Plant growth patterns in a tripartite strip relay intercrop are shaped by asymmetric aboveground competition

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Abstract

Intercropping is a promising model for ecological intensification of modern agriculture. Little information is available on how species growth patterns are affected by size-asymmetric above- and belowground competitive interactions, especially in intercrops with more than two species. We studied plant growth and competitive interactions in a novel intercropping system with three species: wheat, watermelon and maize. Wheat and maize are grown sequentially (as a double cropping system) in narrow strips while watermelon is grown between the cereal strips, with partial overlap in growing period with the two cereals. Growth patterns were monitored over two years and described with logistic growth curves. Root barriers were used to study the effect of belowground interactions. Wheat produced 31% greater yield per plant in the intercrop than in the sole crop but 24% lower yield per unit total (inter)crop area. Wheat yield increase per plant was associated with faster growth and substantial overyielding in the outer rows of wheat strips. Watermelon did not competitively affect wheat. Watermelon biomass was substantially reduced at the time of wheat harvest. However, compensatory growth after wheat harvest and greater allocation to fruits resulted in a good yield of intercropped watermelon, 92% of monoculture yields, at final harvest. Intercropped maize produced 32% lower grain yield per plant and per unit area than sole maize, as a consequence of later sowing and a changed plant configuration in the intercrop as compared to the sole crop, and competitive effects of watermelon, as shown by comparison with a skip-row maize system without watermelon. Root barriers did not affect yield of any of the species, indicating that aboveground competitive interactions in this case played a more important role in shaping the observed growth responses than belowground interactions. Plant interactions in this tripartite intercrop system are consistent with the hypothesis of size-asymmetric competition for light.

Key words: tripartite intercrop, above- and belowground competition, growth patterns, logistic growth.

1. Introduction

Intercropping entails the cultivation of two or more crop species in a field (Vandermeer, 1989). It has been widely practiced by smallholders in developing countries since ancient times (Vandermeer, 1989; Smith, 2001; Zhang and Li, 2003) because of higher land productivity (Rao and Willey, 1980; Yu et al., 2015), improved nutrient utilization (Morris and Garrity, 1993; Stern, 1993; Zhang and Li, 2003), lower disease and pest damage (Trenbath, 1993; Zhu et al., 2000), and enhanced economic return as compared to monoculture (Vandermeer, 1989; Huang et al., 2015). Intercropping provides an attractive model for sustainable intensification by diversification (Brooker et al., 2015).

In an intercropping system, intraspecific and interspecific competition between plants determines crop growth and resource capture (Vandermeer, 1989). When species do not compete for exactly the same resources at the same time, e.g. due to differences in growing period, they show niche differentiation, resulting in complementarity (de Wit, 1960; Vandermeer, 1989; Loreau and Hector, 2001). Niche differentiation can also be the result of different nutrient foraging strategies of crop species in a mixture (Hauggaard-Nielsen and Jensen, 2001; Li et al., 2007; Hinsinger et al., 2011), e.g. as a result of differences in root distribution and rooting depth (Li et al., 2006; Zhang et al., 2014). Legumes can fix nitrogen from the atmosphere by a symbiosis with rhizobia, which reduces competition for soil nitrogen with non-legume species (Andersen et al., 2005). Some species, e.g. faba bean and maize, can release root exudates that mobilize soil nutrients (P and Fe) and thus increase nutrient bioavailability for themselves in a sole crop and for the associated crop species in an intercrop, resulting in facilitation (Zuo et al., 2000; Li et al., 2007; Li et al., 2014; Brooker et al., 2015).

Below- and aboveground plant-plant interactions can greatly influence the structure and composition of plant communities (Cahill, 1999; Zhang et al., 2013). Several studies have

implied a role for belowground interactions in intercrops (Kiær et al., 2013). However, aboveground interactions, notably competition for light, are demonstrably important for shaping plant growth and yield in intercropping (Keating and Carberry, 1993; Zhang et al., 2008a; Li et al., 2014; Zhu et al., 2015). For example, high land equivalent ratio (LER; Willey, 1979) in intercropping of wheat and cotton is explained by the higher radiation interception of the intercrop as compared to the sole crops due to species differences in growing period (Zhang et al. 2008a). Yu et al. (2015) showed in a meta-analysis that high LER in intercropping are associated with temporal niche differentiation. The importance of temporal complementarity between species for high light interception and yield in intercrops does not negate the existence of competitive interactions. These affect not only on resource capture and carbon assimilation, but also plant structural development, with consequences for resource acquisition. For instance, in wheat-maize intercrop, wheat shading lowered leaf appearance rates and decreased biomass accumulation of intercropped maize (Zhu et al., 2014; Li et al., 2001a). Likewise, Zhang et al. (2008b) found a delay in cotton development in an intercrop with wheat. This delay resulted in a lag in resource capture and eventually lower biomass accumulation.

Earlier sown or taller species will tend to have better individual performance than shorter or later sown species in a mixture because of size-asymmetric competition (Weiner, 1990; Yu et al., 2016). Competition for light in plant communities is size-asymmetric because taller individuals have an advantage in the acquisition of light as compared to shorter individuals (Kropff et al., 1992; del Río et al., 2014). With wheat sown first, we hypothesize that wheat in the wheat-maize/watermelon intercrop will have a competitive advantage and show better individual plant performance than wheat in the sole crop. Because of its earlier sowing, we expect wheat negatively affects the growth of later sown watermelon. Furthermore, as maize is sown in an existing watermelon stand, a suppressive effect of watermelon on growth of

maize is expected. However, competitive dominance of watermelon towards maize could be temporary if competition is for light, as maize rapidly outgrows watermelon in height. Li et al. (2001a) described how maize shows recovery after harvest of wheat in a wheat/maize intercrop. A similar response could be anticipated in the interaction of maize with watermelon. Finally, the possibility exists that belowground competitive interactions for nutrients or water are important in this system, resulting for instance in a prolonged competitive effect of watermelon on maize, even after maize grows above the watermelon, due to previous extraction of resources (water, nutrients) from the soil. While competition for light is strongly size-asymmetric, competition for nutrients is comparatively less affected by plant size, with smaller plants having in principle similar access to nutrients in the rooted zone of the soil as larger plants (Dybzinski and Tilman, 2009). Thus, the existence of size-asymmetry in competitive interactions can be used as an indication for a possible role of light capture in competition. On the other hand, differences in sowing date are likely to give first sown species earlier access to soil resources as compared to later sown species, supporting the possibility of pre-emption competition if soil resources are limiting.

Only a few studies investigate plant-plant interaction in intercrops with more than two crop species and little information is available about the impact of such interaction on the crop yield. The studies on tripartite intercropping systems indicated a 5-30% yield increase per plant in the mixture compared to the sole crop (Ghaffarzadeh et al., 1994; Jurik and Van, 2004; Andersen et al., 2007; Zhang et al., 2014; Yang et al., 2014, 2015). Anderson et al. (2007) demonstrated that size-asymmetric interactions between barley, pea and rape resulted in yield advantages while the addition of a third species has a minor effect on the whole intercropping system.

Wheat-maize/watermelon intercropping integrates watermelon into wheat-maize double cropping and has been developed recently by smallholders on the North China Plain to

increase income (Huang et al., 2015). Wheat and maize are grown in the same strip with maize sown after wheat harvest, while watermelon is grown in alternate strips between the cereal strips. Watermelon has a partial overlap in growing period with both wheat and maize. Little is known about how crop growth pattern and final yield are affected by plant-plant interaction occurring in such a system where the species are sown and harvested at different times. Studying the temporal growth patterns may elucidate the role of initial size differences (e.g. due to differences in sowing date) in the interactions between species (Andersen et al., 2007).

We conducted a two-year field study on the growth patterns of wheat-maize/watermelon relay intercropping in order to elucidate the mechanisms responsible for species interactions. In the second year of the study, we used root barriers to investigate the importance of belowground species interactions. Logistic growth equations were fitted to the data to compare growth rates, maximum biomass, and earliness of growth of species between sole and mixed crops.

2. Materials and methods

2.1. Experimental site

Field experiments were conducted in 2012 and 2013 in Quzhou County (36°39' N, 114°55' E; 39 m a.s.l.), Hebei province, China. The study area is a continental monsoon climate, with an average annual precipitation of 480 mm and an annual mean temperature of 13.0 °C. The annual precipitation was 556 mm in 2012 and 546 mm in 2013, and mean temperature was 13.2 °C in 2012 and 13.3 °C in 2013 season (Fig. 1). The soil of the experimental field is a sandy loam, with a pH of 8.3, 11.5 g kg⁻¹ organic matter content, 1.1 g kg⁻¹ total N, 26.7 mg kg⁻¹ Olsen-P and 134 mg kg⁻¹ available K.

2.2. Experimental design

The field experiment

The field experiments were arranged as a randomized block design with three replicates and four treatments (or cropping systems): (1) wheat-maize double cropping (Double cropping, Fig. 2A) which consists of a sole winter wheat and a sole summer maize. Winter wheat is sown in October and harvested in June of the next year, and summer maize is sown in the same field shortly after wheat harvest and it is harvested in October; (2) sole watermelon (Sole watermelon, Fig. 2B), sown in the glasshouse in March, transplanted to the field in mid-May, and harvested at the end of July; (3) wheat-maize/watermelon (Intercropping, Fig. 2C) which is a strip-based intercropping system consisting of alternating strips of wheat-maize double cropping and watermelon; and (4) an intercropping variant (Skip-row, Fig. 2D) which maintained the pattern of wheat and maize rows of the intercropping system, while skipping the rows of watermelon. A skip-row treatment was added to determine plant plasticity and border row effects in wheat and competitive effects in maize in the absence of watermelon.

Each plot was 5.4 m wide and 15.0 m long (81.0 m²). Planting patterns of the wheat-maize double cropping and the intercropping systems were in agreement with the practices of the local farmers who developed this system to increase economic profit (Fig. 2; Huang et al., 2015). Row distance was 15 cm in sole wheat (Fig. 2A), 60 cm in sole maize (Fig. 2A) and 180 cm in sole watermelon (Fig. 2B). Thus, each sole crop plot covered 36 rows of wheat, 9 rows of maize and 3 rows of watermelon. The sowing density of sole wheat was about 25.5 g seeds m⁻². Plant distance within the row was 0.225 m in sole maize and 0.6 m in watermelon. Thus, the respective planting densities were 7.4 plants m⁻² (1/(0.6 m × 0.225 m)) in maize and 0.93 plants m⁻² (1/(1.8 m × 0.6 m)) in watermelon. Rows were oriented east-west.

The intercrop consisted of alternate strips, one of which was grown with wheat and maize in the usual double cropping sequence, while the other was planted with watermelon (Fig. 2C). The wheat strip had seven rows of wheat at 15 cm row distance. Following wheat harvest, maize was sown just outside the wheat strip, 7.5 cm away from the outer rows of the harvested wheat strips. The maize rows had thus a heterogeneous row distance of 1.05 m across the harvested wheat strip and 0.75 m across the watermelon strip (Fig. 2C). Compared to sole wheat, the intercrop skipped 5 wheat rows out of each 12 rows, resulting in a relative density of 0.58 ($= 7/12$). Compared to sole maize, the intercrop skipped one row out of each three, and it changed the row distance from 0.6 m in sole crop to alternating row distances of 1.05 m and 0.75 m in the intercrop, thus increasing spatial heterogeneity (Fig. 2C). We followed the practice of the local farmers to compensate for the loss of maize rows by sowing two seeds per hole, and spacing the seeding holes at 0.3 m in the row, thus maintaining the same overall density of maize plants ($7.4 \text{ plants m}^{-2}$) as in the sole crop. The watermelon strip consisted of a single row of watermelon at a distance of 0.45 m from the nearest wheat row and 0.375 m from the maize rows (Fig. 2C). Watermelon rows were 1.8 m apart, and plant distance in the row was 0.6 m as in the sole crop (Fig. 2C). Thus, the relative density of intercropped watermelon was 1.00.

The expected yield per unit area in the intercrop is calculated by multiplying sole crop yield with the relative density of the species in the intercrop. Departures from this expectation are indicative of differences in yield per plant between the sole crop and the intercrop, indicating interspecific competition being stronger or weaker than intraspecific competition.

The root barrier experiment

In the 2013 season, we used split plots to study the influence of root barriers on crop growth patterns in all four treatments, and assess the importance of belowground interactions.

The length of the split plot in each plot was 3.0 m, and a 0.6 m deep plastic barrier film was buried between the wheat strip and the watermelon strip of the intercrop and the skip-row, and at the same location in sole crops to exclude belowground interactions between plants in neighboring rows (Fig. 2). Including root barriers in all treatments enabled a fair comparison between sole and intercrop treatments, as root systems were in both the sole crops and intercrops confined to the interactions with “own” only, without a difference in space for the root system, which might in itself affect plant growth (Chen et al., 2015). Presence of root barriers in sole crop and intercrop treatments removes belowground competition. The comparison of growth patterns in treatments with and without root barriers thus elucidates the role of belowground competition in interspecific species interactions.

2.3. Crop management

Variety choice and dates of sowing, transplanting and harvesting

We used cultivars that are commonly used by local farmers: winter wheat (*Triticum aestivum* L.) cv. Jimai 22, summer maize (*Zea mays* L.) cv. Nonghua 101, and watermelon (*Citrullus lanatus* (Thunb.) Matsum. and Nakai) cv. Fengshou No.3. Wheat was sown on 18 October in 2011 and harvested on 12 June in 2012, sown on 17 October in 2012 and harvested on 12 June in 2013. Double cropping maize was sown the day after wheat harvest in both years, while in intercropping and skip-row treatment, maize was sown on 23 June in both years in accordance with farmers’ practice. This practice aims at avoiding too strong interspecific competitive effects of watermelon on maize during the co-growth period of the two species. Maize was harvested on 12 October in all treatments in both years. For brevity, the growing seasons are labeled according to the year of harvest. There were no differences in harvesting dates of wheat or maize between treatments. Watermelon was germinated in the greenhouse on 22 March in 2012, and 23 March in 2013. One week after germination, the

watermelon seedlings were grafted onto a rootstock of squash (*Cucurbita moschata* Duch. ex Poir. cv. Heli No.3), after which the grafted seedlings were grown in greenhouse for 40 days before transplanting. The sole and intercropped watermelon were both transplanted on 14 May in 2012 and 16 May in 2013. Watermelons were harvested periodically as fruits matured at the end of July in both years.

Irrigation and fertilization

In both years, the experimental field was irrigated seven times, using flood irrigation, immediately after fertilizer application, except for the 3th irrigation when no fertilizer was applied (Table 1). The first irrigation was given before overwintering, the second at wheat jointing, the third at wheat flowering, the fourth before watermelon transplanting, the fifth after wheat harvest, the sixth during watermelon fruit development, and the seventh after watermelon harvest (Table 1). All plots received the same amount of irrigation water.

Fertilizer was applied three to six times according to crop demands (Table 1). Wheat in the double cropping received fertilizer before sowing and at jointing, while maize was fertilized at seedling stage and at the V8-V10 stage (Ritchie et al., 1986). Sole watermelon was fertilized three times: before transplanting, prior to flowering (i.e. at the time of wheat harvest), and during fruit production. The intercrop and the skip-row system were fertilized six times, by combining the fertilizer applications of the double cropping and sole watermelon, but their 5th fertilizer input was 600 kg ha⁻¹, which was the same amount as applied to the sole watermelon (Table 1).

2.4. Sampling for plant measurements

2.4.1 Aboveground biomass

Samples of aboveground biomass were collected every 20 days to monitor dry matter accumulation and nutrient uptake from wheat tillering till maize harvest. The sampling area of

wheat was 7 rows $\times$ 1 m length at the first and last harvest, and 7 rows $\times$ 0.5 m length at the intermediate harvests. Wheat biomass was determined separately for each row to assess differences between outer and inner rows. Four maize plants were randomly harvested at each periodic harvest, and six plants at final harvest. Twenty watermelon seedlings were taken at watermelon transplanting, while two adjacent plants were taken at periodic harvests and six plants at final harvest. All samples were conducted in subplots which were separated by buffer strips such that harvested plants were surrounded by sufficient neighbor plants to avoid edge effects. Wheat plants were separated into straw and grain, maize plants were separated into straw and ears, and the watermelon plants were separated into straw and fruits. Samples of four plants in sub-plots with root barriers were collected at final harvest in 2013. Procedures were the same as for the sub-plot without barrier. All samples were dried 72 h at 70 °C to determine dry matter.

Table 1. Timing and amount (mm) of irrigation and fertilizer input (kg ha⁻¹) in four cropping systems.

No.	Timing	Irrigation (mm)	Double cropping	Sole watermelon	Intercropping & Skip-row	Percentage of N-P ₂ O ₅ - K ₂ O in fertilizer (%)
1	wheat sowing	80	750	-	750	15-20-10
2	wheat jointing	80	217	-	126	46-0-0 [*]
3	wheat flowering	70	-	-	-	-
4	watermelon transplanting	60	-	750	750	15-15-15
5	maize seedling/before watermelon flowering	80	450	600	600	20-10-10/20-5-20 ^{\$}
6	watermelon fruit development	70	-	450	450	20-5-20
7	maize V8-V10	70	217	-	217	46-0-0

Note: ^{*} 46-0-0 represents urea fertilizer containing 46% N and others with different percentages of N, P₂O₅ and K₂O indicate compound fertilizer;

^{\$}, double cropping used 20-10-10 percentage of compound fertilizer, and sole watermelon, intercropping and skip-row used 20-5-20.

2.4.2 Final yield

Grain and fruit yields were measured at final harvest. Wheat grains were collected from a yield measuring area of 7 adjacent rows times 5 m length in the plot center. All maize cobs were collected from 4 adjacent rows over a length of 5 m in the plot center, and threshed manually after air drying. The air-dried wheat and maize grains were weighed, and a 500-g sub-sample was oven-dried for 72 h at 70 °C to calculate water content and calculate grain dry weight per unit area for each plot for wheat and maize. Grain yields in the intercrop are expressed per unit area of the whole intercrop including the area of the watermelon strip. Fruit yield of watermelon was the fresh weight of all fruits collected from yield monitoring zone of 5.4 m (width) $\times$ 9.6 m (length) in 2012, and 5.4 m (width) $\times$ 6.6 m (length) in 2013.

In the root barrier sub-plots, the samples were collected at final harvest in 2013. Procedures were the same as for the sub-plots without barrier. The sample size was 7 rows $\times$ 2 m length in each plot for wheat, 4 rows $\times$ 2 m length for maize, and 3 rows (5.4 m) $\times$ 2.4 m for watermelon.

2.4.3 Chemical analysis of samples

Dried plant samples were ground to powder for nutrient analysis. The material was digested in a mixture of concentrated H₂SO₄ and H₂O₂ before determining the content of nitrogen (N), phosphorus (P) and potassium (K). Nitrogen content was determined by the micro-Kjeldahl method (KDY-9810, KETUO Instrument Co. Ltd., Beijing, China); P content was determined by the vanadomolybdate method (UV757T, Shanghai Instrument Co. Ltd., Shanghai, China); K content was measured by flame photometry (FP640, Shanghai Instrument Co. Ltd., Shanghai, China) (Horwitz, 1980).

2.4.4 Growth model fitting

Logistic growth curves were fitted to the biomass data of all treatments to characterize the growth patterns (Andersen et al., 2007):

$$Y_t = \frac{K}{1 + e^{r(t_{50}-t)}} \quad (\text{Eqn. 1})$$

where Y_t (g m⁻¹ row or g plant⁻¹) is aboveground biomass at t days after sowing; K (g m⁻¹ row or g plant⁻¹) represents maximum aboveground biomass, r (d⁻¹) is the intrinsic growth rate, and t_{50} (d) is the time (day after sowing) of maximum absolute growth rate. All three parameters (K , r and t_{50}) were estimated using a Nonlinear Least Square function “nls” in R (R Core Team, 2015). Parameter values were determined by fitting the growth curves to the data per plot. Points in figures show average values over replicates, and the curves in figures represent the estimated logistic curves of the mean parameter values across replicates.

2.5. Data analysis

The effects of different cropping systems on aboveground biomass, grain yield and each estimated parameter (K , r and t_{50}) of either wheat, watermelon or maize in both 2012 and 2013, and nutrient uptake of all crops in 2013, were statistically tested using two-way ANOVA with cropping system and block as main effects. As the block effect was not significant, multiple comparisons across treatments were performed using Duncan's multiple range test. The effects of cropping system and root barrier on aboveground biomass and yield of each crop at final harvest in 2013 were statically analyzed using split-plot ANOVA with treatment and block as main plot factors and root barrier as split plot factor. All data were analyzed at the 5% level through using SAS v.9.2 (SAS Institute Inc., 2008).

3. Results

3.1. Grain and fruit yield

Averaged over the two years, wheat grain yield was $6.7 \pm 0.2 \text{ t ha}^{-1}$ in double cropping and $5.1 \pm 0.2 \text{ t ha}^{-1}$ in both intercropping and skip-row (Table 2). Maize grain yield was $9.3 \pm 0.2 \text{ t ha}^{-1}$ in double cropping, $6.3 \pm 0.3 \text{ t ha}^{-1}$ in intercropping and $8.2 \pm 0.3 \text{ t ha}^{-1}$ in skip-row (Table 2). Watermelon fruit yield was $40.5 \pm 1.3 \text{ t ha}^{-1}$ in intercropping, significantly lower than in sole watermelon, $44.0 \pm 2.0 \text{ t ha}^{-1}$. Wheat grain yield was significantly greater in 2013 than in 2012 while both maize grain yield and watermelon fruit yield were considerably lower in 2013 than in 2012 (Table 2).

Average relative yield of wheat, maize and watermelon in the intercrop was 0.76, 0.68 and 0.92, respectively, whilst the relative planting density of these three crops was 0.58, 1.00 and 1.00, respectively, indicating intercropping resulted in a substantial increase in wheat grain yield per plant (+31%), an equally large relative decrease in maize grain yield per plant (-32%), and an 8% decrease in the yield per watermelon plant.

Table 2. Grain yields of wheat and maize, and fruit yields of watermelon in the 2012 and 2013 seasons (t ha⁻¹).

Season	Treatment	Root barrier	Wheat	Maize	Watermelon
2012	Double cropping	-	6.4 ± 0.4	10.7 ± 0.2	-
	Sole watermelon	-	-	-	47.1 ± 1.6
	Intercropping	-	5.0 ± 0.1	7.9 ± 0.3	45.1 ± 1.0
	Skip-row	-	5.0 ± 0.3	8.9 ± 0.5	-
	Block		NS	NS	NS
	Treatment		***	***	NS
2013	Double cropping	-	7.0 ± 0.4	7.8 ± 0.1	-
		+	7.0 ± 0.3	7.9 ± 0.4	-
	Sole watermelon	-	-	-	40.9 ± 3.9
		+	-	-	39.8 ± 4.4
	Intercropping	-	5.2 ± 0.3	4.6 ± 0.4	35.8 ± 1.9
		+	4.8 ± 0.2	4.4 ± 0.5	38.2 ± 5.1
	Skip-row	-	5.1 ± 0.4	7.4 ± 0.5	-
		+	5.2 ± 0.2	7.0 ± 0.4	-
	Block		NS	NS	NS
	Cropping system (C)		***	***	NS
	Root barrier (R)		NS	NS	NS
	C × R		NS	NS	NS
Average	Double cropping	-	6.7 ± 0.2	9.3 ± 0.2	-
	Sole watermelon	-	-	-	44.0 ± 2.0
	Intercropping	-	5.1 ± 0.2	6.3 ± 0.3	40.5 ± 1.3
	Skip-row	-	5.1 ± 0.2	8.2 ± 0.3	-
	Block		NS	NS	NS
	Cropping system (C)		***	***	*
	Year (Y)		*	***	**
	C × Y		NS	*	NS

Note: Values are means ± standard deviation (n = 3). NS, P ≥ 0.05; *, P < 0.05; **, P < 0.01; ***, P < 0.001.

3.2. Crop growth dynamics

There was a large and significant difference in the growth of wheat between border and inner rows of the heterogeneous systems (intercrop and skip-row) while the growth pattern of wheat in the sole crop and in the inner rows of the heterogeneous systems was indistinguishable (Fig. 3A, B; Table 3). Analysis of growth parameters (Table 3) indicated that carrying capacity (K) and intrinsic growth rate (r) were significantly lower in inner rows than in border rows, but there was no difference in the time of maximum growth rate (t_{50}). The ratio of carrying capacity in inner and border rows was approximately 1:1.66, indicating 66% greater aboveground biomass per plant in border rows, while the ratio in intrinsic growth rate was approximately 1:1.37, indicating 37% greater relative growth rate of wheat plants in border rows (Table 3). There were no significant differences in wheat growth in border rows between intercrop and skip-row, or in wheat growth between sole wheat and inner rows in intercrop or skip-row. This indicates that wheat growth in the inner rows of the heterogeneous systems (intercrop and skip-row) was only affected by intraspecific competition. This competition was reduced in the border rows. The lack of difference in wheat growth between skip-row and intercrop indicates that there was negligible influence of watermelon on wheat growth.

There were only minor differences in growth of watermelon between the sole crop and the intercrop (Fig. 3C, D), with no significant differences in K and r in either year, and a significant difference in t_{50} only in 2012 (Table 3). This latter difference indicated a growth delay of 2 days of watermelon in the intercrop as compared to the sole crop. At the time of wheat harvest, intercropped watermelon had a substantially and significantly lower aboveground biomass (49% lower than sole watermelon in 2012 and 59% lower in 2013) (Fig. 3C, D). However, at final harvest, due to compensatory growth in the intercrop, the relative

difference in biomass between the intercrop and sole crop was much smaller (3% in 2012 and 19% in 2013), and the difference in fruit yield was also minor (12% in 2012 and 4% in 2013).

Growth of maize was significantly reduced in the skip-row and intercrop treatments, compared to the double cropping system (Fig. 3E, F). The skip-row and intercrop maize had lower K and greater t_{50} than double cropping maize in both years, indicating a lower maximum biomass in skip-row and intercropped maize and a growth delay of 9 to 14 days (Table 3). The skip-row and intercropped maize had a greater r than double cropping maize in 2012 while a similar value of r was found for maize in all three treatments in 2013 (Table 3). The higher carrying capacity in skip-row maize as compared to intercropped maize indicates a competitive influence of watermelon on maize growth. Maize in the skip-row showed a growth delay compared to the sole crop of 9 days in 2012 and 10 days in 2013, while the delay for the intercrop, as compared to the sole crop, was 10 days in 2012 and 14 days in 2013 (Table 3). These growth delays are mostly the consequence of a 10 days later sowing in the skip-row and intercrop systems as compared to the sole crop. However, part of the growth delay in the intercrop in 2013 may be attributed to a competitive effect of watermelon on maize.

3.3. Nutrient uptake

Uptake dynamics of N and P in the aboveground biomass of the three crop species showed broadly the same dynamic patterns as biomass accumulation. The border rows of wheat in intercrop and the skip-row had significantly increased N and P uptake over the growing season, as well as enhanced K uptake (Fig. 4A, B, C). There were no significant differences between treatments in the nutrient uptake by the inner rows of wheat. No difference in nutrient uptake was found between sole and intercropped watermelon (Fig. 4D, E, F). N, P

and K uptake of maize was significantly lower in both intercropping and the skip-row system than in double cropping (Fig. 4G, H, I), and lower in intercropping than in the skip-row (Fig. 4G, H, I). This pattern was consistent with the dry matter accumulation (Fig. 3F). The total amount of K uptake in wheat and maize (Fig. 4C, I) showed a slight decrease at the end of crop growth due to attrition of leaf biomass.

Table 3. Parameters estimated from fitting logistic growth curves to wheat, maize and watermelon aboveground biomass growth in different cropping system treatments (double cropping, intercropping, and skip-row) in 2012 and 2013.

Year	Crop	Treatment	K (g m ⁻¹ row, g plant ⁻¹)	r (×10 ⁻² d ⁻¹)	t_{50} (d)
2012	Wheat	Double cropping	257.6 ± 6.0 b	7.2 ± 0.9 b	197.1 ± 1.9 a
		Skip-row inner	272.6 ± 5.5 b	7.4 ± 0.4 b	197.4 ± 0.2 a
		Intercropping inner	260.3 ± 8.4 b	7.6 ± 0.3 b	196.2 ± 1.3 a
		Skip-row border	440.9 ± 35.7 a	10.2 ± 2.1 a	195.2 ± 3.8 a
		Intercropping border	460.5 ± 22.4 a	10.4 ± 1.9 a	196.0 ± 1.1 a
	Maize	Double cropping	375.0 ± 4.0 a	5.9 ± 0.7 b	310.0 ± 3.3 b
		Skip-row	293.2 ± 4.9 b	8.4 ± 1.7 ab	319.3 ± 0.6 a
		Intercropping	266.6 ± 15.4 c	11.4 ± 2.3 a	319.8 ± 0.7 a
	Watermelon	Sole watermelon	418.1 ± 11.6 a	18.6 ± 2.8 a	261.8 ± 0.4 b
		Intercropping	410.7 ± 15.7 a	15.0 ± 1.6 a	263.9 ± 0.8 a
2013	Wheat	Double cropping	253.7 ± 13.4 b	6.6 ± 0.8 b	191.0 ± 2.7 a
		Skip-row inner	280.9 ± 14.3 b	5.9 ± 0.7 b	194.2 ± 2.2 a
		Intercropping inner	274.5 ± 3.4 b	6.9 ± 0.4 b	190.8 ± 1.0 a
		Skip-row border	453.0 ± 29.2 a	8.7 ± 0.1 a	194.1 ± 2.0 a
		Intercropping border	425.6 ± 9.1 a	9.5 ± 0.7 a	191.9 ± 0.7 a
	Maize	Double cropping	250.6 ± 7.4 a	7.6 ± 0.2 a	299.8 ± 1.0 c
		Skip-row	195.9 ± 8.4 b	7.3 ± 0.2 a	309.7 ± 0.9 b
		Intercropping	164.3 ± 7.9 c	7.6 ± 0.5 a	313.8 ± 1.6 a
	Watermelon	Sole watermelon	425.4 ± 29.7 a	18.2 ± 2.2 a	254.5 ± 0.6 a
		Intercropping	346.6 ± 16.3 a	38.1 ± 14.1 a	253.5 ± 0.9 a

Note: The table reports means $\pm$ standard deviation ($n = 3$). Means with the same letter within each column in the same crop in each year are not significantly different between treatments at the 5% level.

3.4. Belowground Interactions

There was no significant effect of root barriers on yield or aboveground biomass at final harvest ($P > 0.05$; Table 2, 4). The results indicate that belowground interactions did not play an important role in shaping the crops' growth dynamics.

Table 4. Aboveground biomass of wheat (g m^{-1} row), maize (g plant^{-1}) and watermelon (g plant^{-1}) in the 2012 and 2013 seasons.

Season	Treatment	Root barrier	Wheat	Maize	Watermelon
2012	Double cropping	-	237 ± 1	360 ± 4	-
	Sole watermelon	-	-	-	405 ± 10
	Intercropping	-	300 ± 12	260 ± 15	391 ± 8
	Skip-row	-	298 ± 14	278 ± 4	-
	Block		NS	NS	NS
	Cropping System		***	***	NS
2013	Double cropping	-	242 ± 11	253 ± 5	-
		+	234 ± 15	255 ± 4	-
	Sole watermelon	-	-	-	412 ± 34
		+	-	-	400 ± 42
	Intercropping	-	305 ± 4	168 ± 10	331 ± 22
		+	316 ± 21	164 ± 9	361 ± 40
	Skip-row	-	312 ± 11	200 ± 8	-
		+	296 ± 10	200 ± 5	-
	Block		NS	NS	NS
	Cropping System		***	***	NS
	Root barrier		NS	NS	NS
	C $\times$ R		NS	NS	*

Note: values are means $\pm$ standard deviation (n = 3). NS, $P \geq 0.05$, *, $P < 0.05$, **, $P < 0.01$, ***, $P < 0.001$.

4. Discussion

The objective of this study was to analyze yield and growth patterns as influenced by plant-plant interactions in a tripartite relay intercropping system with wheat, maize and watermelon. Wheat had a greater growth rate and increased yield per plant in border rows in the intercrop as compared to the sole crop. Intercropping with wheat caused an initial growth reduction in watermelon, resulting in almost 50% lower watermelon biomass at wheat harvest. However, compensatory growth after wheat harvest resulted in compensation and the final effect on watermelon fruit yield was small (8%). The intercropped watermelon had no effect on the growth of wheat, but it had a significant and substantial effect on growth and yield of intercropped maize (12% lower in 2012 and 38% lower in 2013). Intercropped maize showed substantial yield reduction compared to the sole crop as a result of the change in planting pattern (greater spatial heterogeneity) and delayed sowing (10 days later than in double cropping) and to a smaller extent by competition from watermelon. Competitive effects in intercrops were mainly driven by aboveground competitive interactions as shown by the absence of significant effects of root barriers on yields. From a farmer's point of view, the intercropping system allows a proliferation of yields from the same land. The tripartite system generates total grain and watermelon yields per unit area that would require 1.66 ha when combining wheat-maize double cropping with sole watermelon.

4.1. Crop productivity and growth pattern

In this study, the relative yield of wheat (0.76) was greater than relative density (0.58) indicating substantially increased grain yield per plant in the intercrop (Table 2). This result is consistent with other studies on wheat-based intercropping (Li et al., 2001a; Zhang et al., 2007; Bedoussac and Justes, 2010). Improved performance of individual wheat plants in intercrops is mainly attributable to the greater light capture per plant (Zhang et al., 2008a; Zhu et al., 2015) resulting from the reduced competition from neighbors in the border rows during early wheat growth (Li et al., 2006).

Watermelon yields were on average 8% lower in the intercrop than in the sole crop ($P < 0.05$; Table 2) indicating weak competitive effects of wheat on watermelon. The effect of intercropping on watermelon biomass (-20% in intercropping in 2013) was greater than the effect on yield. Thus, watermelon experienced competitive effects from wheat before wheat harvest, but yield effects were small due to a higher allocation to fruit in intercrop than in sole crop. Such a pattern was also observed for maize in wheat/maize intercrop, in which intercrop maize has a higher harvest index than sole maize (Li et al., 2001a; Gou et al., 2016). During July and August in 2013, one continuous rainfall (about 165 mm of water in a week) hit the experimental site (Fig. 1). During that period both watermelon and maize suffered from flooding stress, but the biomass reduction of watermelon had slight effect on the fruit yield (Table 2).

Maize had lower yields in the skip-row and intercrop systems than in double cropping (Table 2; Fig. 3E, F). In order to obtain a good watermelon yield, farmers sow the maize later in the intercrop than they do in the conventional double cropping system of wheat and maize. They also modify the planting pattern to deal with the heterogeneity created by the wheat strip, and to limit the work involved in planting by hand (Huang et al., 2015). The planting pattern in intercrop and skip-row (0.75 and 1.05 m row distance, 30 cm plant distance, and two seeds

per hole) is less suitable for capturing radiation and other resources than the more homogeneous pattern used in double cropping (0.60 m row distance, 22.5 cm plant distance, and one seed per hole). These two factors (changed sowing date and changed pattern) resulted in a moderate yield decrease of 12% in the skip-row system compared to the double cropping system. On average over the two years, maize in the intercrop yielded 32% less than maize in double cropping and 23% less than maize in the skip-row. Similar results also found in wheat/maize intercropping, a 14%-31% of yield reduction found in intercropped maize, as compared to skip-row maize (Gou et al., 2016). The yield reduction in intercropped maize can thus be attributed to competitive effects from watermelon and a suboptimal sowing date and spatial configuration.

Growth of intercropped maize speeded up after the competing crop, watermelon, was harvested in 2012 (Fig. 3E). Such recovery growth has also been reported for maize in wheat-maize intercrop (Li et al., 2001a; Zhang et al., 2015). In 2013, the intercropped maize growth was similarly retarded but recovery growth did not occur (Fig. 3E), possibly as a result of less suitable weather in this year.

4.2. Plant-plant interactions

Plant-plant interactions shape the productivity and community structure of natural ecosystems (Armas and Pugnaire, 2005; van Ruijven and Berendse, 2005) and agroecosystems, such as intercrops (Li et al., 1999; Li et al., 2001b; Zhang et al., 2007; Li et al., 2014; Gou et al., 2016). The competitive ability of a species depends on its size and growth rate (Goldberg and Landa, 1991; Andersen et al., 2007). Different sowing date causes size-asymmetric competition that is more important in influencing community structure and ecosystem function than symmetric competition (Weiner and Damgaard, 2006; Chu et al., 2010). In the current study, the earlier sown wheat dominated the later sown watermelon

indicating size-asymmetric competition, with a large benefit to wheat but a minor disadvantage to watermelon. The earlier sown watermelon dominated the later sown maize. In the pea/barley/rape intercropping where three species were sown at the same time, addition of a third species had only minor effects on behavior of the individual crops (Andersen et al., 2007). Differently, the wheat-maize/watermelon includes double relay intercropping, namely wheat with watermelon and watermelon sequentially with maize. Wheat significantly reduced the biomass of watermelon seedlings (Fig. 3C, D; Table 2), and the reduction might alleviate the size-asymmetric competition of watermelon towards maize. However, this alleviation did not occur because watermelon had been growing alone at great rate in the field for around 2 weeks and then fully recovered without yield reduction (Fig. 3 C, D). Consequently, the growth of the intercropped, later sown maize was greatly suppressed compared with that of the sole maize, but the intercropped maize could have recovery growth (Li et al., 2001a; Zhang et al., 2008; Zhu et al., 2014). In current study, the growth of the intercropped maize was fully recovered from competition in 2012 (Fig. 3E) described as a greater initial growth rate (Table 3). However, such recovery growth did not occur in intercropped maize in 2013 (Fig. 3F; Table 3). The reason was that a heavy rainfall (165 mm in one week) hit the field plots in 2013 during a sensitive period for maize and watermelon growth (Fig. 1), causing a reduction in kernel number of maize in double cropping, intercropping and skip row by 19%, 13% and 20%, respectively, compared with those in 2012.

Some studies concluded that more than 20% of the yield advantage in intercropping results from belowground interactions (Li et al., 1999; Zhang et al., 2001; Zhang and Li, 2003). We found, however, no evidence for belowground effects in this case (Table 2, 4). Possible explanations for the absence of belowground interspecific interaction effects are spatial niche differentiation between the roots of wheat, watermelon and maize (Li et al., 2006; Zhang et al., 2014), consequently reducing root competition between species (Hauggaard-Nielsen and

Jensen, 2005) and the high input of fertilizer (Table 1). With ample nutrients and water being supplied to all species in this system, belowground interaction effects could become negligible, resulting in dominance of mechanisms for aboveground resource partitioning (Li et al., 2011; Kiær et al., 2013).

5. Conclusions

The tripartite relay intercropping system showed substantial competitive effects of wheat on early growth of watermelon and negative impacts of watermelon on the early growth of maize. Root barriers did not affect yields, indicating that aboveground competitive interactions mainly shaped the growth patterns of crop species in this system. The tripartite intercrop produced an almost full watermelon yield in the empty strips between wheat and maize, at the expense of a rather moderate 24% reduction in wheat yield and a somewhat greater 32% reduction in maize yield. The total of relative yields in this system is $0.76 + 0.92 + 0.68$, indicating a proliferation of outputs from a parcel of land in this system. The tripartite system generates total grain (wheat plus maize) and watermelon yields per unit area that would require 1.66 ha when combining wheat-maize double cropping with sole watermelon. This system is a good example of a multiple cropping system with high inputs and outputs, and a distinct land use advantage. Wheat is competitively dominant in the size-asymmetric competition with watermelon; watermelon is comparatively insensitive to size-asymmetric competition from wheat, and competitive to later-sown maize, which is sensitive to this competition. Competition is mainly mediated aboveground.

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Figure captions

Fig. 1. Monthly mean temperature and precipitation during the 2012 and 2013 growing seasons.

Fig. 2. Layouts of the four cropping systems: (A) wheat-maize double cropping; (B) sole watermelon; (C) wheat-maize/watermelon intercropping; (D), wheat-maize skip-row treatment. Each panel shows an area of 450 cm width and 240 cm length. In panel A (conventional wheat-maize double cropping), there are 30 wheat rows (15 cm distance) over this width, and 8 maize rows (60 cm distance). In panel C (maize/wheat intercropping), there are three strips of seven wheat rows each (at 15 cm row distance) and two paths between the strips, each measuring 75 cm. Maize is sown after wheat harvest at a distance of 7.5 cm from the outer wheat rows of the strip, and there are six maize rows within panel C, at alternating row distances of 105 (across the wheat strip) and 75 cm (across the path). Watermelon is sown in the middle of the path between the wheat strips. Panels B (sole watermelon) and D (skip-row treatment) are obtained by omitting either the cereals or the watermelon from panel C.

Fig. 3. Aboveground biomass accumulation in wheat (A, B), watermelon (C, D) and maize (E, F) in three cropping systems (double cropping, intercropping and skip-row) in 2012 and 2013. In wheat, distinction is made between inner and outer rows of the strip. DASW means days after sowing of wheat (18 and 17 October in 2012 and 2013, respectively).

Fig. 4. Nutrient accumulation (from left to right: N, P, K) in inner and border rows of wheat (A, B, C), watermelon (D, E, F) and maize (G, H, I) in wheat-maize double cropping, in the maize-wheat/watermelon intercrop, and in the skip-row wheat-maize system in 2013.

Figure 1

Figure 2

Figure 3

Figure 4