Evaluation of Shade Tolerance in Black Soybean Germplasm at Seedling Stage and Root System Response to Low Light Stress: Postprint

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Abstract

Maize-soybean intercropping is one of the important ecological planting patterns in Southwest China; however, specialized shade-tolerant black soybean germplasm is currently extremely scarce, and the shade tolerance mechanism of black soybean remains unclear, which severely restricts further promotion of this pattern. This study aims to establish a mathematical model for evaluating shade tolerance at the seedling stage of black soybean, screen effective indicators capable of determining shade tolerance in black soybean, and explore differential responses of root systems in black soybean germplasms with different shade tolerance types to low light stress, thereby laying a foundation for the breeding of shade-tolerant black soybean germplasm and the elucidation of shade tolerance mechanisms. The experiment utilized 23 black soybean germplasms as research materials, employing a pot experiment method with two treatments: natural light and shading. At the V3 stage of black soybean plants, morphological indicators including plant height, stem diameter, hypocotyl length, leaf dry weight, stem dry weight, main stem node number, total root length, root surface area, and total root volume, as well as physiological indicators such as photosynthetic parameters and chlorophyll fluorescence parameters were measured. Multivariate statistical methods were employed to establish an evaluation model for shade tolerance at the seedling stage of black soybean, and based on the evaluation results, correlation analysis was conducted on differential responses of root systems in black soybean germplasms with different shade tolerance types to low light stress. A mathematical model for evaluating shade tolerance at the seedling stage of black soybean was established through stepwise regression analysis; and through this model, five identification indicators were screened out: transpiration rate, plant height, leaf dry weight, maximum fluorescence intensity, and initial fluorescence intensity. Comprehensive evaluation of shade tolerance at the seedling stage of black soybean can be achieved by measuring the aforementioned five indicators under shaded conditions. Simultaneously, cluster analysis was performed on the comprehensive evaluation value D for shade tolerance of 23 black soybean germplasms, with results indicating that black soybean germplasms can be divided into three categories: shade-tolerant, moderately shade-tolerant, and shade-sensitive. The root architecture of black soybean germplasms with different shade tolerance types exhibited varying degrees of response to low light stress; root vigor indicators including total root length, root surface area, total root volume, and root dry weight all demonstrated the pattern shade-tolerant > moderately shade-tolerant > shade-sensitive. This suggests that black soybean with greater shade tolerance potential possesses more developed root systems.

Full Text

Evaluation for Shade Tolerance of Black Soybean Germplasms and Their Root Structure Response to Shade Stress at Seedling Stage

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Abstract: Maize-soybean relay strip intercropping systems represent an important ecological planting mode in Southwest China. However, shade-tolerant germplasms of black soybean are scarce and the mechanism of shade tolerance remains unclear, which significantly hinders further promotion of this cropping system. This study aimed to establish a mathematical model for evaluating shade tolerance in black soybean seedlings, identify effective indicators for assessing shade tolerance, and explore differential responses of root systems to low light stress among black soybean varieties with varying shade tolerance levels, thereby laying a foundation for breeding shade-tolerant black soybean germplasms and elucidating the underlying mechanisms. Using 23 black soybean germplasms as experimental materials, a pot culture experiment was conducted with two treatments: natural light and shade. Morphological indicators including plant height, stem diameter, hypocotyl length, leaf dry weight, stem dry weight, main stem node number, total root length, root surface area, and total root volume, along with physiological parameters such as photosynthetic and chlorophyll fluorescence parameters, were measured at the V3 stage (third trifoliolate leaf stage). Multivariate statistical methods were employed to establish an evaluation model for shade tolerance at the seedling stage, and correlation analysis was performed based on the evaluation results to determine differential root responses to shade stress.

Through stepwise regression analysis, a mathematical evaluation model for shade tolerance at the seedling stage was established, identifying five key appraisal indicators: transpiration rate, plant height, leaf dry weight, maximum fluorescence intensity, and initial fluorescence intensity. Measurement of these five indicators under shaded conditions enables comprehensive evaluation of shade tolerance in black soybean seedlings. Cluster analysis of the comprehensive shade tolerance evaluation values (D) for the 23 germplasms revealed three distinct groups: shade-tolerant, moderately shade-tolerant, and shade-sensitive types. Root structural responses to low light stress varied significantly among these groups, with root vigor indicators—including total root length, root surface area, total root volume, and root dry weight—consistently following the pattern: shade-tolerant > moderately shade-tolerant > shade-sensitive. These results demonstrate that shade-tolerant black soybean varieties possess more robust root systems.

Keywords: Black soybean; Seedling stage; Shade tolerance; Multivariate statistical analysis; Root structure

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Introduction

Black soybean, the black-seeded cultivar of *Glycine max* (L.) Merrill, constitutes an important economic crop in China with high medicinal value, representing a typical dual-purpose food and medicinal plant [1-2]. In recent years, maize-soybean relay strip intercropping has been extensively promoted as an efficient ecological planting pattern in Southwest China, emerging as a vital approach to alleviate domestic soybean supply-demand imbalances [2]. However, in this intercropping system, shading from the taller maize crop significantly reduces photosynthetically active radiation and the red/far-red ratio within the soybean canopy, altering the light environment [3]. Under shaded conditions, soybean morphogenesis and assimilate distribution patterns change substantially, resulting in thinner and fewer leaves, reduced leaf area index, decreased leaf dry weight, increased plant height, elevated center of gravity, and heightened lodging risk [4-6]. Wang et al. [7] reported that shading during early growth stages significantly affected main stem morphological characteristics, while late-stage shading primarily impacted pod height and branch number. Song et al. [8] found that intercropping shade reduced photosynthesis, gas exchange, and ultimately yield in soybean. Shading from the taller crop thus constrains soybean yield improvement in intercropping systems, making the breeding of shade-tolerant soybean varieties crucial for enhancing production.

Researchers have employed various methods to evaluate and identify shade tolerance in soybean, aiming to establish simplified assessment models. Chen et al. [9] evaluated shade tolerance using agronomic traits and a comprehensive shade tolerance coefficient method, which was simple but failed to consider differential contributions of individual indicators. Wu et al. [10] applied multivariate statistical methods for comprehensive evaluation, overcoming limitations of information overlap inherent in single-indicator assessments.

As the primary organ for nutrient and water absorption, roots also serve as the main site for synthesis of various hormones, amino acids, and organic acids. Root morphology, physiology, and distribution significantly influence water and nutrient uptake, with robust root systems providing essential support for normal growth and stress resistance [11]. Studies have shown that shade stress not only directly reduces leaf photosynthesis but also indirectly affects underground growth [12]. How soybean roots respond to low light stress, and whether these responses correlate with genetic shade tolerance, remain unanswered questions. Previous research has primarily focused on yellow-seeded soybeans, while specialized black soybean varieties suitable for intercropping are severely lacking, and their shade tolerance mechanisms remain unclear. This study aims to establish a mathematical model for evaluating shade tolerance in black soybean seedlings, identify effective indicators for shade tolerance assessment, and investigate differential root responses to low light stress among varieties with varying shade tolerance, providing a foundation for breeding shade-tolerant black soybean germplasms and elucidating shade tolerance mechanisms.

Materials and Methods

1.1 Experimental Design The experiment was conducted in 2016 at the Chengdu Campus of Sichuan Agricultural University (30°41 2.84 N, 103°51 13.60 E). The 23 tested black soybean germplasms were collected from 2014-2015 in Sichuan, Yunnan, Chongqing, Guizhou, and Gansu provinces, with detailed source information provided in . Pot culture experiments (12 cm × 15 cm pots) were performed using a mixed soil substrate (nutrient soil from Hong Kong Pan’ s Technology Co., Ltd. and natural soil at a 1:2 ratio). Shade conditions were simulated using three layers of two-needle green shade netting installed 3.5 m above ground, with light transmittance measured using a lux meter (Tekman TM830). Treatments began at sowing and continued until the V3 stage, with the control group receiving 100% transmittance and the shade treatment receiving 48.5% transmittance. Each treatment had three replications, with two pots per replication and two plants per pot. All environmental conditions and management practices except light environment were consistent between control and shade treatments, with relevant traits investigated at the V3 stage.

1.2 Measurement Parameters 1.2.1 Photosynthetic Parameters

Using a portable photosynthesis system (LI-6400, LI-COR, USA) with an open gas path, net photosynthetic rate (Pn), intercellular CO concentration (Ci), transpiration rate (Tr), and stomatal conductance (Gs) were measured on the uppermost fully expanded trifoliolate leaves on sunny days (June 28-29, 2016) between 14:00-16:00. Three uniform plants were selected per treatment, with three measurements per leaf.

1.2.2 Chlorophyll Fluorescence Parameters

Chlorophyll fluorescence parameters were measured using a portable fluorometer (PAM-2100, Walz, Germany) at the same developmental stage, time, and leaf positions as photosynthetic measurements. The actual photochemical efficiency of PSII (ΦPSII) was measured under light-adapted conditions (8:00-10:00), while initial fluorescence (Fo), maximum fluorescence (Fm), and maximum photochemical efficiency of PSII (Fv/Fm) were measured under dark-adapted conditions (22:00-23:00) [4-5].

1.2.3 Morphological Indicators

At the end of shade treatment, plant height, stem diameter, hypocotyl length, and main stem node number were measured for five plants per treatment. Root systems were collected, washed clean, scanned using an Epson Expression 10000XL scanner, and analyzed using WinRhizo software to determine root length, surface area, and volume. Roots, stems, and leaves were oven-dried at 105°C for 1 hour, then at 80°C to constant weight to determine leaf dry weight, stem dry weight, and root dry weight.

1.3 Data Processing and Analysis Data were organized and calculated using Microsoft Excel 2013. Principal component analysis, correlation analysis, stepwise regression analysis, and one-way ANOVA were performed using SPSS 22.0 (SPSS, Chicago, IL, USA). Cluster analysis was conducted using Multi Experiment Viewer 4.9. Relative values of individual indicators (RVS), membership function values [(Xj)], weights of comprehensive indicators (Wj), and comprehensive evaluation values (D) under low light stress were calculated according to established formulas.

Results

2.1.1 Relative Values and Variation Analysis of Individual Indicators

Relative values (RVS) of 14 individual indicators were calculated for 23 soybean germplasms. As shown in , stomatal conductance and transpiration rate exhibited the highest coefficients of variation (47.01% and 42.29%, respectively), followed by initial fluorescence yield, net photosynthetic rate, hypocotyl length, stem dry weight, and leaf dry weight (27.77%-30.93%), indicating substantial impacts of low light stress on these parameters. Under shade treatment, initial fluorescence yield, maximum photochemical yield of PSII, intercellular CO concentration, hypocotyl length, and plant height generally increased compared to controls ($RVS > 1$), while stomatal conductance, transpiration rate, net photosynthesis, stem diameter, main stem node number, leaf dry weight, and stem dry weight decreased ($RVS < 1$). Other traits showed germplasm-specific variation. Given the wide variation in RVS both among indicators within the same germplasm and among germplasms for the same indicator, shade tolerance cannot be reliably assessed using single-indicator RVS alone, necessitating multivariate statistical analysis to address information overlap.

2.1.2 Principal Component and Membership Function Analysis Principal component analysis of 14 individual indicators extracted five principal components based on eigenvalues > 1, transforming the 14 indicators into five comprehensive indicators (X1–X5). Eigenvectors and contribution rates are presented in . The first five principal components explained 79.53% of total variance, representing most original information. The first component explained 25.48% of variance, representing 3.57 original indicators including stem diameter, main stem node number, leaf dry weight, and stem dry weight, primarily reflecting aboveground dry matter accumulation. The second component explained 20.05% of variance, representing 2.81 original indicators including stomatal conductance, intercellular CO concentration, and transpiration rate, reflecting photosynthetic characteristics. The third component explained 15.91% of variance, representing 2.23 original indicators including actual photochemical yield of PSII, maximum dark-adapted fluorescence yield, and maximum photochemical yield, reflecting light utilization capacity. The fourth component explained 10.71% of variance, representing 1.5 original indicators including initial fluorescence yield and net photosynthetic rate, reflecting light energy conversion capacity. The fifth component explained 7.38% of variance, representing 1.03 original indicators, with plant height and hypocotyl length as major contributors, reflecting morphological characteristics.

Membership function analysis of comprehensive indicators yielded membership values (). For individual comprehensive indicators such as X1, CQ12 showed the highest membership value (1.00) while 13WHJ showed the lowest (0.00). Since the first principal component primarily reflects aboveground growth, CQ12 exhibited the greatest aboveground dry matter accumulation while 13WHJ accumulated the least. Similarly, for X2 (reflecting photosynthetic characteristics), E200 demonstrated the strongest photosynthetic capacity while E1 showed the weakest. For light utilization capacity (X3), QWT43 and E21-2 were strongest while E314 was weakest.

2.1.3 Comprehensive Shade Tolerance Evaluation Weights and comprehensive shade tolerance evaluation values (D) were calculated, with germplasms ranked by shade tolerance capacity. CQ12 showed the strongest shade tolerance while A3 was weakest. Euclidean distance-based cluster analysis of D values for 23 germplasms ([Figure 1: see original paper]) revealed three groups at a distance of 0.13. Group I (A3, E1, MY10, and E314) exhibited poor overall performance and was classified as shade-sensitive. Group II (12-WHJ, QWT10, 13WHJ, G3-1, C103, and 39) showed moderate performance and was classified as moderately shade-tolerant. Group III (E21, QWT49, QWT43, QWT3, E202-1, CQ12, NH20, E200, and E333) demonstrated superior performance and was classified as shade-tolerant.

2.1.4 Regression Model Establishment and Indicator Screening To analyze relationships between individual indicators and shade tolerance and identify key appraisal indicators, regression analysis was performed using 14 individual indicators as independent variables and D values as dependent variables. Direct regression analysis may cause multicollinearity issues, as stomatal conductance affects photosynthesis through transpiration rate, thereby influencing shade tolerance. Therefore, stepwise regression was employed to eliminate non-significant indicators and obtain an optimal model. The analysis identified five evaluation indicators significantly correlated with shade tolerance: transpiration rate, plant height, leaf dry weight, maximum fluorescence yield, and initial fluorescence yield.

2.2.1 Correlation between Root Characteristics and Shade Tolerance Correlation analysis between root indicators and shade tolerance appraisal indicators () revealed that root surface area was extremely significantly positively correlated with total root length ($P < 0.01$), total root volume was significantly positively correlated with total root length and root surface area ($P < 0.05$), and transpiration rate was extremely significantly positively correlated with total root length and root surface area ($P < 0.01$). These results demonstrate that root structure is associated with shade tolerance in black soybean, with transpiration rate showing the strongest correlation with root parameters among aboveground shade tolerance indicators.

2.2.2 Root Morphological Characteristics Under Low Light Stress Phenotypically, low light stress significantly inhibited primary and lateral root growth, reducing root branching number. Compared to controls, shaded conditions increased lateral root thickness, with greater impacts on shade-sensitive than shade-tolerant germplasms ([Figure 2: see original paper]). Total root length, root surface area, total root volume, and root dry weight decreased extremely significantly under shade stress ($P < 0.01$), with significant differences among shade tolerance groups ([Figure 3: see original paper]). Shade-tolerant, moderately tolerant, and sensitive germplasms showed root length reductions of 58.30%, 65.83%, and 71.73%, respectively; root surface area reductions of 32.55%, 37.89%, and 51.87%; root volume reductions of 71.66%, 72.88%, and 75.25%; and root dry weight reductions of 86.64%, 88.59%, and 89.68%. These results indicate that low light stress severely inhibits root elongation, affects dry matter accumulation, reduces soil contact area, and decreases nutrient absorption capacity, with shade-tolerant germplasms experiencing smaller impacts.

Discussion

3.1 Shade Tolerance Evaluation and Indicator Screening The maize-soybean relay strip intercropping system has developed rapidly in Southwest China, and breeding shade-tolerant soybean germplasms is crucial for improving intercropped soybean yields. Single-indicator-based evaluation may provide biased assessments due to correlations among indicators [14-15]. Previous studies using comprehensive shade tolerance coefficients [9,16] were simple but neglected differential indicator contributions. To address these limitations, fuzzy mathematics methods have been introduced to transform multiple indicators into fewer independent ones, with membership function analysis providing simple and accurate comprehensive evaluation [10,17]. This approach informed our methodology.

We selected 14 easily measured indicators that directly reflect soybean growth status and applied multivariate statistical analysis to comprehensively evaluate shade tolerance in black soybean seedlings. Fourteen indicators were transformed into five relatively independent ones, from which comprehensive evaluation values were obtained via membership functions. Stepwise regression identified five key appraisal indicators: transpiration rate, maximum dark-adapted fluorescence, initial fluorescence yield, leaf dry weight, and plant height. Light is essential for plant growth, and numerous studies have shown that shading reduces photosynthetic rate, stomatal conductance, and transpiration rate [18-20]. Transpiration rate rather than net photosynthetic rate was selected, likely because low light stress reduces root number, directly affecting water absorption and leaf stomatal aperture, with transpiration rate responding more sensitively to stomatal conductance than photosynthesis [21-22]. The remaining indicators reflect light energy absorption and transfer [23-24], with leaf dry weight directly indicating assimilatory capacity under shaded conditions.

3.2 Response of Different Shade-Tolerant Black Soybean Roots to Low Light Stress Shade stress significantly altered root morphology, inhibiting root growth, likely through effects on endogenous hormones and assimilate distribution. Under shade, root-synthesized auxin decreases while cytokinin increases [25-26], with most auxin translocating to stems [27], resulting in shorter roots but increased lateral root differentiation. Reduced photosynthetically active radiation decreases photosynthesis, reducing aboveground dry matter production. To capture more light, assimilates are preferentially allocated to stems rather than roots, inhibiting root elongation and reducing surface area and volume, thereby decreasing active absorption capacity [12]. Many studies confirm that low light stress inhibits root growth [11-12,21]. Our findings reveal distinct responses among shade tolerance groups, with shade-tolerant germplasms showing smaller reductions in total root length, surface area, volume, and dry weight compared to shade-sensitive types. Shade-tolerant germplasms also developed thicker roots with more lateral branches under shade, possibly as an adaptive strategy to increase root surface area for adequate water and nutrient uptake under stress [28].

Conclusion

Multivariate statistical analysis classified 23 black soybean germplasms into shade-tolerant, moderately shade-tolerant, and shade-sensitive groups. Stepwise regression established a mathematical evaluation model for seedling shade tolerance, identifying transpiration rate, plant height, leaf dry weight, maximum fluorescence intensity, and initial fluorescence intensity as key appraisal indicators. Measurement of these indicators under controlled conditions enables comprehensive evaluation of black soybean shade tolerance at the seedling stage. Shade stress inhibited root growth, reducing root length, surface area, and volume, with responses varying significantly among shade tolerance groups. Shade-tolerant black soybean germplasms possessed more robust root systems that were less affected by low light stress compared to shade-sensitive types.

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