (positive/neutral, +/0) in cultivated plant population. Yet, few investigations were documented in terms of the third mode, i.e. positive/negative (+/-). We therefore hypothesize that there would be superior and inferior species to co-exist in a same farming system, and total LER of symbiotic system might exceed the average value of two monoculture systems. Under the interspecific competition, the loss of biomass or yield of inferior crops may imply the mechanism of asymmetric facilitation formation in agroecosystems. This phenomenon is likely to contain new implications on the relationship between plant diversity and its productivity under stressful conditions. In present study, maize-faba bean intercropping system, a symbiosis widely found in agricultural ecosystem, was chosen to test and verify the above hypothesis. The major objectives of this study are designed as follows: 1) to determine the differentiate dynamics of growth and yield formation of two crop species under the monoculture and intercropping conditions; 2) to identify the positive and negative interactions between two species and the possible yield loss of inferior species as affected by the co-growth effect; 3) to reveal the yield loss mechanism of inferior species in rainfed environment; 4) to clarify the presence of third facilitation mode with +/- and the relationship between plant diversity and productivity in rainfed agroecosystem.

**MATERIALS AND METHOD**

**Experimental site**

The experiment was conducted in the Experimental Station of Agroecosystem of Lanzhou University (35°51′N, 104°07′E, altitude 1620 m), in Yuzhong County, Lanzhou, China during 2018 and 2019. Local landscape belongs to the semi-arid hilly and gully region of the Loess Plateau, with the characteristics of low & variable rainfall and high evaporation rate. The average rainfall, evaporation rate, and temperature in last 15 years were 346 mm, 1592 mm, and 7.81 ˚C respectively. Almost 60% of annual precipitation mainly occurs from July to September, belonging to typical rainfed agricultural region. The precipitation in 2018 and 2019 was 445.7mm and 415.2mm respectively, and the average temperature in 2018 and 2019 was 7.56 ˚C and 6.88 ˚C, respectively (Fig S1). The soil type of the experimental site was yellow loam soil, and the long-term cropping system was wheat monoculture. The soil bulk density, organic carbon content, pH (1:2.5 H2O), total nitrogen, available phosphorus and available potassium in 0-40 cm soil layer were 1.36 g·cm-3, 7.20 g·kg-1, 8.16, 0.81 g·kg-1, 3.51 mg·kg-1, and 121.54 mg·kg-1, respectively.

**Experimental design**

The experiment was designed in a two-factor randomized block. The faba bean cultivar *Lincan-6* (*Vicia faba*) and maize (*Zea mays* L.) hybrid *Shengdan* 18 were selected as two typical crop species in the present study. The planting patterns were mainly divided into following 6 types: the intercropping with plastic film mulching (2M4F: two rows of maize and four rows of faba bean), the monoculture with plastic film mulching (row to row and plant to plant distance for both species was 0.2 and 0.4 m respectively), the intercropping without mulching (2M4F), and the monoculture without mulching (row to row and plant to plant distance for both species was 0.2 and 0.4 m respectively). The plant to plant distance and row to row distance for monoculture and intercropping were kept equal, and the plot size in each replication was 8m×8m (64m2). The plant density was chosen according to local planting convention. Faba bean was sown in 2.25 × 106 plants ha-1 and maize was in 6.5 × 105 plants ha-1. In the experimental years, faba bean was sown on April 10 and harvested on August 15, while maize was sown on April 25 and then harvested on October 15. Prior to sowing, 238 kg ha-1 of urea and 225 kg ha-1 of superphosphate were applied at one time to ensure nutrient sufficiency in the experimental field. Before sowing, 0.008 mm thick polyethylene black film was used as soil mulching in this experiment. All treatments were under normal field management and there was no irrigation across the whole growth period except natural rainfall.

**Data analysis and methods**

*Soil moisture and water use efficiency*

Soil water content (SWC), soil water storage (SWS), and water use efficiency (WUE) of 0-100 cm soil layer were calculated in faba bean and maize strips before sowing, during grain filling period, and after harvesting according to the method of (Mo *et al.* 2016).

*Determination of remobilization ability and yield-forming parameters*

After 7 days of maize silking period, three samples were randomly taken from the center of each plot (12 replicates) to select for counting their visible silks from the first day to the seventh day of silk emergence; silks were cut and counted once daily to determine their floret numbers per ear. The kernel loss was divided into two parts, in which the first one lost in kernel number by a decrease in visible silks due to failure of silk protruding from the husk (7 days after silking) was represented as loss1. It was calculated as the florets at silking, minus the total visible silks in one week for each plot. The second lost was in kernel number (loss2) by abortion; loss2 was calculated as the final kernel number at harvest minus visible silks.

On the fifteenth day of silking, i.e. when leaf senescence gradually appeared, three maize plants were randomly selected and harvested from the center area of each plot (12 replications). The stem, leaves, sheaths, and ear of maize per plant were separated and weighed after drying at 80 ˚C for 62 hours. After maturity, four plants were randomly selected from each plot and repeated the previous method. Yield-forming parameters such as ear length, ear diameter, kernel number, 100 kernel weight, kernel weight per plant, and bald tip length were measured and recorded. The remobilization of dry matter in vegetative organs and contribution rate of vegetative organs to kernel were calculated using the following equations:

(1)

(2)

(3)

Where DTA (kg ha−1) is a remobilization amount of dry matter in vegetative organ, LDW (kg ha−1) is the largest dry weight of the vegetative organ, DWM (kg ha−1) is the dry weight of the same vegetative organ in maturity, DTR is remobilization rate of dry matter in vegetative organ (%), GCR is contribution rate of vegetative organs to kernel (%), and GDW (kg ha−1) is the dry weight of kernel respectively.

**Statistical analysis**

Multiple destructive sampling method was used in the present study as previously described in (Trinder *et al.* 2012). Thirty days after seed germination, the aboveground plant parts (two samples from each plot i.e., 6 replicates) were collected after every 15 days, 7 times for faba bean and 10 times for maize. After the sample collection, quickly put it into the oven to be sterilized at 100 ˚C for 2 hours, and then kept at 80 ˚C until dried and weighed. Then, a logistic model was fitted to the biomass data of each treatment according to the equation 4 as described in (Zhang *et al.* 2017).

（4）

Where *Mt* (kg ha-1) is the biomass per unit area of the plant in a specific time, *K* (kg ha-1) refers to the maximum biomass that the crop can reach, r (d-1) represents the intrinsic growth rate (), and *t50* is the time in which a crop reaches the maximum growth rate respectively. These factors can be obtained by fitting the logistic 1 model in origin 2018. On the other hand, the instantaneous growth rate of plants was obtained by the following formula:

（5）

As the instantaneous growth rate of plants reaches the maximum at =K/2, the maximum growth rate is *Imax* = r*K*/4.

Data analysis and set of figures were prepared using SPSS 20.0, Origin 2018. One-way and two-way ANOVA was conducted using the SPSS 20.0 program (SPSS Inc., Chicago, USA). The differences among treatments were examined using LSD test (P≤0.05).

**RESULTS**

*Logistic fitting of biomass and carbon assimilation of two species*

In general, planting patterns significantly affected the biomass accumulation in two plant species, regardless of plastic mulching. In 2018 growing season, aboveground biomass in monoculture was 26.4 t ha-1 in maize and 12.0 t ha-1 in faba bean respectively, significantly greater than 23.6 t ha-1 in intercropping maize, while lower than 14.3 t ha-1 in intercropping faba bean respectively (*P*<0.05; Table 1). Importantly, the LER (land equivalent ratio) with the reference of biomass was 1.05 and the LER of yield was 1.07 in intercropping condition, significantly greater than 1 (*P*<0.05). This trend demonstrated that there existed a concurrent plant positive interaction, i.e. +/- asymmetric facilitation in the co-growth system of maize and faba bean. On the other hand, while plastic mulching significantly improved soil water status, the improved soil moisture did not change the above phenomenon of +/- asymmetric facilitation. Two growing seasons’ observations achieved similar results. In such case, maize was identified as inferior species and faba bean as superior species, both of which formed a symbiotic relationship, i.e. asymmetric facilitation under the intercropping condition.

To explore the critical factors causing the biomass and yield loss in inferior species (maize), a logistic model was established over various developmental stages. The results showed that both the intrinsic rate *R* and the maximum growth rate *Imax* were significantly decreased in inferior species (*P*<0.05). Simultaneously, the maximum biomass *K* was observed to decline greatly, as a result of interspecific competition (*P*<0.05; Fig 1a and Table 1). In contrast, the logistic model parameters of superior species (faba bean) showed a significant increasing trend when grown with inferior species (*P*<0.05; Fig 1b and Table 1). On the other hand, the responses of plant morphological and physiological parameters to co-growth environment were also measured and compared in inferior species (Fig. 3S). A general trend was that interspecific competition significantly reduced leaf area index, chlorophyll content (SPAD) and photosynthetic rate in inferior species across the growth stages (*P*<0.05). Accordingly, the carbon assimilation rate was also restricted in inferior species, leading to the occurrence of negative effects.

*Competition trajectories of biomass accumulation in co- growth period*

Cumulative biomass production and corresponding trajectories of instantaneous rates of biomass production were derived simply by plotting the fitted logistic models in Fig. 1 for the competing plants against one another (Fig. 2). The competitive trajectory of instantaneous biomass accumulation and growth rate showed that interspecific competition resulted in significant decrease in the growth ability of the inferior species during the co-growth period (Fig. 2a-b). The cumulative biomass in superior species was consistently greater than that of inferior species in both isolated and competing plants (Fig. 2a). Particularly, interspecific competition delayed the time when inferior species biomass exceeded superior species biomass (Fig. 2a). In addition, during the co-growth period (30-120 days) of two species, the biomass of inferior species did not exceed than superior species. In this period, it can be achieved under monoculture condition. This trend demonstrated that the biomass of superior species occupied a dominant position in the co-growth period across two growing seasons.

On the other hand, the initial advantage of superior species was also evident in light of the trajectories of their instantaneous rates of biomass production (Fig 2b). The growth rate of superior species was remarkably higher than that of inferior species at early growth stage (30-83 days). Until 83 d, the instantaneous growth rate of the inferior species exceeded that of the superior species in both monoculture and intercropping system; whereas the cumulative biomass did not exceed that of the superior species in the co-growth period. And interspecific competition delayed the time when the growth rate of inferior species exceeded that of superior species (Fig. 2b), suggesting that the high growth rate of superior species at early growth stage suppressed the growth of inferior species. Moreover, both root weight and soil water storage of 0-100cm soil layer in the strips of inferior species were significantly decreased (*P*<0.05), while there was no significant differences in both parameters in the strips of superior species (*P*>0.05). Despite plastic film mulching greatly improved soil water status, the above tendencies were not obviously affected (Fig. 2c-e, Table S1). Therefore, it can be argued that superior species can restrain the growth and development of inferior species through capturing more water from the strips of inferior species. This process was closely associated with water migration from the root-zone soils of inferior species to that of superior one.

*Biomass distribution and remobilization in inferior species as affected by competition*

The characteristics of biomass allocation and remobilization among different organs in inferior species are shown in Figure 3 and Table 2. In general, the growth and development of inferior species such as reproductive biomass (ear) and vegetative biomass (leaf, stem, and sheath) showed a decreasing trend at silking and maturity stage in the case of interspecific competition (Fig 3a-b). However, the pattern of biomass allocation followed an opposite trend from above parameters (Fig 3c-d). Relatively, the biomass proportion of vegetative organs in total biomass increased, while the proportion of reproductive organs turned to decrease at two growth stages. Additionally, although plastic film mulching led to a pronounced improvement on total biomass accumulation and reproductive allocation amount, the differentiate effects caused by interspecific competition were still remained as above. Similar tendencies were similar in two growing seasons.

Another pronounced parameter, i.e. biomass remobilization efficiency was recorded and compared between intercropping and monoculture across two growing seasons (Table 2). Totally speaking, interspecific competition significantly restricted the remobilization ability of inferior species (*P*<0.0001). Three typical physiological parameters of inferior species, including the amount of biomass transfer (DTA), the rate of transferring (DTR), and the contribution rate of biomass to grain (GCR), displayed extremely significant downward tendencies (*P*<0.0001). Specifically, the contribution rate of vegetative organs to grain filling followed a decreasing trend in the sequence of stem > leaf > sheath (Table S2). In comparison with monoculture, interspecific competition significantly reduced DTA, DTR and GCR by 29.3%, 22.8% and 17.4%, respectively (*P*<0.05; Table 2). Two growing seasons shared a similar trend in inferior species. Improved soil water status under plastic mulching did not change the general trend. These results suggested that interspecific competition tended to suppress the transfer of remobilization substance to reproductive organs since grain filling in inferior species. The general trend was similar between two growing seasons.

*Yield formation and kernel abortion in inferior species*

Regardless of plastic film mulching, interspecific competition significantly affected the yield formation process of inferior species (Table 2). Relative to the monoculture system, both grain number and grain yield of inferior species decreased significantly in the intercropping system (P<0.0001). Two-way ANOVA results showed that interspecific competition and plastic film mulching had significant effects on bald tip length, floret number, silking number, grains number, loss2 and total abortion rate in inferior species (P<0.05), whereas the interactive effect between two factors was not significant on the number of silking number and Loss1 (*P*>0.05). When comparing with monoculture, interspecific competition significantly decreased bald tip length by 56.2%, final grain number by 6.5%, Loss2 by 33.99%, and total abortion rate by 14.8% in intercropping system, respectively. On the other hand, logistic model estimation on grain filling suggested that interspecific competition significantly reduced *Imax*, *K* and *R* of grain yield (*P*<0.05; Table 1). Although plastic film mulching also significantly affected grain fertilization and development, the significant effect derived from interspecific competition was not remarkable. The above observations demonstrated that interspecific competition significantly had restricted grain fertilization and development process of inferior species, and accordingly elevated the grain abortion rate, and weakened its grain filling ability.

Finally, principle component analysis (PCA) predicted the abundances of kernel growth traits at the horizontal axis and vertical axis. The data presented the highest and the second highest differences between them, accounting for approximately 92.9% under film mulching and 94.3% under non-mulching respectively (Fig S4). The kernel abortion parameters (loss1, loss2, bald tip length and kernel abortion) were negatively associated with yield formation variables (visible silk, ear diameter, yield and ear length), remobilization variables (DTA, DTR, and GCR) and grain filling variables (*R*, *K*,and *Imax*), no matter whether plastic film mulching was applied or not. Also, there were significantly positive associations among the latter three variables. Two growing seasons shared similar trends as indicated above.

**DISCUSSION**

*Differentiate biomass accumulation dynamics of two species in intercropping system*

By using logistic model, the competition between adjacent plants can be analyzed quantitatively (Trinder *et al.* 2012). Previous studies showed that R, K, and Imax were totally increased for maize and decreased for watermelon in maize-watermelon intercropping system (Huang *et al.* 2017). In maize-wheat and maize-barley intercropping systems, it was also found that R, K, and Imax were wholly increased in wheat and barley, while those of maize were decreased (Zhang *et al.* 2015, 2017). In the present study, intercropping significantly increased the R, K and Imax of superior species (Table 1), and significantly decreased the R, K and Imax of inferior species, regardless of soil water status as affected by plastic film mulching. The photosynthetic parameters and physiological indexes of maize during the growth period also provided evidence to support this result (Fig S3).

From the dynamic trajectories of biomass accumulation and instantaneous growth rate of two species, the biomass and growth rate of superior species were observed to be higher than that of inferior species. This phenomenon showed a highly size-dependent competition relationship. On the other hand, the decrease of soil water storage and root biomass in maize strip of intercropping also provided another evidence to support the above relationship. Till now, there have been the similar reports available regarding the logistic model analysis on the cereal-legume (e.g. maize-faba bean) intercropping system. Several relevant studies reported such a phenomenon that after wheat, barley or faba bean was harvested, maize biomass began to rise sharply. And eventually the maximum biomass of intercropped maize was equal to or greater than that of monoculture maize. Theoretically, this phenomenon is defined as "compensation effect" (Li *et al.* 1999; Xia *et al.* 2013; Wang *et al.* 2017; Yin *et al.* 2017; Zhang *et al.* 2017; Ma *et al.* 2020). However, in the current study, when the superior species, faba bean was harvested (105 days after maize sowing), inferior species (maize) continued to grow till silking stage, when its individual development was transited from vegetative growth to reproductive growth. At this critical turning point, plant missed the fast growth period of biomass, and accordingly the physiological compensation effect was massively weakened. Our results showed that the compensation effect was not only dependent on the resources availability for the late-harvesting crop after the early-sowing crop was harvested, but also on the gap of growth at the co-growth period. If the loss of growth and yield during the co-growth period cannot be compensated in the late follow-up period, the intercropping would not increase total production, especially in rainfed agricultural ecosystems, where water resources are scarce. When the superior species showed a pronounced advantage of water capture over inferior one, high-intensity interspecific competition frequently enabled the compensation effect difficult to occur at the late sole growth period.

*Biomass allocation patterns of inferior species*

In higher plant, allocation patterns of biomass indicate energy investment trade-offs (Weiner *et al.* 2009). Generally, high investment in reproductive organs implies that plants provide more opportunities to their offspring, while high input in vegetative organs is to improve the survival ability of plants (Salguero-gómez *et al.* 2017). Previous studies suggested that small individual plants would grow slowly, and lower the number of flowers and branches, when the biomass allocation to reproductive organs was reduced (Echarte & Andrade 2003). (Weiner *et al.* 2009) also proposed that plants tended to allocate most of their biomass to vegetative organs at high density (due to the lowered available resource). Similarly, wheat also tended to allocate more biomass to vegetative organs than reproductive parts under the condition without plastic film mulching, due to the reduced water availability (Luo *et al.* 2020). Our results revealed that under the increased competition intensity particularly under no film mulching, the biomass of vegetative organs in inferior species would significantly decrease, but its proportion to total biomass would increase (Fig. 3). On the other hand, the biomass of reproductive organs not only decreased significantly, but also decreased in proportion to the total biomass. Facing with strong competition stress, inferior species tends to preferentially allocate more biomass to vegetative organs for better survival ability. This provides a theoretical basis for us to elucidate the impacts of interspecific competition on biomass allocation patterns for inferior species.

*Substance remobilization, kernel abortion and final yield formation in inferior species*

A widely-recognized strategy of plant growth and development is to translocate nutrients and photosynthates from senescing parts to newly developed organs, thereby supporting the whole growth and development of plant. This strategy appears to play an essential role in plant life history by recycling numerous essential nutrients (Ning *et al.* 2013; Thomas 2013). Previous studies found that maize-wheat (inferior-superior) intercropping system increased the contribution extent of biomass remobilization to grain for maize, in which the compensation effect was pronounced (Yin *et al.* 2020). In the present study, the ability of inferior species to obtain external resources was relatively weak due to the competitive suppression of superior species at the early growth stage. Simultaneously, the substance remobilization ability was also affected to some extent (Table 2). Also, the DTA, DTR, and GCR of leaves, stem, and sheaths were significantly decreased under intercropping conditions. The results showed that owing to the competition with superior species, the remobilization ability of photosynthetic products was restricted in inferior species, ultimately resulting in the decrease of the kernel formation.

On the other hand, the number and weight of kernel proved to be highly dependent on the size of assimilates in each grain for inferior species. During the developmental process of seeds, the ability to provide assimilates for kernel growth, and the grain filling rate tended to be lowered as a result of strong resource restriction (Borrás *et al.* 2004; Hisse *et al.* 2019). In the present study, we found that Loss1 (fertilization failure) was only affected by film mulching, however the main effect of intercropping was Loss2 (kernel abortion). This phenomenon demonstrated that intercropping mainly affected the availability of assimilates in kernel, when the supply of assimilates was insufficient (Table 2). The potential number of grains was mainly related to the pre-anthesis ear size (Amelong *et al.* 2015). In this study, the increase of Loss1 caused by non-mulching was mainly due to the reduction of ear size in vegetative growth period. The grain filling rate of intercropped maize (inferior species) was also significantly lower than that of monocropping (Table 1).

Finally, the PCA analysis showed that the yield formation parameters were positively correlated with remobilization efficiency and grain filling rate, but negatively correlated with kernel abortion rate. In this case, intercropping was significantly correlated with kernel abortion in the presence or absence of film mulching. All these results revealed that as inferior species, the competition at the co-growth period in the early stage not only caused the developmental damage (briefly in vegetative growth), but also damage the kernel weight and the kernel number by affecting the plant remobilization ability and grain filling during the reproductive growth period, thus resulting in the loss of final yield in inferior species.

**CONCLUSION**

Majority of previous studies showed two major modes of facilitation, i.e. both positive (+/+) and one positive& one neutral (+/0) in the cultivated plant populations. For the first time, we experimentally identified a novel mode of +/- facilitation in agroecosystem. The novel mode provided an insight into facilitation theory and its application in plant diversity management. According to our observations, yield loss of inferior crops in intercropping system was helpful to improve the rainwater resource use efficiency in agroecosystem. Particularly, during the co-growth period, the preferential planting of superior species restricted the growth of inferior species through higher biomass accumulation and growth rate. This was mainly because superior species had a higher competitive ability in capture soil water than inferior one did, consequently declining C assimilation ability of inferior species. On the other hand, the yield of inferior species was not stable or high under compensation effect. Inferior species tended to reduce the reproductive allocation, remobilization capacity, grain filling rate, and therefore restrict the transport of C assimilation to the grain, increase the abortion rate of the grain. This trend consequently wholly declined grain number, grain weight, and finally the yield. In this regard, the occurrence of competition and compensation effect should be based on the result of balance resource conditions. In the rainfed farming system, water restriction frequently led to the yield loss of inferior crops. This trend resulted from lower soil water availability in maize strip of intercropping system, and lower leaf chlorophyll content and photosynthetic rate in maize. Therefore, substance remobilization and seed filling at maturity might be physiological mechanism underlying the plant asymmetric facilitation of +/- in rainfed agroecosystem. This study may offer a novel insight into reduce interspecific competition and improve the compensation effect in intercropping system. Taking together, yield loss of inferior species provided a mechanical explanation on the concurrent +/- facilitation. This study enriched the existing understandings on asymmetric facilitation and the relationship between plant diversity and productivity in agroecosystems.

**Author contributions:** The authors have no conflicts of interest to declare. Specially, Y.C. Xiong, W. Wang and Y.N. Zhou performed experimental design, data collection, field investigations and original draft preparation. Y.N. Zhou, M.Y. Li, B.Z. Wang, S.G. Zhu, J. Wang and H.X. Duan undertook the sample collection, field observations and laboratory work. Y.C. Xiong as corresponding author performed the conceptual design, and provided financial support, data analyses and writing guidance. Rui Zhou and Abid Ullah contributed to conceptual design, data analyses and manuscript revision. All authors have read and approved the final manuscript.

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