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Growth and photosynthetic responses of soybean seedlings to maize shading in relay intercropping system in Southwest China

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Abstract

Intercropping, a traditional and worldwide cropping practice, has been considered as a paradigm of sustainable agriculture based on complementary mechanisms among different crop species. Soybean (*Glycine max*) is widely relay intercropped about 60 days before maize (*Zea mays*) harvest in Southwest China. However, shade caused by tall maize plants may be a limiting factor for soybean growth at a seedling stage. In field research, we studied the ecophysiological responses of two widely cultivated soybean varieties [Gongqiudou494-1 (GQD) and Gongxuan 1 (GX)] to maize shading in a relay intercropping system (RI) compared with monocropped soybean plants (M). Our results showed that soybean seedlings intercropped with maize exhibited significantly downregulated net photosynthetic rate (P_N) (–38.3%), transpiration rate (–42.7%), and stomatal conductance (–55.4%) due to low available light. The insignificant changes in intercellular CO_2 concentration and the maximum efficiency of PSII photochemistry suggested that the maize shading-induced depressions in P_N were probably caused by the deficiency of energy for carbon assimilation. The significantly increased total chlorophyll (Chl) content (+27.4%) and Chl *b* content (+52.2%), with lowered Chl *a*/*b* ratios (–20.5%) indicated soybean plants adjusted their light-harvesting efficiency under maize shading condition. Biomass and leaf area index (LAI) of seedlings under RI decreased significantly (–78.7 and –71%, respectively) in comparison with M. Correlation analysis indicated the relative reduction in biomass accumulation was caused by the decline in LAI rather than P_N, it affected negatively the final yields of soybean (32.8%). Cultivar-specific responses to maize shading were observed in respects of LAI, biomass, and grain yield. It indicated that GX might be a better cultivar for relay intercropping with maize in Southwest China.

Additional key words: carbon accumulation; chlorophyll *a* fluorescence; photosynthetic pigment; planting pattern; productivity.

Introduction

With the fast increase of population and global environmental changes, it is a big challenge to ensure food security with shrinking cropland and limited resources in an environment-friendly way (Godfray *et al.* 2010, Fan *et al.* 2012). Intercropping, a land-use strategy of cultivating two or more crop species in a piece of land, is a traditional cropping practice to make a higher crop harvest, which is of highly economic, ecological, and environmental significance (Altieri 1999, Swinton *et al.* 2007, Pypers *et al.* 2011). This cropping strategy is still commonly practiced in the world, especially in developing countries, such as China, India, Southeast Asia, Latin America, and Africa (Li *et al.* 2007). In China, more than 28 million ha of annually sown area are under intercropping (Li *et al.* 2007). Cereal-legume intercropping, such as maize-soybean relay intercropping, is considered as a paradigm of sustainable agriculture based on the complementary mechanisms between the two species (Rusinamhodzi *et al.* 2012). It has been well known that intercropping systems as a whole can improve the resource-use efficiency,

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Abbreviations: Car – carotenoids; Chl *a*/*b* – chlorophyll *a*/*b* ratio; Chl *b* – chlorophyll *b*; Chl (*a*+*b*) – total chlorophyll; C_i – intercellular CO_2 concentration; E – transpiration rate; F_v/F_m – maximum photochemical efficiency of PSII; g_s – stomatal conductance; GX – soybean variety ‘Gongxuan 1’; GQD – soybean variety ‘Gongqiudou494-1’; LAI – leaf area index; M – monoculture; P_N – net photosynthetic rate; RI – relay intercropping.

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such as nutrients (Li *et al.* 2001, 2007) and light (Gao *et al.* 2010). However, negative effects can influence individual crop species. To our knowledge, such information is very limited.

In the maize-soybean relay intercropping system, soybean is sown into the interstrips between rows of maize plants about two months before maize maturity. Maize canopy can absorb more than 50% of the received PAR (Liu and Song 2012). Consequently, tall, heliophilous maize plants cause considerable changes in microenvironment including light, temperature, and moisture for soybean seedlings (Gao *et al.* 2010), which may affect significantly soybean growth and final yields (Yan *et al.* 2010). Shade caused by maize canopy may be the uttermost, microenvironmental factor for soybean seedlings. A response or adaptation to shade are important index for selecting soybean cultivars that can be suitable for maize-soybean relay intercropping system (Yan *et al.* 2010). Former studies have reported that soybean plants might develop thicker leaves, when intercropped with trees (Reynolds *et al.* 2007), and exhibited slender shape with taller stems, longer internodes, and fewer branches in wheat-soybean intercropping system (Wallace *et al.* 1996) and corn-soybean-oak system (Jurik and Van 2004). Nevertheless, information is limited about the ecophysiological response of the intercropped soybean to shading from maize in the relay intercropping system (Callan and Kennedy 1995, Makoi *et al.* 2010).

Maize-soybean relay intercropping pattern is widely applied in southwestern China (Yan *et al.* 2010). In such intercropping system, soybean usually grows in the interval strips of maize plants at seedling stage (about 60 d), therefore, shade of maize impacts the growth of soybean seedlings. In this study, we selected two soybean varieties widely cultivated in southwestern China to study their responses at seedling stage to maize shading in relay intercropping system in terms of morphological plasticity and photosynthetic parameters. We also analyzed the impacts of relative changes in these parameters at seedling stage on its final grain yields.

Materials and methods

Site description: The experiment was conducted at the Teaching and Experimental Farm of Sichuan Agricultural University (29°58'54"–29°59'11"N, 102°58'27"–102°59'04"E; 576 m a.s.l.), Ya’an, Sichuan Province, China. According to meteorological data provided by Ya’an Meteorological Station, the 30-year (1971–2000) mean annual temperature was 16.2°C, with the mean minimum and maximum temperatures being 6.1°C (January) to 25.4°C (July). The frostless period lasts approximately 300 d, the mean annual precipitation varies from 1,250 to 1,750 mm and solar radiation is averaged at 3,750 MJ m^{-2} y^{-1}. The soil is composed of purple clay loam (pH = 7.5), with total N of 1.33 g kg^{-1}, P_2O_5 of 0.51 g kg^{-1}, total K of 26.16 g kg^{-1}, and organic matter of 24.4 g kg^{-1}.

Experimental design: A randomized complete block design was used to set up the field experiment with three replicates in 12 plots (6 m × 6 m each). Seeds of the two widely cultivated soybean varieties (GX and GQD) were sown on June 30, 2008 with a density of 1.05×10^5 plant ha^{-1}. For the RI treatment, seeds of soybean were sown into the alternating strips with maize plants that were formerly sown on 8 April with a density of 5.25×10^4 plant ha^{-1}. The width for both soybean and maize rows was 0.4 m, and the strip between maize and soybean rows was 0.6 m. Without maize, soybean was planted in the same pattern as RI. Maize was harvested on 29 August and soybean on 25 October, thus duration of intercropping with maize was about 60 d for soybean. All the seeds of soybean were obtained from Zigong Institute of Agricultural Sciences (Zigong, Sichuan Province, China); maize seeds were obtained from Research Institute, Sichuan Agriculture University (Chengdu, Sichuan province, China). Irrigation, weeding, fertilization, and other field agricultural management were carried out equally for all treatments.

Microenvironment for soybean seedlings: On clear days of 34, 40, and 46 d after soybean emergence (DAE), both diurnal temperature and humidity at 10 cm above the canopy of soybean seedling were recorded hourly using temperature and humidity sensor attached to a *HOBO H8* data-logger (*Onset Computer Corp*., Bourne, USA), simultaneously PAR was measured using a quantum sensor *LI-190* (*LI-COR Inc*., Lincoln, NE, USA) in each plot from 06:00 to 18:00 h.

Gas exchange of the latest, fully expanded leaves was examined using an infrared gas analysis instrument (*LI-6400, Li-COR Inc.,* Lincoln, NE, USA) from 10:00 to 14:00 h on 34, 40, and 46 DAE, respectively. P_N, transpiration rate (E), stomatal conductance (g_s), and C_i were automatically recorded. At least four seedlings of each soybean variety were measured under each treatment.

Chl *a* fluorescence was determined with a pulse-amplitude modulation fluorescence analyzer (*Mini-PAM, Heinz Walz*, Effeltrich, Germany) on 34, 40, and 46 DAE. After 30-min dark adaptation, the minimum fluorescence (F_0) was first determined with modulated light (< 1 μmol m^{-2} s^{-1}), and then the maximum fluorescence (F_m) was determined with a 0.8-s saturating pulse at 8,000 μmol m^{-2} s^{-1}. The variable fluorescence (F_v) was calculated as $F_v = F_m - F_o$. The maximum efficiency of PSII photochemistry in the dark-adapted state (F_v/F_m) was calculated as $F_v/F_m = (F_m - F_0)/F_m$ (Genty *et al.* 1989, Zhang *et al.* 2012).

Leaf sampling and pigment analysis: Ten fully developed leaves of soybean seedlings in each treatment were sampled on 34, 40, and 46 DAE. Leaf samples were frozen in liquid nitrogen immediately after removal of leaf veins, and all samples were kept in a freezer at –40°C to be analyzed. Chl and carotenoids (Car) were extracted from frozen leaf samples (0.2 g) in 20 ml of 95% ethanol in the dark for 48 h at 4°C. The extract was then measured at a wavelengths of 663, 645, and 470 nm using a *UV–Vis* spectrometer (*V-1100D, Shanghai MAPADA Instruments Co., Ltd.*, China). Chl and Car concentrations were calculated using extinction coefficients provided by Arnon (1949) and Lichtenthale (1987).

Biomass accumulation and LAI: Twelve soybean seedlings were obtained with roots (30 cm) from each plot to determine the changes in accumulation and allocation of biomass, respectively, on 34, 40, and 46 DAE. After being well washed, each plant was divided into stems, leaves, and roots to determine stem dry mass (SDM), leaf dry mass (LDM), and root dry mass (RDM). Total leaf areas of each plant were calculated by *WINFOLIA Pro[S] 2004a* computer program (*Regent Instruments*, Canada) using their pictures scanned by the *Epson Perfection 4870 PHOTO* scanner. LAI was calculated as total leaf area of one plant (m^2 $plant^{-1}$) × plant density (plants m^{-2}) (Breda 2003). Thereafter, all samples were oven-dried at 80°C to constant mass before dry mass was recorded with an electronic balance (*BP221S*, *Sartorius*, Göttingen, Germany). LDM, SDM, and RDM were calculated with dry mass per plant and plant density. Root/shoot ratio was calculated as the RDM/(SDM + LDM), and the biomass was calculated as the sum of SDM, LDM, and RDM.

Final grain yield: When soybean plants reached physiological maturity (25 October), 12 plants of each variety from each plot were harvested to determine the final grain yield. A number of pods per plant and the number of seeds per pod were counted. The 100-seed mass and the final grain yield were determined.

Statistical analysis: Data were analyzed using the General Linear Models Procedure of *SPSS* (*version 15*, *SPSS*, Chicago, IL, USA). Means of each parameter were compared between treatments using one-way analysis of variance (*ANOVA*). Interactions between treatments (RI and M) and varieties (GX and GQD) were analyzed using two-way *ANOVA*. Linear regression was performed using *SigmaPlot 10.0* (*Aspire Software Intl.*, Ashburn, USA).

Results

Microenvironment: Among the microenvironment parameters for soybean seedlings under RI, the PAR was the most different from the M; it was reduced by 50.5% (Fig 1*A*). Although temperature was lower (Fig. 1*B*) and air humidity higher (Fig. 1*C*) in RI than in M, statistical analyses did not show any significance between the treatments.

Gas exchange and Chl *a* fluorescence: P_N of soybean seedlings growing in RI was considerably lower (38.3%) than that in M (Fig. 2*A*). The significant reduction was also observed in g_s (55.4%) and *E* (42.7%) (Fig. 2*B,D*). Insignificant difference was found in C_i between plants in RI and M (Fig. 2*C*). Statistical analyses showed that the effect of cropping treatment on P_N, g_s, and *E* was significant, while the effect of variety, cropping treatment *vs.* variety or measuring time was not notable. There was the insignificant negative effect of maize shading on F_v/F_m (Table 1), and the insignificant difference was observed between both varieties.

Chl content: Leaf total Chl content [Chl (*a*+*b*)] (Fig. 3*A*) and Chl *b* (Fig. 3*C*) were significantly higher, while the Chl *a*/*b* ratio was notably lower (Fig. 3*B*) in RI than in M, indicating that maize shading in RI caused significant rise namely in Chl *b*. There were not cultivar-specific responses of Chl (*a*+*b*), Chl *b*, and Chl *a*/*b* ratio to cropping treatments. Car content of soybean seedlings was reduced in RI compared with that in M, and the notable reduction was found only in GQD (–23.5%) (Fig. 3*D*). The interactive effect between cropping treatment and variety was statistically significant for Car but not for Chl (*a*+*b*), Chl *b*, and Chl *a*/*b* ratio.

LAI was significantly lower in RI than in M, indicating that maize shading caused a significant reduction in LAI under RI (Fig. 4). The average LAI of GQD declined more (–75%) than in GX (–67%). Statistic analyses showed that the effect of cropping treatment, variety, and cropping treatment *vs.* variety were all significant for LAI (Fig. 4).

Biomass accumulation and partition: The SDM, LDM, RDM, and biomass of soybean seedlings were significantly reduced by maize shading in RI, contrary to the root/shoot ratio (Fig. 5). The average reductions in SDM, LDM, RDM, and biomass were significantly higher in GQD (–74.2, –81.9, –79.5, and –78.7%, respectively) than in GX (–64.1, –72.6, –69.4, and –68.9%, respectively). There were significant interactive effects between intercropping treatment and variety on SDM, LDM, RDM, and biomass, but insignificant interactive effects on the root/shoot ratio (Fig. 5*E*).

Grain yield and yield components: Statistical analysis showed that there were significant negative effects of maize shading on the number of pods per plant, the number of seeds per pod, and the grain yield per plant in RI (Table 2), while insignificant negative effect was found for 100-seed mass. The reductions in the number of pods per plant, the number of seeds per pod, and the grain yield in GQD (–7.03, –62.4, and –42.4%, respectively) were significantly higher than that in GX (–3.4, –25.3, and –23.2%, respectively).

Correlations among LAI, P_N, biomass, and yield: The relative loss of biomass in RI was significantly positively correlated with relative loss in LAI (Fig. 6*B*), but it did not correlate with relative loss in P_N (Fig. 6*A*). A relative loss in the grain yield caused by maize shading exhibited in RI significantly positive relationships with the relative loss in LAI ($r^2 = 0.377$) (Fig. 6*C*) and soybean seedlings biomass ($r^2 = 0.384$) (Fig. 6*D*).

Discussion

Relay intercropping, one of the major, traditional farming systems in developing countries, performs a variety of ecological services besides food supply. However, it is of fundamental importance to understand how is the growth of the relayed crop species influenced in relay intercropping system, if such agroecosystem is to be practiced effectively to achieve sustainable agriculture (Rusinamhodzi *et al.* 2012). In maize-soybean relay intercropping system, light intensity to soybean canopy might be the most important environmental factor as nearly half of PAR was lost due to the interception by tall maize plants (Fig. 1*A*). Low radiation with higher fraction of diffuse lights (Sinclair *et al.* 1992, Greenwald *et al.* 2006) have significant effects on the morphological and physiological characteristic of plants (Zhang *et al.* 2008, Ghanbari *et al.* 2010). Photosynthetic processes are very sensitive to shade conditions (Dai *et al.* 2009, Huang *et al.* 2011), and plants change their photosynthetic characteristics to acclimate to various light environments (Cheng and Fleming 2009, Huang *et al.* 2011). In our experiment, maize shading caused significant reductions in P_N of both two soybean varieties (Fig. 2*A*) with increased C_i (Fig. 2*C*), indicating that the depressions of P_N were caused by limitations of mesophyll processes rather than stomatal limitation (Fay and Knapp 1993, Zhao and Oosterhuis 1998, Zhang *et al.* 2012). These results are consistent with the findings of other researchers (Crookston *et al.* 1975, Araujo *et al.* 2008). However, F_v/F_m was not affected by maize shading (Table 1), implying that the reduction in P_N was not caused by the reduction of PSII photochemical activity (Baker 2008), but it was probably caused by the energy deficiency for carbon assimilation in dark reaction of photosynthesis.

We found notable enhancement in total Chl and Chl *b* contents (Fig. 3), suggesting that soybean seedlings under maize shading formed more Chl *b* to improve light-harvesting efficiency (Murchie and Horton 1998, Evans and Poorter 2001, Wittmann *et al.* 2001). Nevertheless, a tremendous reduction in LAI (Fig. 4) and LDM (Fig. 5*D*) in RI might indicate that the light-harvesting capability of soybean seedlings was still lower under RI. However, it was a result of the decreased number of leaves produced under maize shade conditions (Kennedy *et al.* 2007).

GQD showed larger reduction in LAI and LDM than GX, indicating the cultivar-specific response to shade. As leaf area and LDM are regarded as key traits to alter light-harvesting capability (Niinemets 2010), the GX might be more tolerant cultivar to maize shading than GQD.

The accumulation of biomass represents the net effect of carbon assimilation and maintenance, and shade-induced reductions in biomass generally reflect the recognized differences in shade tolerance among the species (Chen 1997). The SDM, RDM, and total biomass of soybean seedlings were significantly reduced by maize shading in RI compared with M (Fig. 5), suggesting that

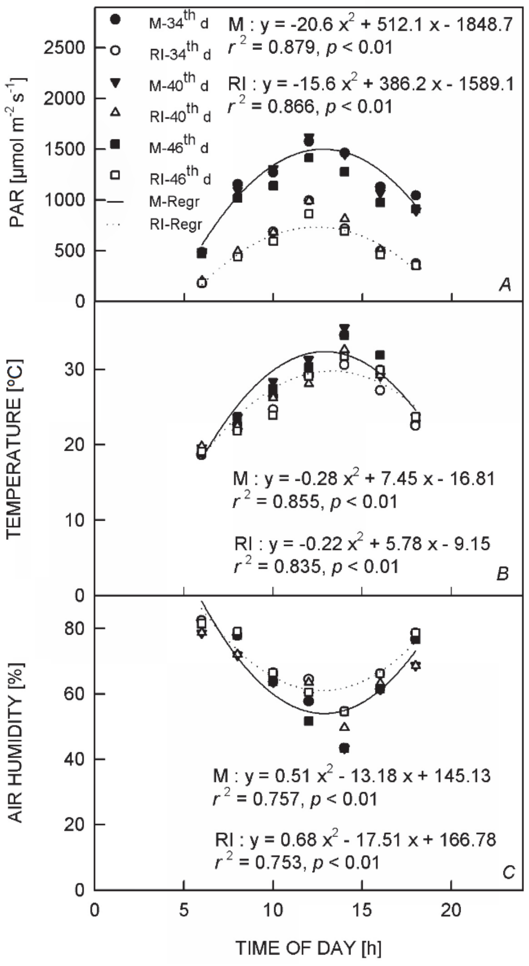

Fig. 1. Diurnal course of average (*A*) incident PAR, (*B*) air temperature, and (*C*) air humidity in relay intercropping soybean system (RI) and monoculture soybean system (M).

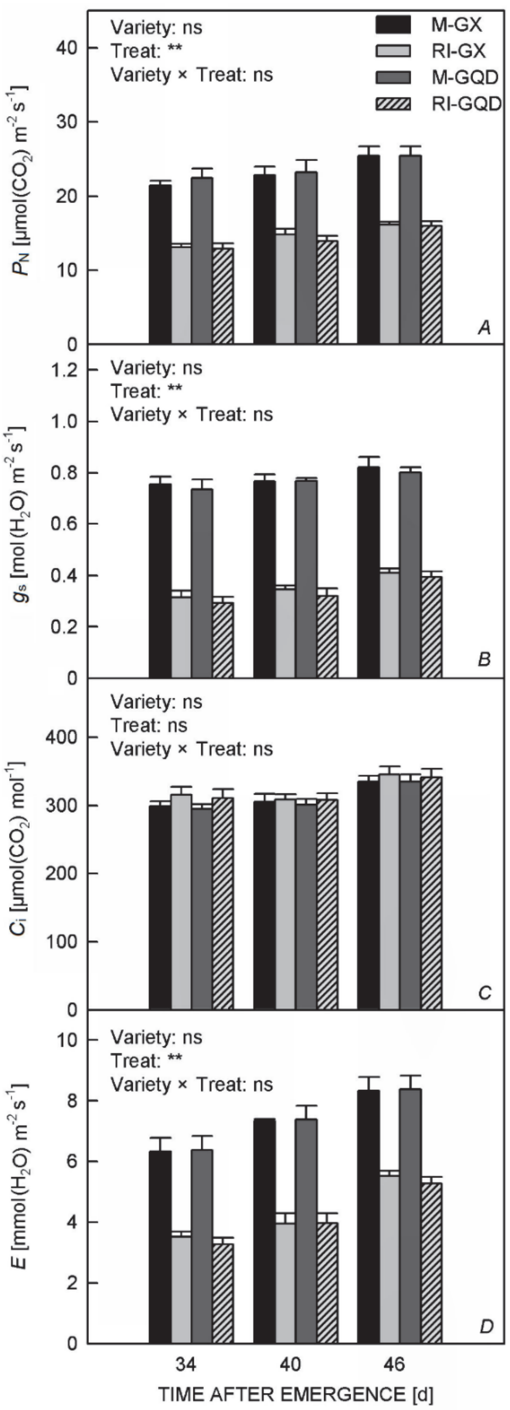

Fig. 2. (*A*) Net photosynthetic rate (P_N), (*B*) stomatal conductance (g_s), (*C*) intercellular CO$_2$ concentration (C_i), and (*D*) transpiration rate (*E*) of Gongxuan 1 (GX) and Gongqiudou494-1 (GQD) under relay intercropping system (RI) and monoculture system (M). Error bars show SD, $n = 9$. Means of each parameter were analyzed using the *Student*'s *t*-test to compare values between treatments in each variety. Effects by variety, intercropping treatment (treat), and variety × relay intercropping treatment interactions (variety × treat) were denoted significant by * at $P \leq 0.05$ and ** at $P \leq 0.01$, or not significant by ns.

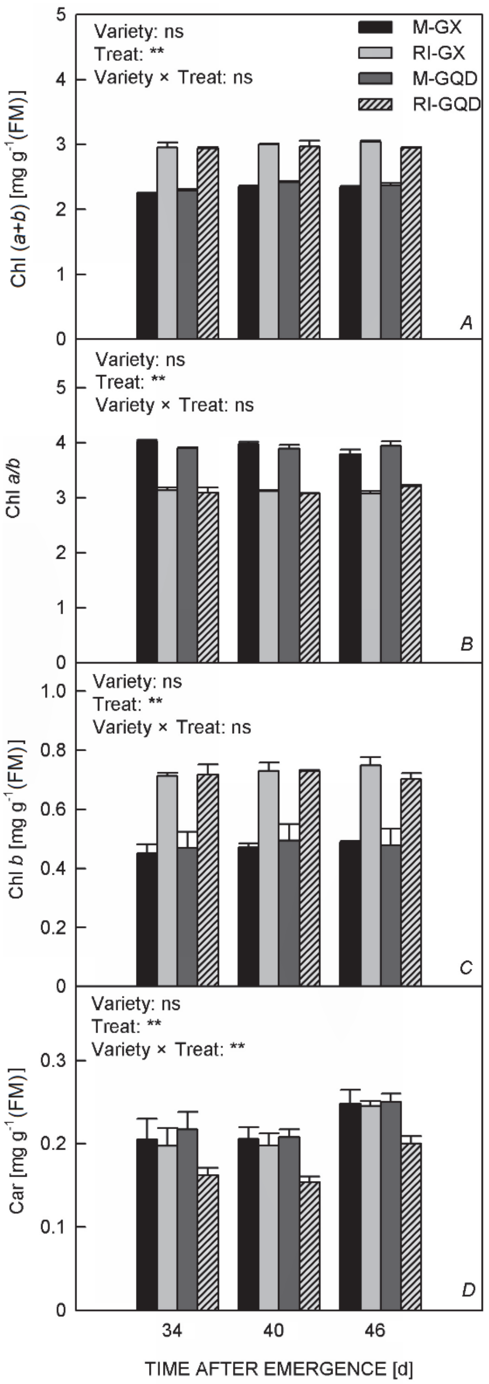

Fig. 3. (*A*) Total chlorophyll (Chl) (*a*+*b*), (*B*) Chl *a/b*, (*C*) carotenoid content (Car), and (*D*) Chl *b* of Gongxuan 1 (GX) and Gongqiudou494-1 (GQD) under relay intercropping system (RI) and monoculture system (M). Error bars show SD, $n = 9$. Means of each parameter were analyzed using the *Student*'s *t*-test to compare values between treatments in each variety. The asterisks * ($P \leq 0.05$) and ** ($P \leq 0.01$) denote significant effects by variety, intercropping treatment (treat), and variety × relay intercropping treatment interactions (variety × treat); ns – not significant.

Table 1. The maximum photochemical efficiency of PSII (F_v/F_m) (mean ± SD) of Gongxuan 1 (GX) and Gongqiudou494-1 (GQD) under relay intercropping (RI) and monoculture system (M) on 34 d, 40, and 46 d after soybean emergence. Letters are comparable within treatments in each species. Values with *different letters* are significantly different ($P<0.05$).

Soybean variety	Treatment	Time after soybean emergence [d] 34	 40	 46
GX	M	0.837 ± 0.031^a	0.831 ± 0.038^a	0.826 ± 0.030^a
	RI	0.829 ± 0.042^a	0.820 ± 0.033^a	0.816 ± 0.041^a
GQD	M	0.840 ± 0.033^a	0.835 ± 0.042^a	0.831 ± 0.036^a
	RI	0.827 ± 0.037^a	0.818 ± 0.037^a	0.815 ± 0.037^a

growth of the relay-sown crop would be negatively influenced by the tall maize plants.

Results of statistical analysis showed that the biomass loss positively correlated with the relative loss in LAI (Fig. 6*B*) but not with that in P_N (Fig. 6*A*), which could be easily understood since the LAI was an important resource of the biomass. The insignificantly changed root/shoot ratio (Fig. 5*E*) indicated that maize shading might not result in the change of biomass partition. The reductions in SDM, RDM, and total biomass of GX were significantly lower than those of GQD, implying that GX might be more tolerant to maize shading than GQD (Wang *et al.* 1994, Khan *et al.* 2000).

Shade can reduce grain yields of the subordinate crop in the intercropping system or agroforestry intercropping system (Kuruppuarachchi 1990, Reynolds *et al.* 2007, Peng *et al.* 2009). We found that the final grain yield of soybean in RI was considerably lower (–32.8%) than in M, and the reduction exhibited significantly positive relationships with the relative loss both in LAI and biomass at the seedling stage (Fig. 6*C,D*). It indicated that growth restrictions of the seedlings might have an important impact on the final yield of soybean under RI. Yield components showed that the reduction in the final grain yield caused by maize shading was primarily due to the significant reductions in the number of seeds per pod (–43.9%) rather than the number of pods per plant (–5.2%) at the seedling stage (Table 2). Our results were consistent with the findings of Yan *et al* (2010). However, the relatively lower degree of the loss in the final grain yield (–32.8%) compared with the loss in biomass at seedling stage (–73.8%) indicated that the plants in RI might recover or compensate their growth after the maize harvest (Li *et al.* 2001). GX showed the lesser reduction in the grain yield (–23.2%) than GQD (–42.4%), suggesting that negative impacts on the seedlings growth caused by maize shading impacted less the grain yields of the former cultivar.

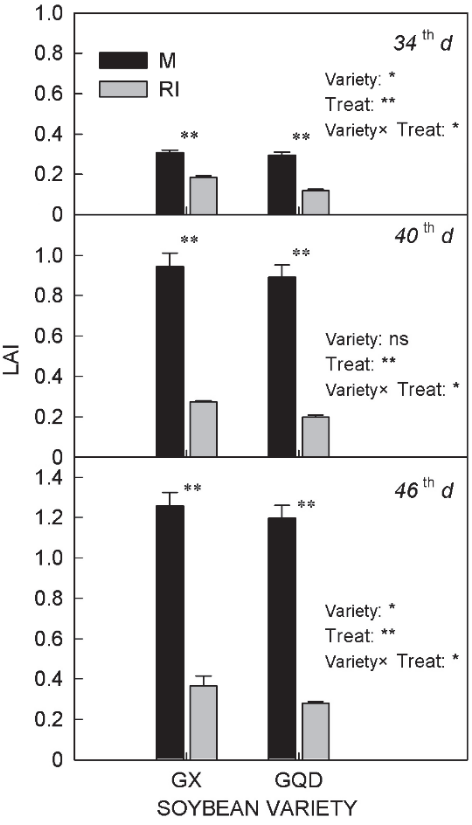

Fig. 4. Leaf area index (LAI) of Gongxuan 1 (GX) and Gongqiudou494-1 (GQD) under relay intercropping system (RI) and monoculture system (M) on 34, 40, and 46 d after soybean emergence. Error bars show SD, $n = 9$. Means of each parameter were analyzed using the *Student*'s *t*-test to compare values between treatments in each variety. * ($P\leq0.05$) and ** ($P\leq0.01$) denote significant effects by variety, intercropping treatment (treat) and variety × relay intercropping treatment interactions (variety × treat); ns – not significant.

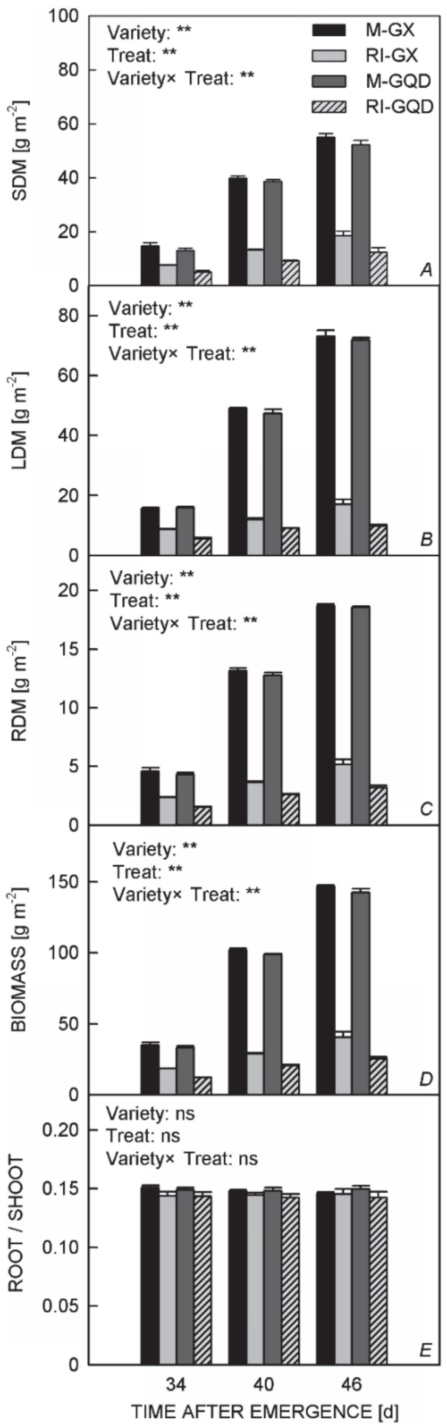

Fig. 5. (*A*) Stem dry mass (SDM), (*B*) leaf dry mass (LDM), (*C*) root dry mass (RSD), (*D*) total biomass, and (*E*) root/shoot ratio of Gongxuan 1 (GX) and Gongqiudou494-1 (GQD) under relay intercropping system (RI) and monoculture system (M). Error bars show SD, $n = 9$. Means of each parameter were analyzed using the *Student*'s *t*-test to compare values between treatments in each variety. * ($P \leq 0.05$) and ** ($P \leq 0.01$) denote significant effects by variety, intercropping treatment (treat), and variety × relay intercropping treatment interactions (variety × treat) ; ns – not significant.

Table 2. Grain yields and yield components of Gongxuan 1 (GX) and Gongqiudou494-1 (GQD) under relay intercropping (RI) and monoculture system (M). [%] – differences between RI and M, (RI – M)/M × 100%, * $P<0.05$, ** $P<0.01$.

Soybean variety	100-seed mass [g]			Number of seed [pod^{-1}]			Number of pods [plant^{-1}]			Yield [kg ha^{-1}]		
	M	RI	[%]	M	RI	[%]	M	RI	[%]	M	RI	[%]
GX	19.5 ± 0.173	18.9 ± 0.167	−3.01	1.69 ± 0.010	1.63 ±0.013	-3.40^{*}	82.3 ± 0.593	71.9 ± 0.700	-25.34^{*}	3002.7 ± 56.161	2305.8 ± 23.611	-23.19^{*}
GGD	17.4 ± 0.190	16.70 ± 0.450	−4.34	1.66 ± 0.010	1.54 ± 0.022	-7.03^{**}	85.9 ± 0.584	59.1 ± 0.478	-62.40^{**}	2935.2 ± 30.161	1689.6 ± 53.129	-42.42^{**}

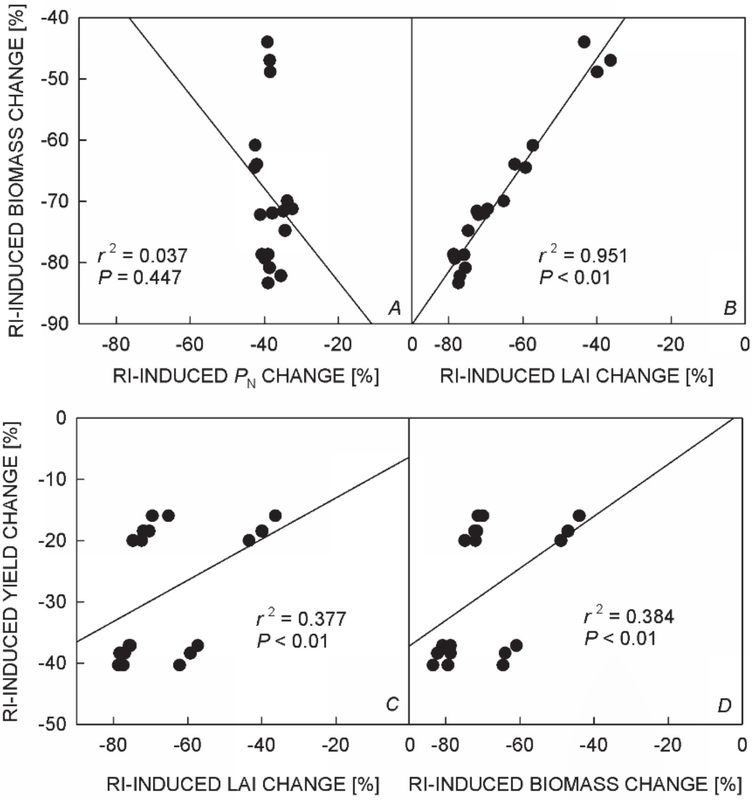

Fig. 6. Relationship between the RI-induced relative reduction in biomass and the RI-induced relative reduction in LAI and in P_N, and relationship between the RI-induced relative reduction in the grain yield and the RI-induced relative reduction in LAI and in biomass using values measured on the days of 34, 40, and 46 d after soybean emergence, n = 18. The RI-induced relative reduction was calculated as (RI-M)/M × 100%.

Conclusion: Maize shading negatively affected physiological and ecological characteristics of soybean seedlings and, consequently, also its final grain yield in a maize-soybean relay intercropping system in Southwest China. Thus, the sensitivity of the relay-sown crop to shade should be considered in relay intercropping systems. Response of LAI to shade might be the important index for soybean variety selection. GX variety might be a more adaptive variety to maize-soybean relay intercropping system.

References

Altieri, M.A.: The ecological role of biodiversity in agroecosystems. – Agr. Ecosyst. Environ. **74**: 19-31, 1999.

Araujo, W.L., Dias, P.C., Moraes, G.A.B.K., *et al.*: Limitations to photosynthesis in coffee leaves from different canopy positions. – Plant Physiol. Biochem. **46**: 884-890, 2008.

Arnon D.I.: Copper enzymes in isolated chloroplasts. Polyphenoloxidase in *Beta vulgaris*. – Plant Physiol. **24**: 1-15, 1949.

Baker, N.R.: Chlorophyll fluorescence: a probe of photosynthesis *in vivo*. – Annu. Rev. Plant Biol. **59**: 89-113, 2008.

Breda, N.J.J: Ground-based measurements of leaf area index: a review of methods, instruments and current controversies. – J. Exp. Bot. **54**: 2403-2417, 2003.

Callan, E.J., Kennedy, C.W.: Intercropping stokes aster: effect of shade on photosynthesis and plant morphology. – Crop. Sci. **35**: 1110-1115, 1995.

Chen, H.Y.H.: Interspecific responses of planted seedlings to light availability in interior British Columbia: survival, growth, allometric patterns, and specific leaf area. – Can. J. Forest Res. **27**: 1383-1393, 1997.

Cheng, Y. C., Fleming, G.R.: Dynamics of light harvesting in photosynthesis. – Annu. Rev. Phys. Chem. **60**: 241-262, 2009.

Crookston, R.K., Treharne, K.J., Ludford, P., Ozbun, J.L.: Response of beans to shading. – Crop. Sci. **15**: 412-416, 1975.

Dai, Y.J., Shen, Z.G., Liu, Y., Wang, L.L., Hannaway, D., Lu, H.F.: Effects of shade treatments on the photosynthetic capacity, chlorophyll fluorescence, and chlorophyll content of *Tetrastigma hemsleyanum* Diels et Gilg. – Environ. Exp. Bot. **65**: 177-182, 2009.

Evans, J.R., Poorter, H.: Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. – Plant Cell Environ. **24**: 755–767, 2001.

Fan, M.S., Shen, J.B., Yuan, L.X., *et al.*: Improving crop productivity and resource use efficiency to ensure food security and environmental quality in China. – J. Exp. Bot. **63**: 13-24, 2012.

Fay, P.A., Knapp, A.K.: Photosynthetic and stomatal responses of *Avena sativa* (Poaceae) to a variable light environment. – Am. J. Bot. **80**: 1369-1373, 1993.

Gao, Y., Duan, A.W., Qiu, X.Q., *et al.*.: Distribution and use efficiency of photosynthetically active radiation in strip intercropping of maize and soybean. – Agron. J. **102**: 1149-1157, 2010.

Genty, B., Briantais, J.M., Baker, N.R.: The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. – Biochim. Biophys. Acta **990**: 87-92, 1989.

Ghanbari, A., Dahmardeh, M., Siahsar, B.A., Ramroudi, M.:

Effect of maize (*Zea mays L.*) - cowpea *(Vigna unguiculata* L.) intercropping on light distribution, soil temperature and soil moisture in arid environment. – J. Food Agric. Environ. **8**: 102-108, 2010.

Godfray, H.C.J., Beddington, J.R., Crute, I.R., *et al*.: Food security: the challenge of feeding 9 billion people. – Science **327**: 812 -818, 2010.

Greenwald, R., Bergin, M.H., Xu, J., *et al*.: The influence of aerosols on crop production: a study using the CERES crop model. – Agr. Syst. **89**: 390-413, 2006.

Huang, D., Wu, L., Chen, J.R., Dong, L.: Morphological plasticity, photosynthesis and chlorophyll fluorescence of *Athyrium pachyphlebium* at different shade levels. – Photosynthetica **49**: 611-618, 2011.

Jurik, T.W., Van, K.: Microenvironment of a corn-soybean-oat strip intercrop system. – Field Crop. Res. **90**: 335-349, 2004.

Kennedy, S., Black, K., O´Reilly, C., Dhubhain, N.A.: The impact of shade on morphology, growth and biomass allocation in *Picea sitchensis*, *Larix* × *eurolepis* and *Thuja plicata*. – New Forest. **33**: 139-153, 2007.

Khan, S.H., Rose, R., Haase, D.L., Sabin, T.E.: Effects of shade on morphology, chlorophyll concentration, and chlorophyll fluorescence of four Pacific Northwest conifer species. – New Forest. **19**: 171-186, 2000.

Kuruppuarachchi, D.S.P.: Intercropped potato (*Solanum spp.*): Effect of shade on growth and tuber yield in the northwestern regosol belt of Sri Lanka. – Field Crop. Res. **25**: 61-72, 1990.

Li, L, Sun, J.H., Zhang, F.S., Li, X.L., Rengel, Z., Yang, S.C.: Wheat/maize or wheat/soybean strip intercropping: II. Recovery or compensation of maize and soybean after wheat harvesting. – Field Crop. Res. **71**: 173-181, 2001.

Li, L., Li, S.M., Sun, J.H., *et al*.: Diversity enhances agricultural productivity via rhizosphere phosphorus facilitation on phosphorus-deficient soils. – P. Natl. Acad. Sci. USA **104**: 11192-11196, 2007.

Lichtenthaler, H.K.: Chlorophylls and carotenoids: pigments of photosynthetic biomembranes. – Methods Enzymol. **148**: 350-382, 1987.

Liu, T.D., Song, F.B.: Maize photosynthesis and microclimate within the canopies at grain-filling stage in response to narrow-wide row planting patterns. – Photosynthetica **50**: 215-222, 2012.

Makoi, J.H.J.R., Chimphango, S.B.M.; Dakora, F.D.: Photosynthesis, water-use efficiency and $\delta\ {}^{13}$C of five cowpea genotypes grown in mixed culture and at different densities with sorghum. – Photosynthetica **48**: 143-155, 2010.

Murchie, E.H., Horton, P.: Contrasting patterns of photosynthetic acclimation to the light environment are dependent on the differential expression of the responses to altered irradiance and spectral quality. – Plant Cell Environ. **21**: 139-148, 1998.

Niinemets, U.: A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. – Ecol. Res. **25**: 693-714, 2010.

Peng, X.B., Zhang, Y.Y., Cai, J., Jiang, Z.M., Zhang, S.X.: Photosynthesis, growth and yield of soybean and maize in a tree-based agroforestry intercropping system on the Loess Plateau. – Agroforest. Syst. **76**: 569-577, 2009.

Pypers, P., Sanginga, J.M., Kasereka, B., Walangululu, M., Vanlauwe, B.: Increased productivity through integrated soil fertility management in cassava-legume intercropping systems in the highlands of Sud-Kivu, DR Congo. – Field Crop Res. **120**: 76-85, 2011.

Reynolds, P.E., Simpson, J.A., Thevathasan, N.V., Gordon, A.M.: Effects of tree competition on corn and soybean photosynthesis, growth, and yield in a temperate tree-based agroforestry intercropping system in southern Ontario, Canada. – Ecol. Eng. **29**: 362-371, 2007.

Rusinamhodzi, L., Corbeels, M.C., Nyamangara, J., Giller, K.E.: Maize-grain legume intercropping is an attractive option for ecological intensification that reduces climatic risk for smallholder farmers in central Mozambique. – Field Crop. Res. **136**: 12-22, 2012.

Sinclair, T.R., Shiraiwa, T., Hammer, G.L.: Variation in crop radiation-use efficiency with increased diffuse radiation. – Crop Sci. **32**: 1281-1284, 1992.

Swinton, S.M, Lupi, F., Robertson, G.P., Hamilton, S.K.: Ecosystem services and agriculture: cultivating agricultural ecosystems for diverse benefits. – Ecol. Econ. **64**: 245-252, 2007.

Wallace, S.U., Bacanamwo, M., Palmer, J.H., Hull, S.A.: Yield and yield components of relay-intercropped wheat and soybean. – Field Crop. Res. **46**: 161-168, 1996.

Wang, G.G., Qian, H., Klinka, K.: Growth of *Thuja plicata* seedlings along a light gradient. – Can. J. Botany **72**: 1749-1757, 1994.

Wittmann, C., Aschan, G., Pfanz, H.: Leaf and twig photosynthesis of young beech (*Fagus sylvatica*) and aspen (*Populus tremula*) trees grown under different light regime. – Basic Appl. Ecol. **2**: 145-154, 2001.

Yan, Y.H., Gong, W.Z., Yang, W.Y., *et al*.: Seed treatment with uniconazole powder improves soybean seedling growth under shading by corn in relay strip intercropping system. – Plant Prod. Sci. **13**: 367-374, 2010.

Zhang, L., Su, B.Y., Xu, H., Li, Y.G.: Growth and photosynthetic responses of four landscape shrub species to elevated ozone. – Photosynthetica **50**: 67-76, 2012.

Zhang, L., van der Werf, W., Bastiaans, L., *et al*.: Light intereption and utilization in relay intercrops of wheat and cotton – Field Crop. Res. **107**: 29-42, 2008.

Zhao, D.L., Oosterhuis, D.M.: Influence of shade on mineral nutrient status of field-grown cotton. – J. Plant Nutr. **21**: 1681-1695, 1998.