Postprint: Response of Morphological and Photosynthetic Characteristics of Relay-Intercropped Soybean to Maize Shading and Light Recovery

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Abstract

To explore the response strategies of morphogenesis and photosynthetic physiology in soybean under shade stress and subsequent light recovery, three soybean cultivars— 'Jianyang Jiuyuehuang' , 'Jiangpu Heidou' , and 'Yongsheng Heidou' —were selected as experimental materials. Using monoculture and maize-soybean strip relay intercropping planting patterns as research subjects, the response characteristics of soybean morphological traits, photosynthetic rate, leaf anatomical structure, photosynthetic pigment content, and other parameters were analyzed following intercropping shade and light recovery. The results showed that under intercropping conditions, soybean experienced significant maize shade stress at the fifth compound leaf expansion (V5) stage. Compared with monoculture soybean, plant height increased significantly, while stem diameter and aboveground biomass decreased significantly. The biomass allocation of stems, leaves, and petioles accounted for 58%, 37%, and 6% of aboveground biomass, respectively, whereas under monoculture they were 36%, 50%, and 14%, respectively. The allocation center of aboveground biomass in soybean under intercropping shade shifted from leaves to stems. Simultaneously, leaf thickness, palisade tissue thickness, spongy tissue thickness, chlorophyll a content, chlorophyll a/b ratio, and net photosynthetic rate decreased, while chlorophyll b content and the ratio of palisade tissue thickness to spongy tissue thickness increased. After maize harvest alleviated the shade stress, at the soybean seed filling stage (R6), the differences in plant height, stem diameter, leaf area, and aboveground biomass accumulation compared with monoculture were reduced; the biomass of stems, leaves, and petioles accounted for 41%, 49%, and 10% of aboveground biomass, respectively. Leaf, palisade tissue, and spongy tissue thickness increased by 117%, 99%, and 81% compared with the V5 stage (maize-soybean co-growth period), respectively. Photosynthetic pigments showed no significant difference compared with monoculture, but net photosynthetic rate was significantly lower than that of monoculture. The three soybean materials under maize-soybean strip relay intercropping exhibited substantial differences in yield per plant. The yield per plant of ‘Jianyang Jiuyuehuang’ , ‘Jiangpu Heidou’ , and ‘Yongsheng Heidou’ decreased by 33%, 64%, and 40% compared with monoculture, respectively. Therefore, soybean can adapt to light environments through plasticity in morphological and photosynthetic physiological traits, but inter-varietal differences exist.

Full Text

Preamble

Effects of Shading and Light Recovery on Soybean Morphology and Photosynthetic Characteristics in Soybean-Maize Intercropping System

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Abstract: To explore the morphological development and photosynthetic physiological response strategies of soybean under shading stress and subsequent light recovery, three soybean materials— ‘Jianyangjiuyuehuang’ , ‘Jiangpuheidou’ , and ‘Yongshengheidou’—were selected for analysis. Using both monoculture and maize-soybean relay strip intercropping systems, we examined the response characteristics of soybean morphological traits, photosynthetic rate, leaf anatomical structure, and photosynthetic pigment content under intercropping shading and light recovery conditions. The results showed that under intercropping, soybean at the V5 stage (fifth trifoliate leaf fully expanded) experienced significant shading stress from maize. Compared with monoculture soybean, plant height increased significantly while stem diameter and above-ground biomass decreased significantly. The biomass allocation to stem, leaf, and petiole accounted for 58%, 37%, and 6% of total above-ground biomass, respectively, under intercropping, compared with 36%, 50%, and 14% under monoculture. Thus, the biomass allocation center shifted from leaves to stems under intercropping shade. Concurrently, leaf thickness, palisade tissue thickness, spongy tissue thickness, chlorophyll a content, chlorophyll a/b ratio, and net photosynthetic rate decreased, while chlorophyll b content and the palisade/spongy tissue thickness ratio increased.

After maize harvest removed the shading stress, at the soybean R6 stage (seed filling stage), differences in plant height, stem diameter, leaf area, and above-ground biomass accumulation between intercropped and monoculture soybean narrowed. The biomass allocation to stem, leaf, and petiole was 41%, 49%, and 10% of above-ground biomass, respectively. Leaf, palisade tissue, and spongy tissue thickness increased by 117%, 99%, and 81% compared with the V5 stage (maize-soybean symbiotic period). Photosynthetic pigments showed no significant differences compared with monoculture, but net photosynthetic rate was significantly lower than in monoculture. The three soybean materials showed substantial differences in yield per plant under maize-soybean relay strip intercropping, with yield reductions of 33%, 64%, and 40% compared with monoculture for 'Jianyangjiuyuehuang', 'Jiangpuheidou', and 'Yongshengheidou', respectively. Therefore, soybean can adapt to light environment changes through morphological and photosynthetic physiological plasticity, though significant variation exists among varieties.

Keywords: Soybean; Relay strip intercropping; Shading; Light recovery; Photosynthetic physiological characteristics; Morphological characteristics

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1.1 Experimental Design

The experiment was conducted in 2014 at the modern grain production demonstration base of Sichuan Agricultural University in Zhujia Township, Renshou County (N30°4 16 , E104°12 53). The site is at an altitude of 482 m in a subtropical monsoon humid climate zone, with an average annual temperature of 17.4°C, annual rainfall of 1,009.4 mm, annual sunshine of 1,196.6 h, and a frost-free period of 312 days. The soil was purple clay with a pH of 6.8. A randomized block design with three replications was employed, totaling 18 plots. Three soybean varieties with different shade tolerance from three provinces were selected: 'Jianyangjiuyuehuang' from Sichuan, 'Jiangpuheidou' from Jiangsu, and 'Yongshengheidou' from Yunnan. Soybean was planted in both monoculture and maize-soybean relay strip intercropping systems [Figure 1: see original paper]. Under the intercropping system, maize was seeded on March 27, transplanted on April 10, and harvested on August 10, using a wide-narrow row configuration with a strip width of 200 cm (150 cm wide row spacing and 50 cm narrow row spacing). Soybean was sown in the wide maize rows on June 17 with 50 cm row spacing and two plants per hole, and harvested on October 21. Monoculture soybean was planted with equal row spacing of 50 cm and one plant per hole. The planting density for intercropped soybean was 100,050 plants $\cdot$ hm^{-2}, identical to the monoculture density. Basal fertilizer application included 75 kg $\cdot$ hm^{-2} urea, 600 kg $\cdot$ hm^{-2} calcium superphosphate, and 60 kg $\cdot$ hm^{-2} potassium chloride. Topdressing consisted of 75 kg $\cdot$ hm^{-2} urea applied after initial flowering. Other field management practices followed standard production protocols.

1.2.1 Soybean Canopy Light Environment

During the maize-soybean symbiotic period at the soybean V5 stage, diurnal variations in photosynthetically active radiation (PAR) at the soybean canopy were measured every two hours from 9:00 to 17:00 on clear days using a LI-1400 quantum sensor (LI-COR, USA). PAR was measured along the soybean canopy from west to east at positions 1, 2, 3, 4, and 5 using LI-1400 PAR sensor rods [Figure 1: see original paper], with three replications per variety, and the mean values were calculated.

1.2.2 Morphological Parameters and Biomass

At the soybean V5 stage (maize-soybean symbiotic period, when the fifth trifoliate leaf was fully expanded) and R6 stage (seed filling stage, after maize harvest when maize stalks were cut at the base and soybean entered the recovery period after shading removal), five representative soybean plants per treatment were selected to measure plant height, stem diameter, and leaf area per plant. The stems, leaves, and petioles were then placed in paper bags, killed at 105°C for 30 minutes, dried to constant weight in an oven at 80°C, and weighed for biomass determination [14].

1.2.3 Leaf Anatomical Structure of Soybean

At the V5 and R6 stages, functional leaves (the middle leaflet of the third leaf from the top) from three representative soybean plants per treatment were sampled. Tissue sections approximately 5 mm × 5 mm were taken near the basal one-third of the main vein, fixed in standard FAA solution, dehydrated in alcohol and n-butanol series, embedded in paraffin, and sectioned at 10 m thickness using a Leica microtome (Germany). After dewaxing and rehydration in turpentine and alcohol series, sections were stained with safranin, mounted in neutral balsam, observed under a Nikon eclipse 50i microscope, and photographed and analyzed using an ACT-2U imaging system [15].

1.2.4 Net Photosynthetic Rate and Chlorophyll Content

At the V5 and R6 stages, five representative and uniformly growing soybean plants per treatment were selected. Net photosynthetic rate (Pn) of functional leaves (the middle leaflet of the third leaf from the top) was measured in the field between 9:00 and 11:00 on clear days using a LI-6400 portable photosynthesis system (LI-COR, USA), with 15 leaves measured per treatment. Subsequently, following the Arnon method [16], the third leaf from the top was sampled. Two discs were punched from each middle leaflet using a 14.17 mm diameter punch, placed in 10 mL of 80% acetone solution, extracted in the dark at room temperature for 24 h, and absorbance was measured at 663 nm and 645 nm. Chlorophyll a and chlorophyll b contents were calculated from the OD values, with three replications per treatment.

1.2.5 Yield and Yield Components

At soybean maturity, 10 consecutive plants per plot were sampled, air-dried, and used to determine pods per plant, seeds per plant, 100-seed weight, and yield per plant.

1.3 Data Analysis

Data were organized and graphed using Microsoft Excel 2013 and analyzed statistically using SPSS 17.0 software.

2.1 Soybean Canopy Light Environment Under Intercropping

As shown in [Figure 2: see original paper], PAR at the soybean canopy in both monoculture and intercropping systems increased initially then decreased from 9:00 to 17:00. Compared with monoculture soybean, PAR under intercropping decreased by approximately 50% on average, stabilizing around 1,200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ between 11:00 and 13:00, while maximum PAR in monoculture soybean reached 1,900 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

2.2 Effects of Shading and Light Recovery on Soybean Morphological Characteristics and Biomass Accumulation Under Intercropping

As shown in , shading in the maize-soybean intercropping system significantly affected plant height, stem diameter, and leaf area per plant of the three soybean materials. At the V5 stage (maize-soybean symbiotic period), plant height under intercropping was significantly higher than in monoculture, while stem diameter and leaf area were lower. Among the different materials, 'Jiangpuheidou' showed the greatest increase in plant height (2.2 times that of monoculture) and the greatest reductions in stem diameter and leaf area (48.9% and 84.6% lower than monoculture, respectively). At the R6 stage (after maize harvest, light recovery period), morphological characteristics of the three materials under intercropping showed some recovery compared with monoculture. For 'Jianyangjiuyuehuang' , plant height and stem diameter showed no significant differences from monoculture, while 'Jiangpuheidou' plant height remained 27.6% higher than monoculture and 'Yongshengheidou' plant height was 32.2% lower. Similarly, stem diameter and leaf area of 'Yongshengheidou' were 52.9% and 75.5% lower than monoculture, respectively.

Biomass accumulation reflects photosynthetic productivity [17]. As shown in , during the maize-soybean symbiotic period, biomass accumulation in all above-ground organs was significantly lower under intercropping, approximately 10% of that in monoculture. Total above-ground biomass accumulation followed the pattern 'Jianyangjiuyuehuang'< 'Jiangpuheidou'< 'Yongshengheidou'. Biomass allocation differed significantly between planting systems: during the symbiotic period, the average allocation to stem, leaf, and petiole under intercropping was 57.7%, 36.3%, and 6.3%, respectively, compared with 37.0%, 49.3%, and 14.7% under monoculture. The biomass allocation center shifted from leaves to stems under intercropping shade. After maize harvest at the R6 stage, above-ground biomass accumulation recovered to some extent, with differences in plant height, stem diameter, leaf area, and biomass accumulation between intercropped and monoculture soybean narrowing. The biomass allocation to stem, leaf, and petiole was 41.7%, 49.0%, and 9.3%, respectively. The recovery degree followed the order 'Jianyangjiuyuehuang' > 'Yongshengheidou' > 'Jiangpuheidou' .

2.3 Effects of Shading and Light Recovery on Soybean Leaf Anatomical Structure Under Intercropping

As shown in [Figure 3: see original paper], soybean leaves are bifacial with distinct palisade and spongy tissues. However, leaf anatomical structure differed significantly among the three materials between monoculture and intercropping conditions. Quantitative analysis of leaf structure in revealed that at the V5 stage, shading from maize reduced leaf thickness by 41.5%, 34.8%, and 27.7% for the three materials compared with monoculture. Upper epidermis thickness decreased by approximately 25% on average, with weaker differentiation of palisade and spongy tissues and loosely arranged cells. Intercellular spaces increased, with palisade tissue thickness 47.9%, 36.0%, and 34.2% lower than controls, and spongy tissue thickness 59.8%, 38.1%, and 21.8% lower. However, the palisade/spongy tissue ratio increased by 25% and 4% for 'Jianyangjiuyuehuang' and 'Jiangpuheidou' , respectively, while decreasing by 16.8% for 'Yongshengheidou' .

At the R6 stage (after maize harvest), leaf anatomical structure under intercropping recovered significantly compared with the V5 stage. Leaf thickness recovered to 78.7%, 73.7%, and 94.5% of control values for the three varieties. The palisade/spongy tissue ratio of 'Jianyangjiuyuehuang' and 'Jiangpuheidou' was higher than in monoculture, at 100.7% and 111.6% of control values, respectively, while that of 'Yongshengheidou' was 87.5% of the control.

2.4 Effects of Shading and Light Recovery on Soybean Chlorophyll and Net Photosynthetic Rate Under Intercropping

Chlorophyll content is an indicator of leaf light absorption capacity [18]. As shown in , during the maize-soybean symbiotic period, chlorophyll a content, chlorophyll a/b ratio, and net photosynthetic rate decreased significantly ($P<0.05$), while chlorophyll b content increased. At the R6 stage (after maize harvest), no significant differences ($P>0.05$) in chlorophyll a and chlorophyll b contents were observed between monoculture and intercropping for the three materials. However, chlorophyll a and chlorophyll b contents in intercropped soybean were higher than in monoculture. The chlorophyll a/b ratio of 'Jianyangjiuyuehuang' and 'Jiangpuheidou' decreased compared with monoculture, while that of 'Yongshengheidou' increased slightly, though not significantly. The pattern of net photosynthetic rate differences between monoculture and intercropping remained consistent with that observed during the symbiotic period.

2.5 Effects of Shading and Light Recovery on Soybean Yield Components Under Intercropping

As shown in , shading under intercropping had clear effects on soybean yield and yield components. Pods per plant, seeds per plant, and yield per plant were consistently and significantly lower than in monoculture across all three varieties, following the pattern ‘Jianyangjiuyuehuang’ > ‘Yongshengheidou’ > ‘Jiangpuheidou’ . ‘Jianyangjiuyuehuang’ had the highest yield per plant at 13.61 g, followed by ‘Yongshengheidou’ at 9.98 g, and ‘Jiangpuheidou’ at 4.90 g.

3.1 Effects of Light Environment on Soybean Morphology and Biomass Under Intercropping

When environmental conditions change, plants adapt by altering their morphology, structure, and physiological-biochemical characteristics to maintain optimal growth and development [19]. In maize-soybean relay strip intercropping, shading is a key factor affecting soybean production, reducing above-ground biomass accumulation, which is significantly correlated with yield [20-21]. During the maize-soybean symbiotic period, plant height increased while stem diameter, leaf area, and above-ground biomass decreased to approximately 10% of monoculture values. After shading removal, above-ground biomass of the three materials recovered to about 80% of monoculture values. Biomass allocation adjustment represents an environmental adaptation strategy, where plants modify growth strategies in response to environmental changes [17,22], affecting individual development and population yield. Varieties with different yield potentials show different allocation patterns among roots, stems, leaves, and pods during biomass accumulation [15,23]. Under intercropping shade, biomass was allocated primarily to stems, whereas monoculture allocated biomass mainly to leaves. During the light recovery period, ‘Jianyangjiuyuehuang’ showed allocation pattern leaf > stem > petiole, while ‘Jiangpuheidou’ and ‘Yongshengheidou’ showed stem > leaf > petiole. Since leaves are the primary photosynthetic organs and photosynthesis is the source of dry matter accumulation and closely related to yield [24-25], these results indicate that ‘Jianyangjiuyuehuang’ can rapidly alter matter transport direction after light recovery, increasing photosynthetic area and enhancing later-stage photosynthetic capacity to increase yield.

3.2 Effects of Light Environment on Soybean Anatomical Structure Under Intercropping

Leaf anatomical structure reflects plant responses to environmental changes. Thick leaf structure, well-developed palisade tissue, and tightly arranged, straight epidermal cells are typical characteristics of sun leaves, whereas well-developed spongy tissue and convex epidermal cells represent adaptations to low light and adequate moisture [26]. Under intercropping shade, palisade and spongy tissue thicknesses were lower than in monoculture. The reduction in palisade tissue thickness resulted from decreased cell length rather than cell layer number, with cells loosely arranged and shaped as short cones or funnels. Epidermal cell walls became convex, an adaptation to weak light that reduces scattering light reflection and increases internal leaf light intensity [27], enhancing light capture capacity and facilitating light penetration to mesophyll tissue to improve photosynthesis [28]. Thus, intercropped soybean exhibited clear shade leaf characteristics, demonstrating good adaptability to shaded environments.

The palisade/spongy tissue ratio reflects palisade tissue development [29]. This ratio has been studied extensively in dwarf fruit trees, where higher ratios correlate with greater dwarfing, weaker growth vigor, and more dwarfed trees [30]. Zhang et al. [31-33] suggested that the palisade/spongy tissue ratio can serve as a selection index for dwarf soybeans as well as dwarf fruit trees. In this study, the ratio increased for ‘Jianyangjiuyuehuang’ and ‘Jiangpuheidou’ under intercropping shade, indicating more developed palisade tissue. The ratio decreased significantly for ‘Yongshengheidou’ , possibly due to its more developed spongy tissue, showing significant variation among materials.

3.3 Effects of Light Environment on Soybean Photosynthetic Characteristics Under Intercropping

In low-light environments, plant leaves adjust their structure and physiological characteristics to absorb and utilize more light for growth and development, such as through thinner leaves, larger leaf area [34], and increased photosynthetic pigment content [35-36]. Chlorophyll is the primary pigment for light absorption and utilization, and its content changes reflect the quality of the initial photosynthetic reaction. Both chlorophyll a and chlorophyll b can absorb light energy, but only excited chlorophyll a can convert light energy to electrical energy. The chlorophyll a/b ratio reflects light energy utilization, with higher ratios in sun plants and lower ratios in shade plants. Increased chlorophyll b content under weak light helps utilize blue-violet light that dominates diffuse radiation, thereby improving light capture capacity. Additionally, increased chlorophyll b content promotes higher light-harvesting chlorophyll protein complex (LHCP) content and regulates excitation energy distribution between photosystems, enhancing soybean adaptability to weak light [18]. In this study, chlorophyll a content and chlorophyll a/b ratio decreased significantly while chlorophyll b content increased under intercropping shade, improving light capture capacity by absorbing more diffuse light. However, reduced leaf area per plant and leaf thickness decreased light interception under intercropping.

Photosynthetic capacity forms the basis for crop yield and quality. Shading from maize reduced PAR in the soybean canopy, causing decreased net photosynthetic rate (Pn) in soybean seedlings, consistent with previous studies [37]. The photosynthetic capacity reduction was greatest in 'Yongshengheidou' , possibly related to lower chlorophyll content in its leaves. After maize harvest, soybean entered the light recovery period, during which plant height, stem diameter, and chlorophyll a content recovered to some extent across the three materials, with 'Jianyangjiuyuehuang' showing the best recovery and strongest adaptability to weak light. Shading stress reduced pods per plant, consequently decreasing seeds per plant. Among the tested varieties, 'Jianyangjiuyuehuang' showed the highest yield per plant, consistent with previous reports [8,38-39].

In the maize-soybean relay strip intercropping system, early-stage maize shading altered the light environment of the soybean canopy, affecting plant morphology, leaf anatomical structure, and photosynthetic characteristics, resulting in increased plant height and chlorophyll b content but decreased stem diameter, leaf area, leaf thickness, and above-ground biomass. After maize harvest, soybean entered the light recovery period, during which stem diameter, above-ground biomass, chlorophyll a content, and leaf thickness increased rapidly, providing the material and energy foundation for later-stage photosynthetic compensation. The three soybean materials showed different response degrees in morphological and photosynthetic parameters during shading and recovery. From a yield perspective, 'Jianyangjiuyuehuang'demonstrated good light adaptability. Therefore, in maize-soybean relay strip intercropping, selecting soybean varieties with strong early shade tolerance and strong post-shading recovery ability, combined with optimized population configuration, is key to achieving coordinated high yields of both crops.

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Note: Figure translations are in progress. See original paper for figures.