


Article

High Density and Uniform Plant Distribution Improve Soybean Yield by Regulating Population Uniformity and Canopy Light Interception

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Abstract: Optimizing the spatial distribution of plants under normal conditions of water and fertilizer is widely used by farmers to improve soybean yield. However, the relationship between soybean yield and spatial plant distribution in the field has not been well studied. This study examined the effect of planting density and plant distribution pattern on soybean plant growth, yield components, canopy light interception, and dry matter accumulation. We also analyzed the relationship between photosynthetic rate, dry matter accumulation, and yield under different planting densities and plant distribution. A two year field experiment was conducted during the 2018 and 2019 soybean planting seasons. Two planting densities (1.8×10^5 and 2.7×10^5 plants ha^{-1}) and two plant distribution patterns (uniform and non-uniform plant spacing) were tested. Higher planting density significantly increased the canopy light interception and dry matter accumulation during soybean growth, leading to increased soybean productivity. The seed yield of soybean under higher planting density was 22.8% higher than under normal planting density. Soybean planted under uniform spacing significantly reduced the differences plant-to-plant. Uniform plant spacing significantly increased the canopy light interception and dry matter accumulation of the soybean population. In addition, the coefficient of variation of seed weight per plant between individual plants under uniform plant distribution decreased by 71.5% compared with non-uniform plant distribution. Furthermore, uniform plant distribution increased soybean seed yield by 9.5% over non-uniform plant distribution. This study demonstrates that increasing planting density under uniform plant distribution can be useful to obtain higher seed yield without increasing other farm inputs.

Keywords: soybean; high planting density; uniform plant distribution; seed yield



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1. Introduction

Soybean plays a significant role in global food security by providing plant-based protein, vegetable oil, and animal feed [1]. The global consumption of soybean is increasing yearly due to the increasing demand for meat, eggs, and milk [2]. At present, China contributes to a third of total soybean production worldwide, with domestic consumption exceeding 100 million tons per year (<http://www.stats.gov.cn/> 10 December 2020). However, annual soybean production in China is less than 20 million tons, indicating that China imports more than 80 percent of its soybean [3]. The average soybean yield in China is 1980 kg ha^{-1} , which is 60% lower than in the US. Such low production restricts the development of the soybean industry in China [4]. Thus, improving soybean yield and production is essential for China's economic development.

Soybean yield in various countries, including China, has improved in recent years mainly because of genetic improvement, increased inputs (e.g., irrigation and fertilizer), and better field management practices, such as the optimization of planting density and

tillage methods [5–9]. Increasing the planting density of soybeans can remarkably improve light interception and canopy photosynthesis, resulting in a significant increase in total dry matter accumulation and seed yield [9–11]. In the United States, a soybean record yield of 10,414 kg ha⁻¹ was recorded in 2007, with a planting density of 520,000 plants ha⁻¹ in Missouri by Kip Cullers [12]. In China, a soybean yield record of 6803 kg ha⁻¹ was obtained in Xinjiang Province in 2020, with a planting density of 300,000 plants ha⁻¹ [13]. Suhre et al. [14] used 116 soybean cultivars released over the last 80 years to investigate the relationship between the genetic gain of soybean yield and planting density. According to their results, higher seed yield was positively correlated with higher plant populations. Xu et al. [9] showed that the soybean yield could increase significantly by 16.2%, 31.4%, 41.4% and 46.7% for every increase in planting density of 45,000 plants ha⁻¹, within the range of 135,000 to 315,000 plants ha⁻¹. These studies collectively show that higher planting density improves seed yield.

However, high planting density or dense planting alone does not necessarily lead to higher grain yield for soybean or other crops [9,15,16]. Benjamin [17] found that uneven distribution of individual plants in a specific planting density can affect plant growth, leading to yield losses at the crop canopy level. In addition, planting quality (seed depth and distance), soil compaction and crusts, and seed vigor all affect seed emergence and can lead to uneven distribution plant-to-plant [18–20]. This uneven distribution causes local crowding or a lack of seedlings in crop population in the field and can cause a significant decrease in yield [21–23]. The uneven plant distribution can also cause differences in the light environment within the plant population, affecting the development of soybean plants. Moreover, crowding planting can decrease the leaf thickness and photosynthetic rate of soybean due to reduced light intensity in the population, resulting in poor yield or even failure of harvest [24–26]. Strong light radiation, which mainly occurs in the sparse section of soybean fields, has been shown to promote the growth of axillary buds, leading to numerous branches and thus enhancing the production capacity of a single plant [9]. Although soybean plants have a strong branching compensation ability for seedling loss, soil waste and light leakage loss occur when the distance between individual soybean plants is too large, leading to lower yield [23,27].

Several lines of evidence regarding spatial plant distribution indicate that the consistency and uniformity of canopy populations can reduce competition among plants in a specific population and ensure efficient use of light energy and nutrient resources [25,28]. Soybeans exhibit a strong self-compensation ability, especially when the number of seedlings is insufficient, and can increase branching to improve yield [9,29]. The main objective of crop production is to obtain the maximum production benefit, that is, to obtain high yield as far as possible under constant input. At present, it is not clear whether the yield of sparsely planted soybean can compensate for the yield loss of soybean under crowding and seedling deficient conditions. In addition, the light energy utilization of the canopy and yield levels of a soybean population under non-uniform conditions are still unclear. In this study, two plant distribution patterns were examined under normal and high planting density conditions. This study aimed to (1) examine the effect of planting density and plant distribution pattern on soybean growth, yield components, canopy light interception, and dry matter accumulation and (2) analyze the relationship between photosynthetic rate, dry matter accumulation, and yield under different planting conditions.

2. Materials and Methods

2.1. Site Description

Field experiments were conducted from 2018 to 2019 at the Xinxiang Experimental Station (35°09' N, 113°48' E; altitude: 79 m) of the Institute of Crop Sciences, Chinese Academy of Agricultural Sciences. The site exhibits a warm temperate continental monsoon climate with an annual average temperature of 14.1 °C. The annual sunshine is more than 2407.7 h, and the number of frost-free days is 200.5 d. The average annual precipitation is 548 mm, with nearly 70–80% occurring in summer. The soil at Xinxiang is sandy loam (U.S. classification system: TypicPaleustalfs). Before the experiment, the organic matter, available nitrogen (N), available phosphorous (P), and available potassium (K) in the upper 0.4 m of soil were 12.9 g kg⁻¹, 63.8 mg kg⁻¹, 15.9 mg kg⁻¹, and 112.1 mg kg⁻¹, respectively. The monthly air temperature and rainfall during the soybean growing season are shown in Figure 1.

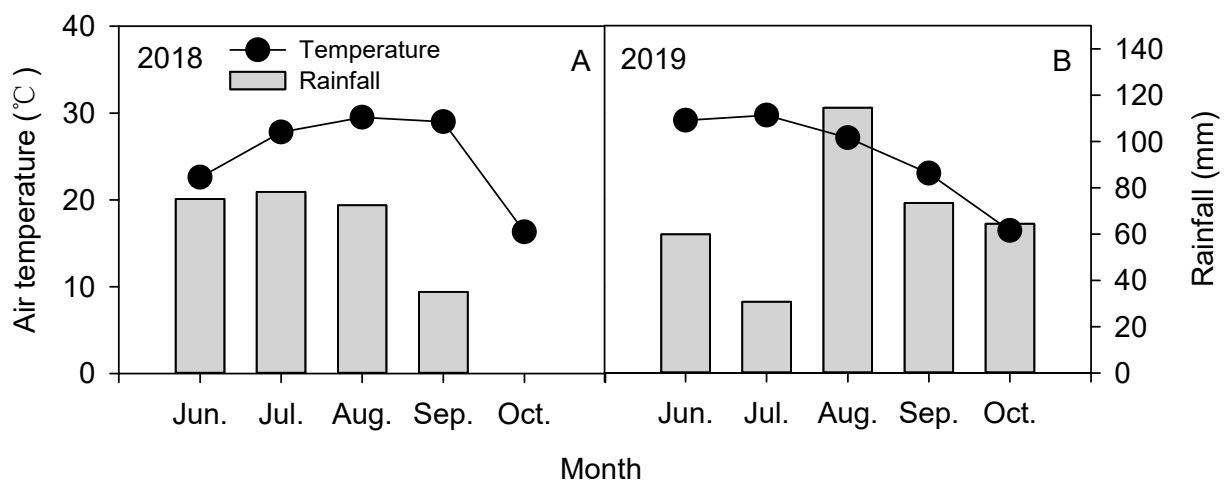


Figure 1. Mean monthly air temperature and rainfall during the 2018 (A) and 2019 (B) growing seasons.

2.2. Experimental Design

The experimental design was a split plot with four replicates. Two planting density treatments were applied as the main plots, and two plant distribution patterns were designated as sub-plots. The main plot size was 20 m × 10 m, while the sub-plot size was 10 m × 10 m (Figure S1). A subfinite growth habit soybean cultivar ZZXA12938 (MG 3.9) was used in this study. The soybean was planted at two planting densities (1.8×10^5 and 2.7×10^5 plants ha⁻¹), with an equal row spacing of 0.4 m. Under a uniform plant distribution pattern, the soybean plants in each row were equally spaced, which were 13.9 and 9.3 cm in 1.8×10^5 and 2.7×10^5 plants ha⁻¹ planting density, respectively. Under a non-uniform plant distribution pattern, the soybean plants in each row were not equally spaced and varied from one centimeter to twenty-seven centimeters in the two planting densities. The detailed planting information is shown in Figure 2. Soybean was seeded on 10 June 2018 and on 15 June 2019. Each plot received 75 kg N ha⁻¹, 100 kg P₂O₅ ha⁻¹, and 75 kg K₂O ha⁻¹ before sowing. No topdressing was added during growth. Each plot was irrigated with 60 mm of water immediately after sowing, and seeds were harvested on 6 October 2018 and 12 October 2019.

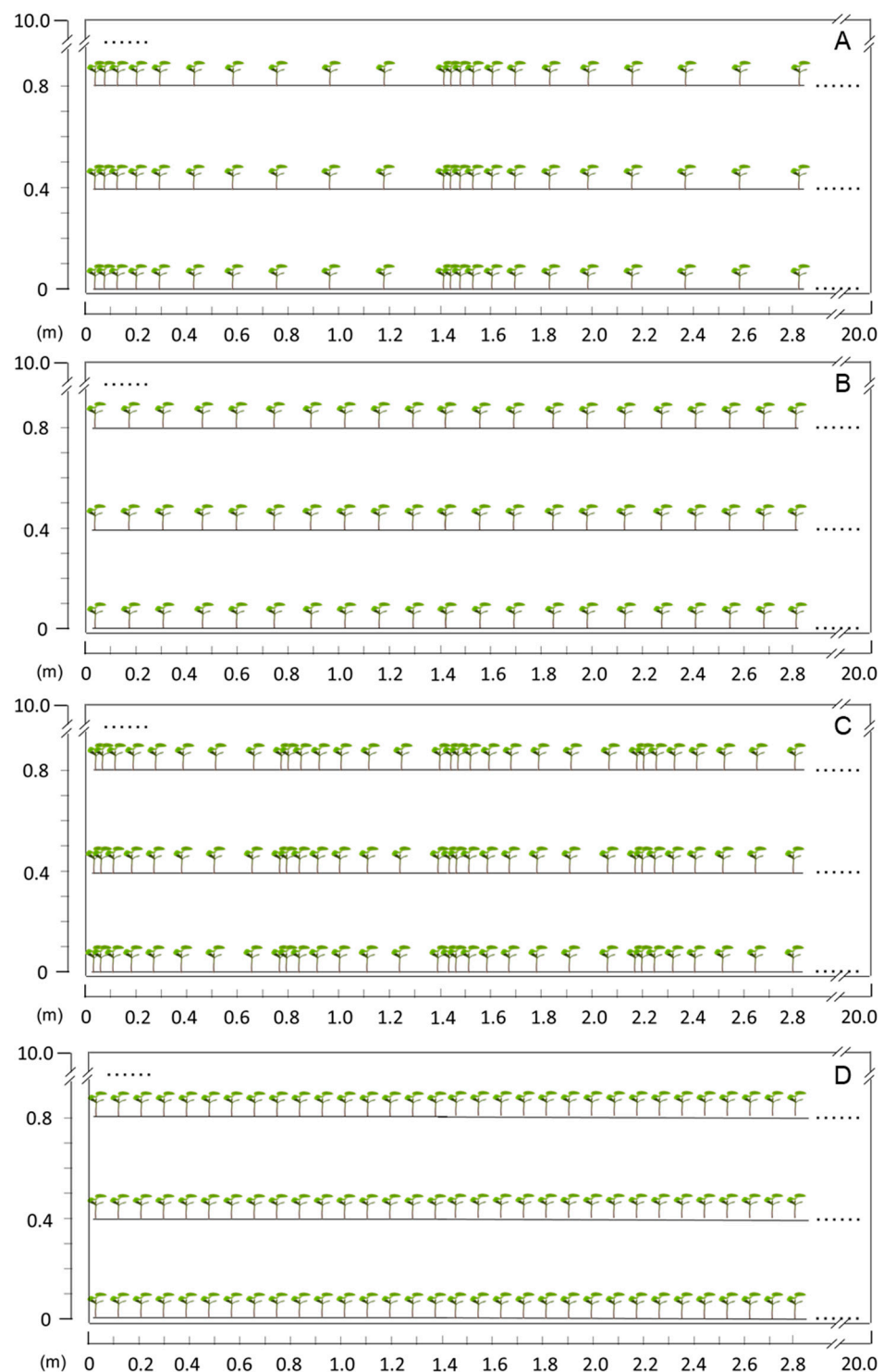


Figure 2. Soybean plant distribution patterns. (A,B) Non-uniform and uniform styles, respectively, under normal planting density (1.8×10^5 plants ha^{-1}). (C,D) Non-uniform and uniform styles, respectively, under high planting density (2.7×10^5 plants ha^{-1}).

2.3. Sampling and Measurements

2.3.1. Dry Matter Accumulation

A 1.4 m length in the plant row (including 10–11 and 16–17 soybean plants in 1.8×10^5 and 2.7×10^5 plants ha^{-1} treatments, respectively) was randomly selected from the center of each plot during the V3, R1, R3, R5, and R7 stages, according to the method described

by Fehr et al. [30], from which the aboveground plant parts were sampled. Samples were oven-dried at 80 °C to a constant weight and weighed to record dry matter accumulation (kg ha^{-1}).

2.3.2. Photosynthetic Rate (P_n)

A 1.4 m length in the plant row (including 10–11 and 16–17 soybean plants in 1.8×10^5 and 2.7×10^5 plants ha^{-1} treatments, respectively) was randomly selected from the center of each plot at the R5 stage. The P_n of the functional leaf of each plant was measured using a portable photosynthesis measurement instrument (LI-6400, LI-COR Inc., Lincoln, NE, USA) from 10:00–12:00 on a clear day. The chamber was equipped with a red/blue LED light source. The photosynthetically active radiation (PAR) was set at $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$. The measurement was conducted with an open system.

2.3.3. Light Interception

The light radiation in the upper and bottom portions of the soybean canopy was measured using a plant canopy analyzer (AccuPAR-LP-80, METER Group Inc., Pullman, WA, USA) on a sunny day from 10:00 to 11:30 at the R5 stage. The measurement was conducted every 20 cm, perpendicular to row direction. The measured length of each row was 1.4 m, including five rows. The canopy light interception rate was calculated in accordance with the following formula, described by Purcell et al. [11]:

$$\text{Canopy light interception rate (\%)} = \frac{\text{Light radiation in upper} - \text{Light radiation in bottom}}{\text{Light radiation in upper}} \times 100$$

2.3.4. Plant Height and Branch

A length of 1.4 m in the plant row (including 10–11 and 16–17 soybean plants in 1.8×10^5 and 2.7×10^5 plants ha^{-1} treatments, respectively) was randomly selected from the center of each plot at the R7 stage. The plant height (cm) and branch number of the soybean plants in the sample area were measured according to the method described by Xu et al. [9].

2.3.5. Yield and Yield Components

At harvest, soybean seed yield (kg ha^{-1} , determined after drying to 13.5% water content) was measured from a randomly selected 2.4 m^2 area in each plot according to the method described by Xu et al. [9]. The number of harvested plants, pods per plant, seeds per plant, seed weight per plant, seed No. per area, and 100-seed weight were also determined.

2.3.6. Statistical Analyses

Univariate analysis of variance (ANOVA) was used to analyze the effects of planting density and plant distribution pattern on the measured parameters (including plant height, branch number, P_n , dry matter accumulation, yield, and yield components). Before ANOVA, we conducted a normal distribution test and variance homogeneity test on the data of each indicator, and the results showed that the p values were both greater than 0.05, indicating that the data was reliable. After verifying the homogeneity of error variances, all the data across planting densities, the plant distribution pattern, and the growing season were pooled for use in the ANOVA according to methods as described in previous studies [31]. A violin plot was employed to analyze plant height, branch number, P_n , pods, seeds per plant, and seed weight per plant. The black line in the violin box plot represents the median. The box in the center represents the interquartile range. The thin black line represents the rest of the distribution, except for points that are determined to be “outliers” using a method that is a function of the interquartile range. On each side of the box plot is a kernel density estimation to show the distribution shape of the data. Wider sections of the violin plot represent a higher probability that members of the population will take on the given value, and the skinnier sections represent a lower probability. ANOVA was

performed using SPSS 17.0 (SPSS Inc., Chicago, IL, USA), whereas a violin plot was drawn using R 3.53. For ANOVA, statistical significance was determined at $p < 0.05\%$ according to the least significance difference (LSD) test.

3. Results

3.1. Effect of Plant Distribution on Yield and Yield Components of Soybean under Different Planting Densities

Planting density and plant distribution had significant effects on seed yield, seed No. per area, and the harvest density of soybean. Growing season and planting density had significant effects on the hundred-seed weight of soybean. In addition, growing season also significantly affected the seed No. per area of soybean (Table 1).

Notably, close planting significantly increased soybean yield. The average yield under higher planting density ($4560.4 \text{ kg ha}^{-1}$) was 22.8% higher than under normal planting density. The higher yield can be attributed to the higher harvest density and seed No. per area. Furthermore, the harvest density ($25.71 \times 10^4 \text{ p ha}^{-1}$) and seed No. per area ($3207.5 \text{ seed m}^{-2}$) under high planting density were higher by 46.7% and 24.3%, respectively, than under normal planting density.

Uniform plant spacing increased the soybean yield significantly. The average yield under uniform plant spacing ($4324.6 \text{ kg ha}^{-1}$) was 9.5% higher than under non-uniform plant spacing. The harvest density ($22.33 \times 10^4 \text{ p ha}^{-1}$) and seed No. per area ($3042.5 \text{ seed m}^{-2}$) significantly increased, by 6.8% and 10.8%, respectively, under uniform plant spacing over non-uniform plant spacing.

3.2. The ANOVA of Phenotypic Index of Soybean under Different Planting Densities

Planting density and plant distribution had significant effects on plant height, branch number, dry matter accumulation, canopy light interception rate, photosynthetic rate, and seed weight per plant of soybean (Table 2). In addition, the interaction of plant distribution and year significantly affected the dry matter accumulation. The interaction of planting density and plant distribution significantly affected the canopy light interception rate and photosynthetic rate.

Table 1. Effect of plant distribution on yield and yield components of soybean under different planting densities.

Sources of Variances		Effective Plant (10 ⁴ p ha ⁻¹)	Seed No. per Area (/m ⁻²)	Hundred-Seed Weight (g)	Yield (kg ha ⁻¹)
Year	2018	21.68	2666.7	15.78	4081.1
	2019	21.57	3121.7	16.49	4192.5
Planting density	Np	17.53	2581.2	16.37	3713.1
	Hp	25.71	3207.5	15.89	4560.4
Plant distribution	Non-uniform	20.91	2747.0	16.14	3948.8
	Uniform	22.33	3042.5	16.12	4324.6

Analysis of Variance												
Sources of Variances	Effective Plant			Seed No. per			Hundred-Seed			Yield		
	MS	df	F	MS	df	F	MS	df	F	MS	df	F
Year	0.094	1	1.476 ^{NS}	1,656,204.39	1	254.414 ^{***}	4.013	1	359.921 ^{***}	99,404.63	1	6.291 ^{NS}
Residual error I	0.064	3		6509.87	3		0.011	3		15,802.03	3	
Planting density	534.645	1	6569.017 ^{***}	3,135,103.43	1	339.914 ^{***}	1.900	1	194.534 ^{***}	5,743,874.16	1	412.809 ^{***}
Residual error II	0.081	6		9223.24	6		0.010	6		13,914.12	6	
Plant distribution	16.245	1	264.624 ^{***}	702,836.44	1	349.496 ^{***}	0.001	1	0.028 ^{NS}	1,131,006.09	1	135.933 ^{***}
Residual error III	0.061	12		2011.00	12		0.049	12		8320.30	12	
Year × Planting density	0.014	1	0.071 ^{NS}	374,230.85	1	40.575 ^{***}	0.378	1	38.698 ^{***}	644,642.02	1	46.330 ^{***}
Year × Plant distribution	0.014	1	0.226 ^{NS}	4620.58	1	2.978 ^{NS}	0.086	1	1.732 ^{NS}	833.14	1	0.100 ^{NS}
Planting density × Plant distribution	3.125	1	50.905 ^{***}	16,895.38	1	8.402 [*]	0.004	1	0.083 ^{NS}	25,509.29	1	3.066 ^{NS}
Year × Planting density × Plant distribution	0.067	1	1.095 ^{NS}	24.08	1	0.012 ^{NS}	0.048	1	0.969 ^{NS}	68.24	1	0.008 ^{NS}

* and *** indicate significance at the 0.05 and 0.001 probability levels, respectively. MS, mean square. NS, not significant.

Table 2. The ANOVA of plant height, branch number, dry matter accumulation, canopy light interception rate, photosynthetic rate, and seed weight per plant for soybean under different planting densities.

Sources of Variances	Plant Height			Branch Number			Dry Matter Accumulation			Canopy Light Interception Rate			Photosynthetic Rate			Seed Weight per Plant		
	MS	df	F	MS	df	F	MS	df	F	MS	df	F	MS	df	F	MS	df	F
Year	165.763	1	0.289 ^{NS}	2.836	1	1.002 ^{NS}	45,607.235	1	0.244 ^{NS}	-	-	-	75.543	1	1.725 ^{NS}	47.263	1	0.546 ^{NS}
Residual error I	573.221	53		2.831	53		187,093.817	3		-	-	-	43.783	53		86.543	44	
Planting density	179,414.108	1	75.253 ^{***}	7.002	1	1.282 ^{NS}	5,852,634.147	1	386.414 ^{***}	8.703	1	363.984 ^{***}	265.158	1	1.318 ^{NS}	221.527	1	1.397 ^{NS}
Residual error II	2384.144	106		5.463	106		15,146.033	6		0.006	3		201.193	106		158.502	88	
Plant distribution	3693.690	1	19.495 ^{***}	3.891	1	2.315 [*]	15,485,470.042	1	303.928 ^{***}	1.337	1	130.381 ^{***}	1354.156	1	79.786 ^{***}	528.529	1	17.713 ^{***}
Residual error III	189.465	212		1.681	212		50,951.110	12		0.010	6		16.972	212		29.838	176	
Year × Planting density	2548.196	1	1.068 ^{NS}	0.669	1	0.123 ^{NS}	468,985.567	1	30.964 ^{**}	-	-	-	35.851	1	0.178 ^{NS}	3.136	1	0.020 ^{NS}
Year × Plant distribution	134.000	1	0.707 ^{NS}	0.188	1	0.112 ^{NS}	1,209,921.322	1	23.746 ^{**}	-	-	-	14.246	1	0.839 ^{NS}	42.573	1	1.427 ^{NS}
Planting density × Plant distribution	524.482	1	2.768 ^{NS}	0.113	1	0.068 ^{NS}	124,266.055	1	2.439 ^{NS}	0.439	1	42.804 ^{***}	2.217	1	0.131 [*]	11.607	1	0.389 ^{NS}
Year × Planting density × Plant distribution	146.767	1	0.775 ^{NS}	0.021	1	0.012 ^{NS}	411,254.445	1	8.072 [*]	-	-	-	0.008	1	0.001 ^{NS}	6.572	1	0.220 ^{NS}

*, ** and *** indicate significance at the 0.05, 0.01 and 0.001 probability levels, respectively. MS, mean square. NS, not significant.

3.3. Effects of Plant Distribution on Plant Productivity of Soybean under Different Planting Densities

Uniform plant spacing with normal planting density had the highest pods per plant (Np-U, 73.7), followed by non-uniform plant spacing with normal planting density (Np-Nu, 66.7). On the other hand, uniform plant spacing with high planting density (Hp-U, 52.0) and non-uniform plant spacing with high planting density (Hp-Nu, 46.4; Figure 3A,B) had the least pods per plant. Notably, close planting density decreased the number of pods per plant. The average pods per plant (49.2) under high planting density was 29.9% lower than under normal planting density. Uniform plant spacing significantly increased the number of pods per plant by 11.1% compared with non-uniform plant spacing. However, non-uniform plant spacing increased the coefficient of variation of pods per plant between individual soybean plants by 32.4% compared to uniform plant spacing.

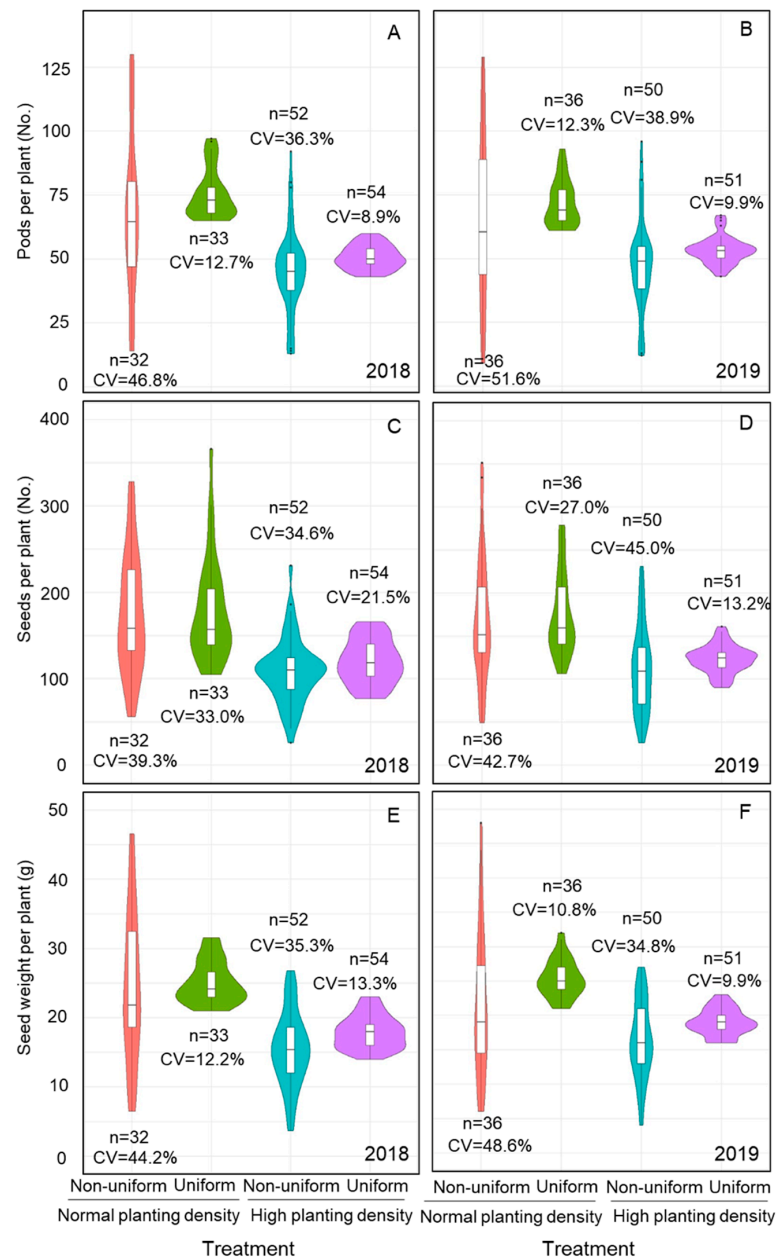


Figure 3. Effects of plant distribution on plant productivity of soybean under different planting densities. CV, coefficient of variation. (A,B) The pods per plant in the 2018 and 2019 growing seasons, respectively. (C,D) The seeds per plant in the 2018 and 2019 growing seasons, respectively. (E,F) The seed weight per plant in the 2018 and 2019 growing seasons, respectively.

The number of seeds per plant was consistent with the number of pods per plant under various conditions (Figure 3C,D). The highest number of seeds per plant was in Np-U (176.2), followed by Np-Nu (171.9) and Hp-U (121.4), whereas Hp-Nu (110.2) had the least. High planting density reduced the average seed number per plant by 33.5% compared to normal planting density. Meanwhile, uniform treatments increased the average seed number per plant by 5.5% compared with non-uniform treatments. Moreover, the coefficient of variation of seeds per plant between individual soybean plants was higher by 23.7% under non-uniform plant spacing than in uniform plant spacing.

The seed weight per plant was highest in Np-U (25.2 g), followed by Np-Nu (23.0 g), Hp-U (18.5 g), and Hp-Nu (15.9 g; Figure 3E,F). High planting density reduced the average seed weight per plant by 28.6% compared to normal planting density. Meanwhile, uniform treatments increased the average seed weight per plant by 12.4% compared to non-uniform treatments. In addition, non-uniform plant spacing increased the coefficient of variation of seed weight per plant between individual soybean plants by 29.1% compared to uniform plant spacing.

3.4. Effect of Plant Distribution on Soybean Plant Height under Different Planting Densities

The order of soybean plant height from high to low among the four treatments was as follows: Hp-U (112.1 cm), Hp-Nu (106.9 cm), Np-U (103.3 cm), and Np-Nu (99.1 cm; Figure 4). High planting density increased soybean plant height by 8.2% compared to normal planting density. In addition, the coefficient of variation of plant height between individual soybean plants increased by 6.6% under non-uniform plant spacing compared to uniform plant spacing.

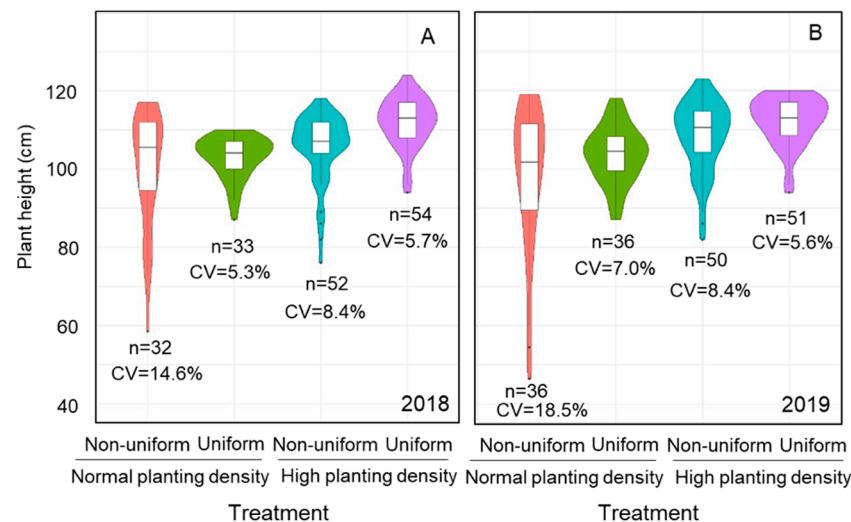


Figure 4. Effect of plant distribution on soybean plant height during the 2018 (A) and 2019 (B) growing seasons under different planting densities. CV, coefficient of variation.

3.5. Branch Number

The order of soybean branch number from high to low among the four treatments was as follows: Np-Nu (3.7), Np-U (3.3), Hp-Nu (2.1), and Hp-U (1.8; Figure 5). High planting density decreased the soybean branch number by 42.9% compared to normal planting density. Meanwhile, the branch number under uniform treatments was 10.2% lower than in non-uniform treatments. Furthermore, the coefficient of variation of branch number between individual soybean plants increased by 36.3% under non-uniform plant spacing compared to uniform plant spacing.

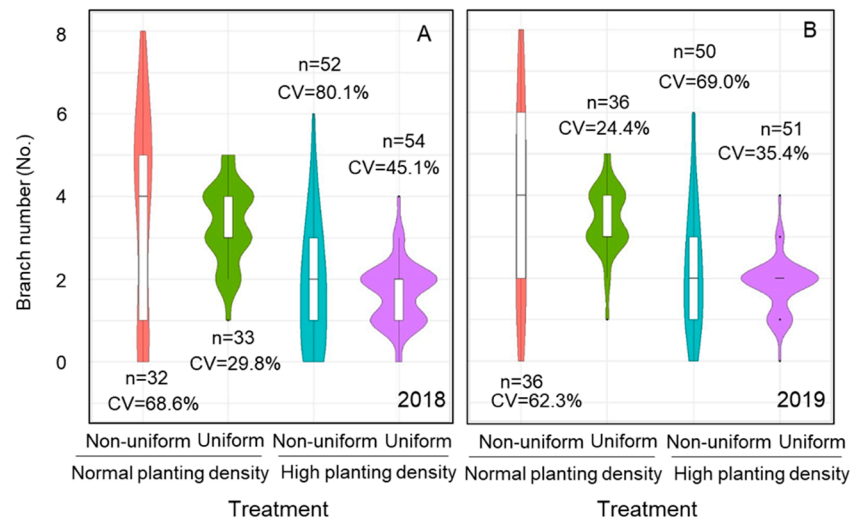


Figure 5. Effect of plant distribution on soybean branch number during the 2018 (A) and 2019 (B) growing seasons under different planting densities. CV, coefficient of variation.

3.6. Effect of Plant Distribution on Dry Matter Accumulation in Soybean under Different Planting Densities

The dry matter accumulation increased gradually after the V3 stage (Figure 6). Notably, close planting was beneficial to dry matter accumulation in soybean. Specifically, soybean dry matter at the R5 and R7 stages increased by 16.3% and 14.6%, respectively, under high planting density over normal planting density. Furthermore, uniform plant spacing increased the soybean dry matter at the R5 and R7 stages by 5.7% and 8.6%, respectively, compared to non-uniform plant spacing. Uniform plant spacing under the high planting density increased the soybean dry matter at the R5 and R7 stages by 6.1% and 9.4%, respectively, compared with non-uniform spacing. In comparison, uniform plant spacing under the normal planting density increased soybean dry matter at the R5 and R7 stages by 5.4% and 7.9% compared with non-uniform spacing. These results show that uniform plant distribution under high planting density should be applied to improve soybean yield.

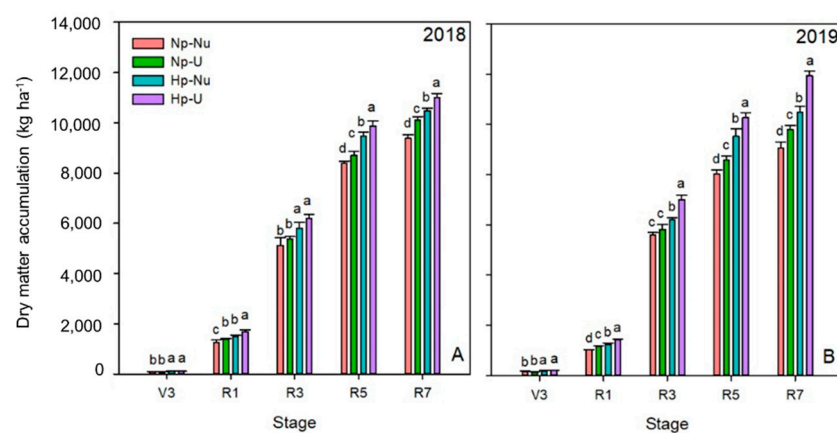


Figure 6. Effect of plant distribution on dry matter accumulation in soybean during the 2018 (A) and 2019 (B) growing seasons under different planting densities. Np, normal planting density. Hp, high planting density. Nu, non-uniform plant distribution. U, uniform plant distribution. The same letters at the same stage are not significantly different at $p < 0.05$ as determined by the least significance difference (LSD) test.

3.7. Effect of Plant Distribution on Canopy Light Interception Rate of Soybean under Different Planting Densities

The order of average canopy light interception rate of soybean from high to low among the four treatments was as follows: Hp-U (98.59%), Hp-Nu (98.35%), Np-U (97.44%), and Np-Nu (96.54%; Figure 7). Close and uniform planting reduced the field light leakage loss and improved the canopy light interception rate of the soybean population. In addition, it can be seen from Figure 7 that uniform planting promoted the uniform distribution of light radiation in the soybean canopy.

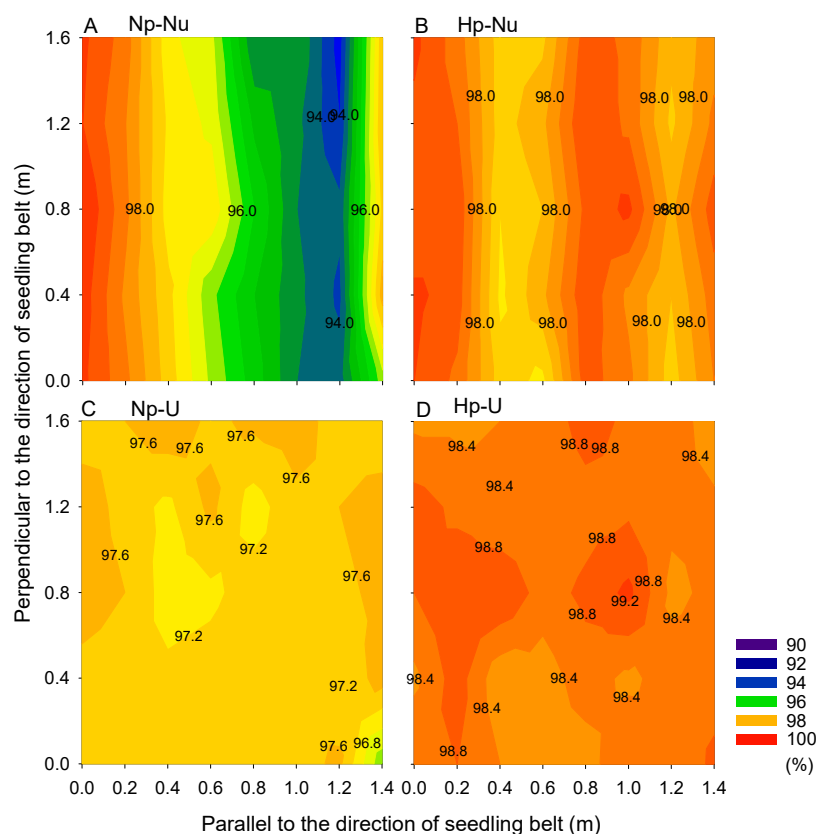


Figure 7. Effect of plant distribution on canopy light interception rate of soybean under different planting densities. (A–D), the canopy light interception rate under Np-Nu, Hp-Nu, Np-U, and Hp-U treatments, respectively. Np, normal seeding density. Hp, high seeding density. Nu, non-uniform plant distribution. U, uniform plant distribution. The change from dark blue to deep red indicates that the canopy light interception rate gradually increases. The number represents the value of canopy light interception rate on the contour line.

3.8. Effect of Plant Distribution on the Photosynthetic Rate of Soybean under Different Planting Densities

In this study, the net photosynthetic rate (P_n) was measured at the R5 stage. The order of P_n from high to low among the four treatments was as follows: Np-U ($28.1 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$), Np-Nu ($22.7 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$), Hp-U ($19.8 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$), and Hp-Nu ($16.8 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$; Figure 8). High planting density reduced the average P_n by 28.0% compared to normal planting density. Meanwhile, the average P_n under uniform plant spacing was 21.0% higher than under non-uniform plant spacing. Furthermore, the coefficient of variation of P_n between individual soybean plants increased by 23.1% under non-uniform plant spacing compared to uniform plant spacing.

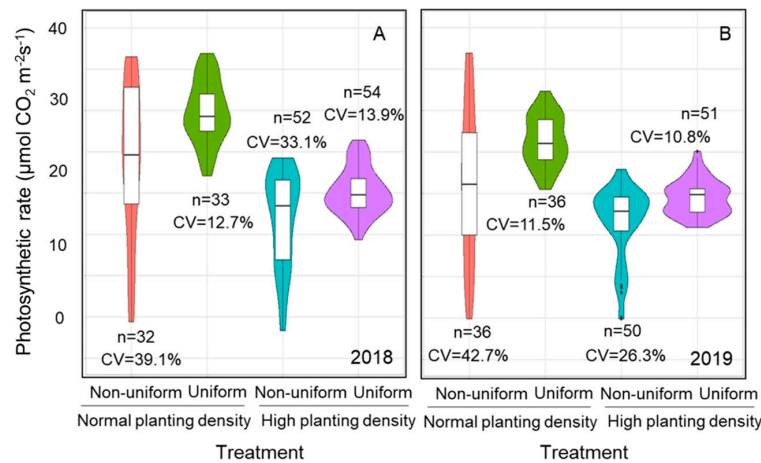


Figure 8. Effect of plant distribution on photosynthetic rate (R5 stage) of soybean during the 2018 (A) and 2019 (B) growing seasons under different planting densities. CV, coefficient of variation.

3.9. Correlation Analysis

The variation ranges of seed weight per plant and P_n of soybean were high under non-uniform plant spacing (Figure 9). The seed weight per plant increased exponentially with an increase in P_n . However, non-uniform plant spacing reduced the variation ranges of seed weight per plant and P_n of soybean. Functional relationships were found between seed weight per plant and P_n , indicating that the contribution rate of P_n to the seed weight was consistent. Generally, the seed weight per plant and P_n of soybean under high density were lower, and their variation ranges were smaller than the normal planting density.

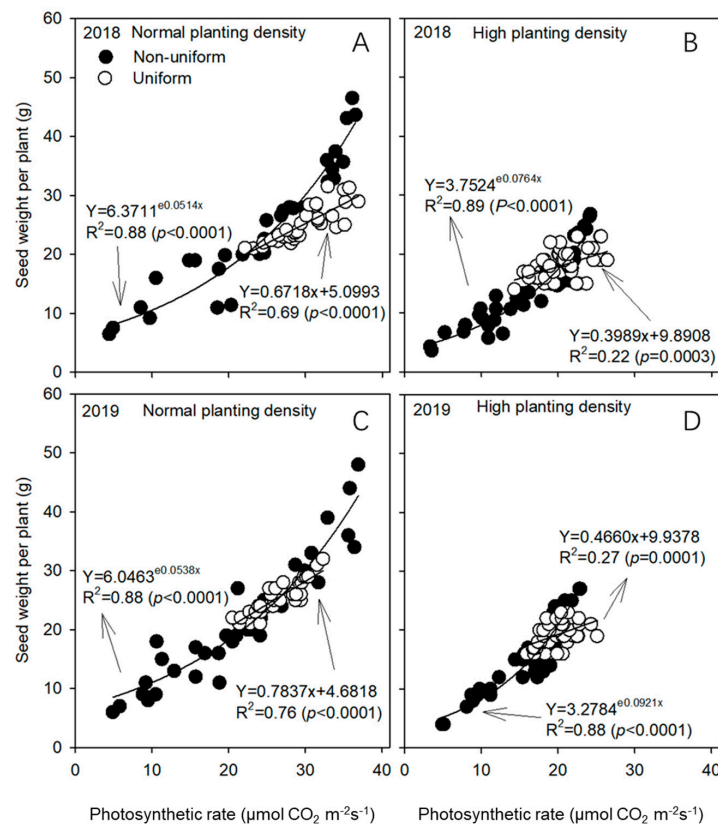


Figure 9. The relationship between seed weight per plant and photosynthetic rate of soybean under normal planting density in 2018 (A) and 2019 (C) and under high planting density in 2018 (B) and 2019 (D).

Positive correlations were found between yield and dry matter weight at maturity of the soybean (Figure 10). The contribution rate of dry matter weight to soybean yield (i.e., harvest index) was greater under uniform plant spacing, indicating that uniform plant distribution can improve the efficiency of material conversion to increase soybean yield.

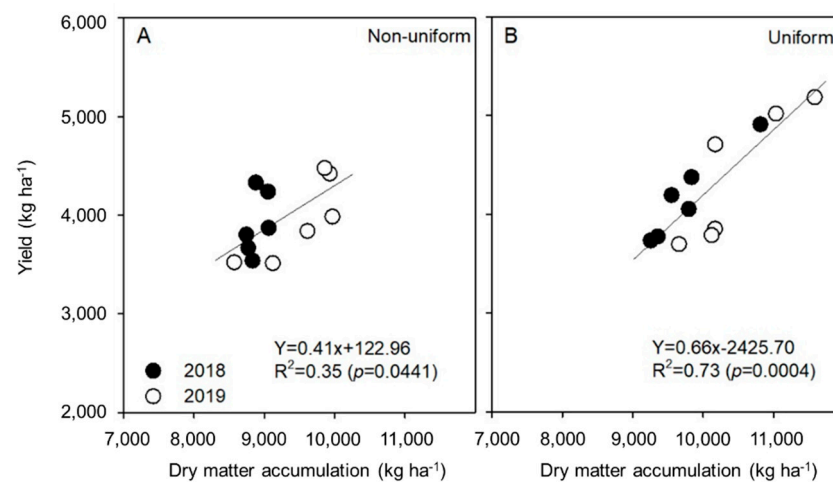


Figure 10. The relationship between yield and dry matter accumulation at maturity of the soybean under different plant distributions. (A,B) Non-uniform and uniform, respectively.

4. Discussion

4.1. Increasing Planting Density Is Beneficial to Seed Yield Increase

From the production manager's standpoint, plant density is one of the major factors that the growers can most easily control [32,33]. Previous research based on conditional inference trees revealed that planting density presented more influence than variety (i.e., MG) and row spacing across seed yield [34]. The optimum planting densities were 255,200, 228,200, and 342,500 plants ha⁻¹ at maximum seed yield for MG_V, VII and VIII soybean cultivars, respectively [35]. Close planting allows the soybean plants to intercept more solar radiation, which accelerates the P_n of soybean, resulting in high yield [9,14]. In addition, the increase in seed yield under high planting density can be attributed to increased dry matter accumulation per area [36,37]. Similar results were observed in this study (Figures 6 and 10). Herein, the average seed yield was significantly higher (22.8%) at a planting density of 2.7×10^5 p ha⁻¹ (Table 1). In comparison, the planting density of 2.7×10^5 p ha⁻¹ is considerably higher than the planting densities typically applied by local farmers in China ($<1.8 \times 10^5$ p ha⁻¹) [9] and more similar to planting densities ($>2.3 \times 10^5$ p ha⁻¹) commonly used in the United States [38–40], Brazil [41], and Japan [23,42]. Planting density affects seed yield due to its significant influence on several yield components, including effective number of plants, seed No. per plant, and seed weight [43,44]. In this study, higher planting density significantly increased the effective number of plants and seed No. per area, increasing seed yield (Table 1).

4.2. Uniform Plant Distribution Can Increase Seed Yield

Crop yield per area depends on the production capacity of individual plants in a specific area [45]. Soybean pods are borne on the nodes, and their number is regulated by plant height and branch number [46–48]. In this study, uneven plant distribution affected the structure and productivity of soybean plants (Figures 3–5). Furthermore, non-uniform plant spacing significantly increased the coefficient of variation of plant height and branch number between individual soybean plants. Specifically, the average plant height under non-uniform and uniform distribution ranged between 67–116 and 86–117 cm, respectively. And the average branch number under non-uniform and uniform distribution ranged between 0–7 and 1–4, respectively. The diversity of soybean canopy shape led to variation in the number of pods per plant (Figure 3). Compared with other crops, the soybean

plant has a strong self-regulation ability in the plant structure [29]. In sparse planting environments, soybean plants exhibit optimal growth and make full use of land and light energy resources to improve the production capacity of each plant [29,48]. However, in a crowded environment, soybean plants exhibit slow growth with poor production capacity, which limits their ability to form effective pods [29]. In this study, non-uniform plant distribution in the field affected the yield compensation ability of soybean plants. Thus, high soybean productivity was not realized under high planting density and non-uniform plant distribution (Table 1). These results show that non-uniform plant distribution can reduce the total soybean yield despite the strong branching compensatory ability of soybean plants.

4.3. Adequate Dry Matter Accumulation Increases Soybean Yield

Crop yield is directly associated with dry mass accumulation [31,49]. High planting density increases crop yield by increasing the dry matter production per area, although the harvest index may remain unchanged [50,51]. In this study, higher planting density increased the soybean dry matter at physiological maturity by 14.6% compared to normal planting density (Figure 6). Furthermore, a significant positive correlation was found between yield and dry matter accumulation (Figure 10). The rapid accumulation of biomass in the crop population relies on full utilization of light energy [52]. In this study, light radiation at the bottom of the soybean canopy under high planting density was significantly lower than under normal planting density (Figure 7), indicating that incident light was sufficiently intercepted by the high density canopy population.

Consistency in growth between individual plants also significantly affects the biomass accumulation in a crop population [18,53]. In this study, uniform plant spacing significantly increased soybean dry matter at the R5 and R7 stages by 5.7% and 8.6%, respectively, compared with non-uniform spacing (Figure 6). The reduction in dry matter accumulation of a crop population occurs because of variations in the growth rate of individual plants caused by unequal resource allocation [25,29]. Photosynthesis is the basis of plant productivity and crop yield. In this study, correlation analysis showed that P_n was positively correlated with seed weight per plant (Figure 9). The average P_n of soybean plants under non-uniform treatments was significantly lower than under uniform treatments (Figure 8), further suggesting that uneven planting negatively affects yield formation. Moreover, uneven planting of soybean increased light leakage in the field (Figure 7). Notably, poor light energy and land utilization were not conducive to overall dry matter accumulation and yield formation.

Under farm management practice in China, the planting density of soybean is lower. Increasing the planting density of soybean under optimal management measures can significantly improve soybean yield, which was also confirmed by previous studies. In the practice of dense planting, the yield of soybean under poor sowing quality cannot reach the expected high yield. The uneven distribution of soybean plants caused by poor sowing quality in the field is a common problem in farming. In 2020, China's total soybean production was 19.6 million tons, and a full spread of uniform planting technology could theoretically increase China's soybean production by 1.8 million tons.

5. Conclusions

Ultimately, the findings of this study show that the optimization of high planting density and uniform plant distribution can enhance seed yield in soybean. This can be attributed to higher light interception and dry matter accumulation of the soybean population. Under high planting density, the light interception rate of the soybean canopy increased, which promoted dry matter accumulation and seed number per unit area and improved soybean yield. Meanwhile, uniform planting further optimized the distribution of light energy in the canopy, reduced the growth differences among individuals, highlighted the population production advantages, and was conducive to the increase in seed

yield. Therefore, we recommend applying higher planting density with uniform plant distribution for improving seed yield in soybean.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/agronomy11091880/s1>, Figure S1: The experimental design in the field, Table S1: Yield and yield components of soybean under different plant distributions.

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Abbreviations

CV	coefficient of variation
Hp	high planting density
Np	normal planting density
Nu	non-uniform plant distribution
PAR	photosynthetically active radiation
P_n	photosynthetic rate
U	uniform plant distribution

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