

## Effects of Shade Signals on Growth and Photosynthetic Characteristics of Soybean Seedlings: Postprint

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### Abstract

The decrease in the red/far-red light ratio (R/FR) is an important signal for shade occurrence in nature. To investigate the response mechanism of soybean seedlings to shade signals, this study employed indoor pot experiments, using seedlings of two soybean varieties, 'Nandou 12' and 'Nan 032-4', as materials. After treatment with two light conditions (normal light and low R/FR), their morphological traits, photosynthetic characteristics, and chlorophyll fluorescence parameters were investigated. The results showed that: compared with normal light, under low R/FR, seedlings of both soybean materials exhibited typical shade-avoidance responses, i.e., increased plant height, leaf area, petiole length, and internode length, and thinner stems; specifically, for 'Nandou 12', plant height, petiole length, and internode length increased significantly by 7.86%, 81.48%, and 26.55%, respectively, while for 'Nan 032-4', they increased by 3.95%, 76.67%, and 20.00%, respectively. Leaf photosynthetic rate ( $P_n$ ), transpiration rate ( $T_r$ ), and stomatal conductance ( $G_s$ ) increased, while intercellular  $CO_2$  concentration ( $C_i$ ) and initial fluorescence intensity ( $F_0$ ), maximum fluorescence ( $F_m$ ), maximum photochemical efficiency ( $F_v/F_m$ ), actual PSII photochemical efficiency ( $\Phi_{PSII}$ ), photochemical quenching coefficient ( $q_P$ ), etc. decreased, non-photochemical quenching coefficient ( $q_N$ ) increased, and total dry matter accumulation increased; specifically,  $P_n$  of 'Nandou 12' and 'Nan 032-4' increased by 37.21% and 39.04%, respectively, total dry matter accumulation increased by 12.35% and 17.36%, respectively, and  $C_i$  decreased by 9.29% and 11.72%, respectively. However, different soybean materials showed varying sensitivity to low R/FR. Under low R/FR light conditions, 'Nandou 12' exhibited lower plant height, internode length, and petiole length, larger leaf area and stem thickness, and higher light energy transfer and conversion efficiency,  $P_n$ ,  $G_s$ , and dry matter accumulation compared with 'Nan 032-4', demonstrating stronger adaptability to shade. This study further confirms that soybean has the ability to perceive shade signals (low R/FR), but its sensitivity

varies among varieties. In intercropping systems, to improve shade tolerance of soybean, reduce lodging rate caused by shade-avoidance responses, and ensure soybean yield, varieties insensitive to shade signals should be selected.

## Full Text

### Effect of Shading Signal on Growth and Photosynthetic Characteristics of Soybean Seedlings

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#### Abstract

The reduction in the ratio of red light (R) to far-red light (FR) serves as an important signal of shade stress in nature. To investigate the response mechanism of soybean seedlings to low R/FR signals, we conducted a pot culture experiment examining morphological, photosynthetic, and chlorophyll fluorescence parameters in two soybean varieties— ‘Nandou 12’ and ‘Nan 032-4’ — under normal and low R/FR light conditions. Compared with normal light, low R/FR induced typical shade avoidance responses in both varieties, increasing plant height, leaf area, petiole length, and internode length while reducing stem diameter. Specifically, ‘Nandou 12’ showed significant increases of 7.86%, 81.48%, and 26.55% in plant height, petiole length, and internode length, respectively, while ‘Nan 032-4’ exhibited increases of 3.95%, 76.67%, and 20.00%. Low R/FR also enhanced net photosynthetic rate (Pn), transpiration rate (Tr), and stomatal conductance (Gs), but decreased intercellular CO<sub>2</sub> concentration (Ci) and chlorophyll fluorescence parameters including initial fluorescence (Fo), maximum fluorescence (Fm), maximum photochemical efficiency (Fv/Fm), actual PSII photochemical efficiency (ΦPSII), and photochemical quenching coefficient (qP), while increasing non-photochemical quenching coefficient (qN). Total dry matter accumulation increased under low R/FR, with Pn rising by 37.21% and 39.04% and total dry matter accumulation increasing by 12.35% and 17.36% for ‘Nandou 12’ and ‘Nan 032-4’, respectively. Ci decreased by 9.29% and 11.72% for the two varieties. However, the sensitivity to low R/FR differed between varieties. Under low R/FR, ‘Nandou 12’ demonstrated superior shade tolerance compared with ‘Nan 032-4’, exhibiting lower plant height, internode length, and petiole length, but greater leaf area, stem diameter, light energy conversion efficiency, Pn, Gs, and dry matter accumulation. This study confirms that soybean can perceive shade signals (low R/FR), though sensitivity varies by variety. For intercropping systems, selecting varieties with low sensitivity to shade signals is recommended to improve shade tolerance, reduce lodging risk from shade avoidance responses, and ensure soybean yield.

**Keywords:** Soybean; Shading signal; Ratio of red light to far-red light (R/FR); Photosynthetic characteristics; Chlorophyll fluorescence

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## Introduction

In natural sunlight, the ratio of red light (R) to far-red light (FR) ranges from 1.0 to 1.2. However, beneath plant canopies or when neighboring plants are present, the R/FR ratio drops below 1.0 due to absorption of R by leaf photosynthetic pigments and reflection of FR [1]. Numerous studies have demonstrated that shade signals (low R/FR) or shade stress (low R/FR combined with low photosynthetic photon flux density) alter plant height, stem diameter, root biomass, and shoot biomass [2-4], including responses such as stem thinning, height increase, and enhanced dry matter allocation to stems [5,6]. The sensitivity to these signals varies among species and cultivars [7]. Previous research on crop responses to shade signals and shade stress has extensively examined photosynthetic physiology, endogenous hormone regulation, and gene expression [6,8,9]. Wang et al. [10] reported that photosynthetic rate increases nonlinearly with R/FR ratio, while Zhang et al. [11] found that at an R/FR of 0.6, shade-tolerant soybean varieties maintained higher PSII reaction center activity and primary light conversion efficiency than shade-intolerant varieties. In chrysanthemum, chlorophyll fluorescence parameters Fv/Fm and qP initially increase then decrease with rising R/FR values [12].

As the native home of soybean, China has a long history of soybean production and food applications. Soybean serves as a crucial source of edible oil and protein for both human consumption and animal feed, playing a vital role in national food security. In recent years, maize-soybean strip intercropping technology has rapidly developed in southwestern China, improving resource use efficiency for light, temperature, water, and nutrients while achieving high yields [13]. However, during the co-growth period in relay intercropping systems, shading from tall crops affects soybean growth and yield formation [14-16], with reduced R/FR ratio being an early signal and notable characteristic of shade stress [17]. Few studies have reported the effects of shade signals (reduced R/FR) on soybean seedling growth, photosynthetic characteristics, and chlorophyll fluorescence parameters. Therefore, this study employed pot experiments using far-red LED supplementation to investigate how reduced R/FR affects soybean seedling growth, photosynthetic characteristics, chlorophyll fluorescence parameters, and dry matter accumulation, aiming to elucidate the response mechanism to low R/FR shade signals and provide a foundation for understanding shade tolerance mechanisms in intercropping systems.

## Materials and Methods

**1.1 Experimental Materials** Two soybean materials were used: the shade-tolerant cultivar 'Nandou 12' (a major cultivar for relay intercropping in south-

western China, bred by Nanchong Academy of Agricultural Sciences, Sichuan Province) and the shade-sensitive breeding line ‘Nan 032-4’ (from Nanchong Academy of Agricultural Sciences). Seeds were provided by the Soybean Research Group of Crop Cultivation and Farming Systems at Sichuan Agricultural University.

**1.2 Experimental Design** The experiment was conducted in a phytotron at the Chengdu campus of Sichuan Agricultural University from November to December 2014. A two-factor randomized block design was employed. Factor one was R/FR ratio: CK (normal light) with R/FR of 1.15, and FR (far-red supplemented) with R/FR of 0.35. Factor two was soybean variety: ‘Nandou 12’ and ‘Nan 032-4’. Four treatments with six replicates yielded 24 pots total. Pots measured 15 cm in diameter and 12 cm in height, filled with sandy soil. One seed hole per pot was retained with two plants. R/FR values were measured using a Field Scout® R/FR meter (Spectrum, USA). Photosynthetic photon flux density from growth lamps in the phytotron was  $360 \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ . After the first compound leaf fully expanded, far-red LED lamps ( $\approx 730 \text{ nm}$ ) supplemented far-red light to reduce the R/FR ratio while maintaining essentially unchanged photosynthetically active radiation. The photoperiod was 12 h with daytime temperature at  $25^\circ\text{C}$  and nighttime temperature at  $15^\circ\text{C}$ .

### 1.3 Measurement Parameters

**1.3.1 Morphological Indices** On day 10 of treatment under normal light (R/FR=1.15) and far-red supplemented light (R/FR=0.35), six uniform seedlings per treatment were selected. Plant height, internode length of the third node from bottom, petiole length of the first compound leaf, and length and width of the terminal leaflet were measured with a ruler. Stem diameter at the middle of the third internode was measured with vernier calipers. Leaf area was calculated using the length-width coefficient method, with correction coefficients of 0.67 for ‘Nan 032-4’ and 0.70 for ‘Nandou 12’ [18].

**1.3.2 Photosynthetic Parameters** Concurrent with morphological measurements, a portable photosynthesis system (LI-6400, LI-COR, USA) was used to measure net photosynthetic rate ( $P_n$ ) of the terminal leaflet of the first compound leaf between 15:00-16:00, simultaneously obtaining transpiration rate ( $Tr$ ), stomatal conductance ( $G_s$ ), and intercellular  $\text{CO}_2$  concentration ( $C_i$ ).

**1.3.3 Chlorophyll Fluorescence Parameters** Chlorophyll fluorescence parameters were measured using a CFImager chlorophyll fluorometer (Technologica, UK) on the same leaves and at the same time as photosynthetic measurements. Under light adaptation (14:00-15:00), actual PSII photochemical efficiency ( $\Phi_{\text{PSII}}$ ), photochemical quenching coefficient ( $q_P$ ), and non-photochemical quenching coefficient ( $q_N$ ) were determined. At night (22:00-23:00) after full dark adaptation, initial fluorescence intensity ( $F_0$ ),

maximum fluorescence intensity ( $F_m$ ), and PSII maximum photochemical quantum yield ( $F_v/F_m$ ) were measured.

**1.3.4 Plant Sample Collection and Determination** After 30 days of treatment under normal light ( $R/FR=1.15$ ) and far-red supplemented light ( $R/FR=0.35$ ), plants were separated into roots, stems, and leaves, killed at  $105^\circ\text{C}$ , then dried at  $85^\circ\text{C}$  to constant weight. Organ dry weights were measured using an electronic balance with 0.0001 g precision. Allocation proportion of each organ was calculated as its percentage of total dry weight.

**1.4 Data Processing** Data were organized using Microsoft Excel 2007. SPSS software was used for analysis of variance and LSD significance testing.

## Results

**2.1 Effects of Low R/FR on Soybean Seedling Morphology** As shown in Table 1, both light environment and variety significantly affected soybean seedling morphology. Reduced R/FR increased plant height, petiole length, and internode length. Specifically, 'Nandou 12' showed significant increases of 7.86%, 81.48%, and 26.55% in plant height, petiole length, and internode length, respectively, while 'Nan 032-4' showed increases of 3.95%, 76.67%, and 20.00%. Under both normal and low R/FR light, 'Nandou 12' exhibited morphological advantages over 'Nan 032-4'. Under low R/FR, 'Nandou 12' had significantly greater leaf area and stem diameter (20.40% and 27.12% higher, respectively) but 40.42% shorter internode length compared with 'Nan 032-4'.

**2.2 Effects of Low R/FR on Photosynthesis in Soybean Seedlings** Table 2 shows that low R/FR significantly increased  $P_n$  and decreased  $C_i$  in soybean seedling leaves. Under low R/FR,  $P_n$  increased by 37.21% and 39.04% for 'Nandou 12' and 'Nan 032-4', respectively, while  $C_i$  decreased by 9.29% and 11.72%. The interactive effect of light environment and variety on photosynthetic characteristics was not significant, though genotype had minor effects on  $P_n$ ,  $T_r$ ,  $G_s$ , and  $C_i$  under low R/FR treatment.

**2.3 Effects of Low R/FR on Chlorophyll Fluorescence Characteristics** Although the light environment  $\times$  variety interaction did not significantly affect chlorophyll fluorescence parameters, low R/FR treatment increased  $F_o$  and  $q_N$  while decreasing  $F_m$  and  $q_P$  compared with normal light (Table 3). For 'Nan 032-4',  $F_o$  and  $q_N$  increased by 7.04% and 8.28%, respectively, while  $F_m$  and  $q_P$  decreased by 9.94% and 15.11%, with all differences reaching significance. These parameters were not significantly affected in 'Nandou 12', indicating that low R/FR impaired PSII electron transport more severely in 'Nan 032-4'.

Under normal light, genotype had minimal influence on  $F_o$ ,  $F_m$ ,  $q_P$ , and  $q_N$ . However, varieties responded differently to low R/FR: 'Nandou 12' showed

significantly lower  $F_o$  and  $qN$  (by 6.35% and 7.40%, respectively) but higher  $qP$  (by 12.63%) compared with ‘Nan 032-4’. Low R/FR reduced  $F_v/F_m$ ,  $F_v/F_o$ , and  $\Phi PSII$  in both varieties, with decreases of 1.96% and 4.18% in  $F_v/F_m$  for ‘Nandou 12’ and ‘Nan 032-4’, respectively. While genotype had little effect on  $F_v/F_m$ ,  $F_v/F_o$ , and  $\Phi PSII$  under normal light, under low R/FR, ‘Nandou 12’ exhibited significantly higher  $F_v/F_m$  and  $F_v/F_o$  (by 2.44% and 12.30%, respectively) than ‘Nan 032-4’.

#### 2.4 Effects of Low R/FR on Dry Matter Accumulation and Allocation

Dry matter accumulation is a crucial indicator of organic matter accumulation and nutrient content. Table 4 shows that low R/FR increased total dry matter accumulation and leaf allocation proportion while decreasing root and stem allocation proportions. Compared with normal light, low R/FR increased leaf and total dry matter accumulation by 20.25% and 12.35% for ‘Nandou 12’, respectively, while decreasing root allocation proportion by 9.79%. For ‘Nan 032-4’, leaf and total dry matter accumulation increased by 24.32% and 17.36%, respectively, while root allocation proportion decreased by 8.77%.

Variety comparisons revealed that ‘Nandou 12’ had significantly higher dry matter accumulation than ‘Nan 032-4’ under both light conditions. Under low R/FR, ‘Nandou 12’ showed 33.33% and 13.15% higher stem and total dry matter accumulation, respectively, compared with ‘Nan 032-4’. Under normal light, ‘Nandou 12’ had 38.61%, 6.43%, and 17.57% higher stem, leaf, and total dry matter accumulation, respectively. The light environment  $\times$  variety interaction did not significantly affect dry matter accumulation.

#### Discussion and Conclusion

As a shade signal, low R/FR significantly increases internode length, leaf length, and leaf width while decreasing stem diameter [1,19]. Our results similarly demonstrate that low R/FR increased soybean seedling plant height, leaf area, petiole length, and internode length while inhibiting stem thickening. Casal [17] proposed that phytochromes, particularly phytochrome B, play a crucial role in strongly perceiving low R/FR signals, stimulating transcription of genes related to auxin and gibberellin synthesis and triggering shade avoidance responses. These morphological changes, including increased plant height, petiole length, and internode length, help plants capture more light, as confirmed by Chen et al. [20] who reported that far-red light increased gibberellin content and internode length. However, Gong et al. [21] found that under combined low light intensity and low R/FR, soybean leaf area decreased due to insufficient energy and material accumulation. In contrast, our study indicates that upon perceiving shade signals (low R/FR), soybean actively increases light-receiving area to mitigate shading effects on photosynthesis. Furthermore, under low R/FR, ‘Nandou 12’ showed less pronounced changes in leaf area, stem diameter, plant height, internode length, and petiole length compared with ‘Nan 032-4’, suggesting lower sensitivity to low R/FR signals and better mainte-

nance of desirable plant architecture under shade. This characteristic is crucial for controlling excessive stem elongation and improving lodging resistance in intercropping environments [22,23].

Chlorophyll fluorescence techniques uniquely characterize light energy absorption, transfer, dissipation, and allocation during photosynthesis, with parameters reflecting “intrinsic” properties [24]. Li et al. [25] reported that moderate to heavy shading (combined low R/FR and low photosynthetic photon flux density) reduced Fv/Fm,  $\Phi$ PSII, and qP while increasing Fo and NPQ in soybean seedlings. Our similar results indicate that early shade stress signals also reduce light energy transfer efficiency and PSII reaction center openness, decreasing the proportion of light energy captured by antenna pigments that flows to photochemistry. This affects photosynthetic electron transport rate, causing excess energy accumulation at PSII reaction centers. The increased qN helps dissipate this excess energy, protecting photosynthetic apparatus from damage. However, Zhang et al. [26] found that shading increased Fv/Fm and Fv/Fo in *Ardisia violacea*, as this species is shade-adapted and may experience photoinhibition under full light [27].

Our study further revealed that under low R/FR, ‘Nandou 12’ maintained higher qP, Fv/Fm, and Fv/Fo but lower Fo and qN compared with ‘Nan 032-4’, indicating that ‘Nan 032-4’ was more sensitive to shade signals, exhibiting lower light energy transfer efficiency, greater heat dissipation, and reduced metabolic activity [28]. In contrast, ‘Nandou 12’ showed a more moderate response.

Shading effects on photosynthesis vary with crop variety, growth stage, and shading duration and intensity. Many studies report that shading reduces Pn, Tr, and Gs [29,30]. However, our study found that low R/FR increased Pn, Tr, and Gs while decreasing Ci, consistent with results from Liu et al. [31] on tomato at flowering stage and Tan et al. [32] on soybean seedlings. This may relate to increased photosynthetic pigments that enhance light capture under shaded conditions [33,34], suggesting that when external stress factors (shading) increase but have not yet caused damage, plants respond to early signals by accumulating chlorophyll a, chlorophyll b, and other photosynthetic pigments to improve photosynthetic capacity in anticipation of potential stress. Our results demonstrate that upon perceiving shade signals, soybean increases leaf area, plant height, and petiole length to capture more light energy, enhances photosynthesis to promote dry matter accumulation, and thereby improves shade tolerance. However, the two tested varieties showed different sensitivities, and their molecular mechanisms warrant further investigation.

In conclusion, low R/FR increased soybean seedling plant height, petiole length, and internode length while decreasing stem diameter. It enhanced photosynthesis and dry matter accumulation but reduced photosynthetic electron transport rate, with ‘Nan 032-4’ being more sensitive than ‘Nandou 12’. Soybean can perceive shade signals (low R/FR), but sensitivity varies by variety. For intercropping systems, selecting varieties with low sensitivity to shade signals is recommended to improve shade tolerance and ensure soybean yield.

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