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Planting Density Tolerance of High-Yielding Maize and the Mechanisms Underlying Yield Improvement with Subsoiling and Increased Planting Density

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Abstract: This study examined the planting density tolerance, grain yield improvement potential, and mechanisms of high-yielding spring maize varieties under increasing planting density and subsoiling. We planted two high-yielding spring maize varieties with a high or low tolerance to high planting densities (LM33 and XD20, respectively) at five different densities (D1: 60,000 plants ha^{-1}, D2: 75,000 plants ha^{-1}, D3: 90,000 plants ha^{-1}, D4: 105,000 plants ha^{-1}, and D5: 120,000 plants ha^{-1}) using two tillage methods (35-cm subsoiling and 15-cm traditional rotary tillage). The response characteristics used to compare the performance of the two maize varieties under different planting densities and tillage methods included root characteristics, canopy physiology, yield, and yield components. The results show that: (1) Under rotary tillage, with the increase of planting density from 75,000 plants ha^{-1} to 90,000 plants ha^{-1}, yields of high-yielding spring maize varieties improved. However, when the planting densities were beyond 90,000 plants ha^{-1}, the yields stopped increase, or even decrease. Subsoiling increased the planting density by 15,000 plants ha^{-1}, enhanced the highest yield by 1080 kg ha^{-1}–1940 kg ha^{-1}, and raised the yield gain by 11.17–30.72%. (2) Under rotary tillage, the functional indexes of the roots and canopy of high-yielding spring maize decreased as planting density increased, and the largest reductions of root dry weight, leaf area index (LAI) of post-anthesis, light transmission percentage (LTP) of ear leaves, bottom leaves LTP, and dry matter accumulation all occurred between D2 and D4. The largest decline of high tolerance variety emerged between D3 and D5, and the extent was smaller than the low tolerance variety. (3) Compared with rotary tillage, subsoiling reduced the extent declines in root dry weight, root length, and root surface area; delayed the attenuation of LAI and the relative chlorophyll content (SPAD) determined in leaves; and improved the LTP of ear layers and bottom layer during the late growth stage. The post-anthesis populations dry matter accumulation of XD20 and LM33 increased by 7.07% and 13.18%, respectively. In addition, subsoiling significantly increased the number of kernels/spike and 1000-grain weight as the planting density increased. Meanwhile, the planting densities at which dry root weight, population LAI, ear leaf LTP, bottom leaf LTP, and dry matter accumulation arose the largest reductions was raised to 15,000 plants ha^{-1}. The effects of subsoiling in the high density-tolerant variety were more pronounced than the low density-tolerant variety.

Keywords: high-yielding spring maize; density tolerance; subsoiling; root–canopy coordination; yield

1. Introduction

In recent years, methods of achieving high maize (*Zea mays* L.) grain yields have been based mainly on "structurality," i.e., increasing the maize population and inhibiting individual growth redundancy [1]. Chen et al. (2012) have analyzed high-yielding and super-high yielding maize farmland in China and found that the optimal planting density for 80.5% of this farmland is 67,500–97,500 plants ha^{-1} [2]. However, because of resource conditions, the availability of varieties and planting technology constraints, maize crops in China are typically planted at a density of only 60,000–67,000 plants ha^{-1}, and just equivalent to the level of the U.S. in the 1990s. [3,4]. The consensus of the scientific community is that the U.S. has achieved large-scale improvements in maize yield by using maize varieties that are tolerant to high planting densities and increasing planting density. These approaches have also been used in China [5,6].

Maize yield improvements have typically been achieved through genetic improvement, farmland management, and planting techniques [6–8]. As a result, previous research on maize planting density tolerance and the physiological mechanisms that regulate this tolerance has been approached from the perspective of these three factors [9–14]. However, most of these studies have focused on planting densities below 90,000 plants ha^{-1}, and therefore fail to fully explain the mechanisms that limit yield improvements in high-yielding maize varieties at higher planting densities (>90,000 plants ha^{-1}).

Long-term use of low-horsepower agricultural machinery for rotary tillage in China has caused the tillage layer to become shallow and the soil in the plow pan to become compacted, reducing soil water holding capacity [15,16]. Increasing planting densities exacerbated competition among plants for water and nutrients. Previous studies have shown that high soil bulk density, soil compactness, and a hard plow pan hindered root growth and elongation, limited the distribution of roots in deep soil, and reduced water and nutrient absorption by roots in deep soil. These effects impacted the maize canopy and severely limited the potential for increased maize yields [17–21]. Therefore, an important method for increasing yield is to break the plow pan, improve soil quality, and thus make maize grow with good canopy structure.

A large number of studies carried out both in China and the rest of the world have shown that subsoiling can break the plow pan, promote the distribution of roots into deeper soils, and maintain high physiological root activity. These allow roots to more effectively meet the canopy demand for nutrients and water, thus, delaying crop aging, improving lodging resistance, and increasing yields [22–26]. However, few studies have examined the effects of subsoiling on the planting density tolerance of high-yielding spring maize.

In this study, we examined the problems of lodging and premature aging in high-yielding spring maize varieties after planting densification under current rotary tillage practices and the barriers to achieving maximum maize yields at high planting densities. We conducted subsoiling to break the plow pan and planted maize at planting densities between 60,000–120,000 plants ha^{-1} to explore the mechanisms underlying yield improvements in high-yielding spring maize varieties after increasing planting density and their responses to subsoiling measures. The results of this study can provide a theoretical basis for using subsoiling measures to achieve densification and yield improvement of high-yielding spring maize

2. Materials and Methods

2.1. Site Description

The experiment was conducted at the Science and Technology Park of Inner Mongolia Agricultural University (Bei Zhitu Village, Goumen Town, Moteyou Qi, Baotou, Inner Mongolia, China) between 2016 and 2017. The geographical position of the experimental fields used in this study were 40°35′49′′ N and 110°33′43′′ E in 2016, 40°35′31′′ N and 110°33′57′′ E in 2017. Different plots were utilized during the two-year experiment, but the previous crop was always maize. The soil texture was sandy loam. In 2016, the soil in the 0–20 cm plow layer of the experimental field contained 19.52 g/kg of organic matter, 100.10 mg/kg of alkaline N, 14.20 mg/kg of available P, and 112.90 mg/kg of available K. In 2017, the soil in the 0–20 cm plow layer of the experimental field contained 16.17 g/kg of organic matter, 86.45 mg/kg of alkaline N, 21.85 mg/kg of available P, and 183.89 mg/kg of available K.

2.2. Experimental Design and Field Management

Treatments consisted of two soil tillage practices: Subsoiling (SS) with a depth of 35 cm and rotary tillage (RT) with a depth of 15 cm; planting densities: Five different plant densities included 60,000 plants ha^{-1} (D1), 75,000 plants ha^{-1} (D2), 90,000 plants ha^{-1} (D3), 105,000 plants ha^{-1} (D4), and 120,000 plants ha^{-1} (D5). The experiment was manual planting with row spacing (60 cm); and maize varieties: A high density-tolerant variety (LM33) and a low density-tolerant variety (XD20), they have been grown in the region for many years, yielding more than 15,000 kg ha^{-1}.

This experiment adopted a split–split plot arrangement. Soil tillage practices were the main factors; the planting densities were sub-plot factors, with three randomized replicates; the secondary sub-plots factors were maize varieties. Area of subsoiling and rotary tillage treatments were 1800 m^2, respectively, every sub-plot area was 120 m^2, and the experimental plots were 12 m long and 5.0 m wide and consisted of 20 rows. The sowing dates were 1 May, 2016, and 23 April, 2017, the 5–10 cm soil temperature of sowing dates was the same between two years. Harvest dates were 2 October, 2016, and 1 October, 2017, respectively. In addition, fertilizers were applied as follows: 465.0 kg ha^{-1} pure N, 210.0 kg ha^{-1} P_2O_5, and 202.5 kg ha^{-1} K_2O. The proportion of nitrogen top-dressing was 30% at V6 and 70% at V12, respectively, whereas P_2O_5 and K_2O were each used once as base fertilizers. The other management measures were the same as those typically used in large-scale farming. The annual accumulated temperature for maize growth was 3103.3 °C in 2016 and 3220.7 °C in 2017. Annual rainfall during the growing season were 319.3 mm and 335.9 mm.

2.3. Measurement Indicators and Methods

2.3.1. Leaf Area Index and Light Transmission Percentage

During the R1 (18 July, 2016; 15 July, 2017) and at R3 (25 August, 2016; 23 August, 2017), a Sunscan crop canopy analyzer (SSI-UM-2.0, Delta-t, Cambridge, UK) was used to measure the photosynthetically active radiation (PAR) at the top of the canopy, and leaf area index (LAI) and PAR transmittance (TPAR) at two levels: Ear layer and bottom layer. Above parameters were measured three times in each plot during 9:00–11:00 and 13:00–15:00 on a sunny day, respectively. To avoid the impacts of senescent leaves, the detector was placed between rows, at 10 cm above the ground. The interception of photosynthetic active radiation (IPAR) and light transmission percentage (LTP) were calculated as follows [27,28].

$$\text{IPAR} = \text{PAR} - \text{TPAR} \tag{1}$$

$$\text{LTP} = \text{TPAR}/\text{IPAR} \times 100 \tag{2}$$

2.3.2. Relative Chlorophyll Content (SPAD)

A SPAD-502 chlorophyll meter (Konica Minolta, Tokyo, Japan) was used in R1, R2 (5 August, 2016; 2 August, 2017), and R3 to determine the relative chlorophyll content (SPAD value) in each ear leaf of maize. Ten points were measured on each leaf and three plants were measured for each plot.

2.3.3. Accumulation and Distribution of Dry Matter in Plants

During the silking and maturity stages, three plants meeting the density standard were selected in each plot. The fresh weights of the leaves, stem sheaths, ears, and kernels were collected. Subsequently, these plant organs were treated at 105 °C for 30 min and then dried at 80 °C to a constant weight, which was recorded.

2.3.4. Root Index

Three representative plants in the same growing status at the silking stage were selected, and the root soil profiles were excavated at 1/2 plant and row distances between adjacent plants. Soil samples (0–80 cm) were collected every 10 cm in depth. The samples was sealed in gauze bags with labels, and brought to the lab to gather roots. After root samples were rinsed, they were preserved in plastic bags at 4–5 °C. Subsequently, root images were scanned using an Epson Twain Pro root scanner (Seiko Epson Corporation, Nagano, Japan) and analyzed using a WinRhizo root image analysis system (Regent Instrument Inc., Québec, QC, Canada) to obtain root length, root length distribution, surface area, and volume for different diameter ranges. The dry weight of the roots was determined using a drying method.

2.3.5. Yield and Yield Components

During the harvest period (2 October, 2016 and 2017), after the yield of the experimental plot was measured, 20 representative plants were randomly selected in each plot to assess the number of spikes, number of kernels per spike, and 1000-grain weight.

2.4. Statistical Analysis

Data recording and organization were performed using Microsoft Excel 2013. Analysis of variance and significance tests among different treatment groups were carried out using SPSS 22.0 (IBM, New York, NY, USA) and the Sigma Plot 12.5 software (Systat Software, Inc., San Jose, California, USA) was used to plot graphs. Because there was no significant difference ($p < 0.05$) between the two-years of data, the average of the two-year data was used for analysis.

3. Results

3.1. Response of Yield and Yield Components to Planting Density, Increasing Planting Density and Subsoiling

The effect of year on Spikes per unit area, Kernels per spike, and yield showed no significant difference. The interaction effects of year and others (tillage pattern, variety, and density) were not almost significant on yield and yield compositions. Therefore, we combined the date of two years (Table 1).

Table 1. Variance analysis of yield and yield composition between years.

Source of Variance	df	Spikes Per Unit Area (ears × 10^4 ha^{-1})	Kernels Per Spike	1000-Kernel Weight (g)	Yield (kg ha^{-1})
Year(Y)	1	0.01 ns	432.6 ns	126.9 *	490 ns
Y × Tillage pattern (TP)	1	0.046 ns	284.5 ns	106.6 ns	5.0 ns
Y × Variety(V)	1	0.074 ns	7077 **	3686 **	120.0 ns
Y × Density(D)	4	0.051 *	482.5 ns	199.9 *	28.0 ns
Y × TP × V	1	0.018 ns	26.96 ns	0.216 ns	36.0 ns
Y ×TP × D	4	0.009 ns	316.2 ns	88.4 ns	19.0 ns
Y × TP × V × D	4	0.002 ns	33.76 ns	29.21 ns	53.0 ns
Error	80	0.018	563.15	116.01	570.0

* Significant at $p < 0.05$, ** Significant at $p < 0.01$, and ns, not significant.

As shown in Table 2, under rotary tillage, the yield of high-yielding spring maize increased initially and then decreased as the planting density increased. Maize yields were significantly different among the five different planting densities evaluated, which increased in increments of 15,000 plants ha^{-1}. XD20, a variety with low tolerance to high planting densities, showed the highest yield (14,640 kg ha^{-1}) at the D2 planting density and a yield increase of 7.33% over the D1 planting density. AS planting density continued to increase, XD20 yield decreased. In contrast, LM33, a variety with high tolerance to high planting densities, showed the highest yield (15.38 t ha^{-1}) at the D3 planting density and a yield increase of 20.06% over the D1 density. As the LM33 planting density continued to increase, yield also increased, but the magnitude of the yield increase gradually decreased with increasing densification.

Table 2. Grain yield and yield components of different high-yielding spring maize varieties under different tillage methods and planting densities.

Variety	Tillage Pattern	Densities	Spikes Per Unit Area (ears × 10^4 ha^{-1})	Kernels Per Spike	1000-Kernel Weight (g)	Yield (t ha^{-1})	The Yield Increase Amplitude (%)
XD20	RT	D1	6.35 h	634.67 ab	397.82 b	13,640.0 e	0.00
		D2	7.64 g	619.63 c	363.71 d	14,640.0 c	7.33
		D3	8.95 f	545.90 e	319.36 f	13,260.0 f	−2.79
		D4	10.49 d	490.54 g	290.50 h	12,710.0 g	−6.82
		D5	11.97 b	445.52 h	260.92 j	11,830.0 h	−13.27
	SS	D1	6.39 h	643.78 a	404.10 a	14,140.0 d	0.00
		D2	7.60 g	624.48 bc	374.74 c	15,130.0 b	7.00
		D3	9.37 e	567.28 d	348.01 e	15,720.0 a	11.17
		D4	10.65 c	513.49 f	301.31 g	14,010.0 d	−0.92
		D5	12.13 a	452.29 h	274.48 i	12,810.0 g	−9.41
LM33	RT	D1	6.26 f	614.35 a	391.61 b	12,800.01 h	0.00
		D2	7.77 e	564.20 c	370.65 d	13,820.0 f	7.88
		D3	9.23 d	544.31 d	360.41 e	15,380.0 c	20.06
		D4	10.73 c	471.16 f	339.17 g	14,580.0 d	13.82
		D5	12.01 b	435.40 g	316.86 i	14,090.0 e	9.99
	SS	D1	6.25 f	620.01 a	402.00 a	13,250.0 g	0.00
		D2	7.75 e	583.32 b	377.44 c	14,510.0 d	9.51
		D3	9.24 d	569.59 c	367.02 d	16,420.0 b	23.92
		D4	10.74 c	538.58 d	352.19 f	17,320.0 a	30.72
		D5	12.25 a	480.09 e	331.73 h	16,590.0 b	25.21
Source of variance							
Variety			**	**	**	**	
Tillage pattern			**	**	**	**	
Density			**	**	*	**	
Variety × Tillage pattern			**	**	**	**	
Variety × Density			**	**	**	**	
Variety × Tillage pattern × Density			**	**	**	**	

Different letters indicate statistically significant differences at the $p < 0.05$ level. * Significant at $p < 0.05$, ** Significant at $p < 0.01$, and ns, not significant.

A further analysis of yield components showed that, for high-yielding spring maize varieties, the number of kernels per spike and 1000-kernel weight both decreased significantly as the planting density increased ($p < 0.05$). Between adjacent densities (D1–D2, D2–D3, D3–D4, and D4–D5), the number of kernels per spike of XD20 dropped by 15.04 grains, 73.73 grains, 55.36 grains, and 45.02 grains, respectively, and the largest decline was observed between D2 and D3. Similarly, the number of kernels per spike of LM33 decreased by 50.15 grains, 19.89 grains, 73.15 grains, and 35.76 grains, respectively, and the largest decline was observed between D3 and D4. The 1000-kernel weight of XD20 decreased by 34.11 g, 44.35 g, 28.86 g, and 29.58 g, respectively, whereas that of LM33 decreased by 20.96 g, 10.24 g, 21.24 g, and 22.31 g, respectively. The largest declines in 1000-kernel weight were observed between D2 and D3 for XD20 and between D4 and D5 for LM33. These results show that significant reductions in the number of kernels per spike and 1000-kernel weight limited the yield increases achievable by high-yielding spring maize under high planting density conditions. Compared to XD20, higher yield in LM33 variety had a less decrease in 1000-kernel weight and number of kernels per spike at different densities.

Compared with rotary tillage, subsoiling significantly increased the yield of high-yielding spring maize at each planting density. For XD20 and LM33, the planting densities with the highest yields (15.38 t ha^{-1} and 17.32 t ha^{-1}, respectively) were D3 and D4, respectively. These yields were 1.08 t ha^{-1} and 1.94 t ha^{-1} higher, respectively, than the corresponding highest yields achieved with rotary tillage. Subsoiling improved yields by 11.17% for XD20 and 30.72% for LM33 compared with traditional rotary tillage. These findings suggest that subsoiling can be utilized to raise the potential for densification and yield improvement of high-yielding spring maize varieties.

Subsoiling significantly increased the number of kernels per spike of XD20 (in D3–4) and LM 33 (in D1–D4), and their 1000-kernelweights in all planting densities.

Significant or extremely significant interactions were identified between variety and tillage pattern, between variety and planting density, and among variety, tillage pattern, and planting density.

3.2. Response of Root Traits to Planting Density, Increasing Planting Density and Subsoiling

As shown in Figures 1–3, the single root dry weight, root length, and root surface area of the tested varieties decreased as the planting density increased, but the degree of reduction between adjacent densities was different for each variety. For the variety with low tolerance to high planting densities, XD20, the total root dry weight of each plant between adjacent densities decreased by 23.61%, 29.54%, 29.92%, and 25.65%, respectively, and the maximum reduction emerged between D2 and D4. In addition, the root length of each plant decreased by 11.75%, 22.63%, 24.26%, and 25.62%, respectively, and the maximum reduction occurred between D4 and D5. The root surface area of each plant decreased by 20.12%, 18.40%, 38.17%, and 22.44%, respectively, and the maximum reduction occurred between D3 and D4. For the high density-tolerant variety, LM33, the total root dry weight of each plant between adjacent densities decreased by 12.06%, 18.28%, 23.63%, and 13.48%, respectively, and the maximum reduction occurred between D3 and D4. The root length of each plant decreased by 12.15%, 13.19%, 8.40%, and 16.14%, respectively, and the maximum reduction occurred between D4 and D5. The root surface area of each plant decreased by 13.67%, 11.54%, 6.23%, and 15.59%, respectively, and the maximum reduction emerged between D4 and D5. These results indicate that increasing the planting density limited root growth and the development of high-yielding spring maize. Nevertheless, compared with the low density-tolerant variety, the roots of the high density-tolerant variety were less sensitive to high planting densities and maintained better root architecture.

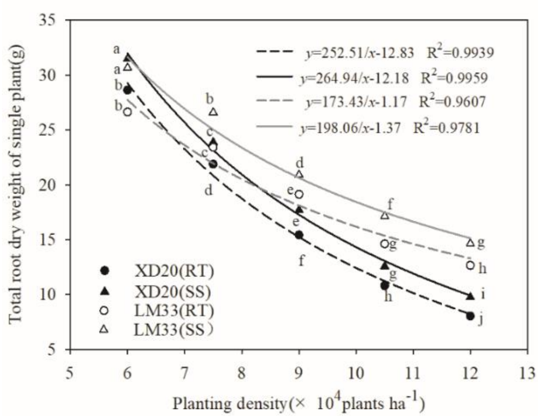

Figure 1. Root dry weight of high-yielding spring maize under different tillage methods and planting densities. Different letters on the graph indicate significant differences at $p < 0.05$.

After subsoiling, the total root dry weight of each XD20 plant decreased by 24.12%, 25.92%, 29.00%, and 22.37% between adjacent densities, respectively, and the maximum reduction occurred between D3 and D4. The root length of each plant decreased by 10.03%, 17.88%, 23.88%, and 21.50%, respectively, and the maximum reduction occurred between D3 and D4. The root surface area of each plant decreased by 17.12%, 18.40%, 37.21%, and 13.64%, respectively, and the maximum reduction occurred between D3 and D4. For LM33, the total root dry weight of each plant between adjacent densities decreased by 13.27%, 21.36%, 18.08%, and 14.59%, respectively, and the maximum reduction occurred between D2 and D3. The root length of each plant decreased by 9.21%, 11.73%, 9.87%, and 12.59%, respectively, and the maximum reduction occurred between D4 and D5. The root surface area of each plant decreased by 11.96%, 12.08%, 8.24%, and 13.18%, respectively, and the maximum reduction occurred between D4 and D5. These results indicate that subsoiling tillage significantly alleviated the sensitivity of high-yielding spring maize roots to stress caused by high planting densities by reducing decreases in root dry weight, root length, and root surface area.

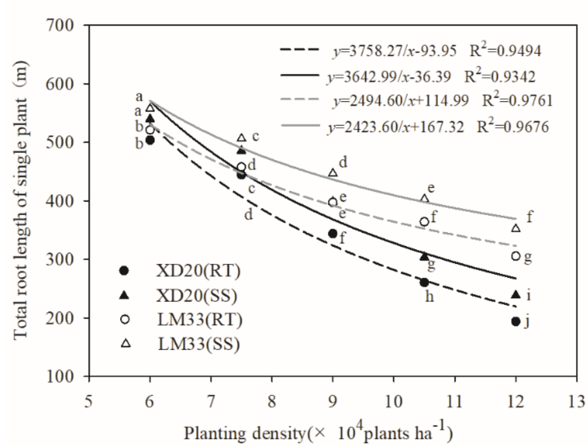

Figure 2. Root length of high-yielding spring maize under different tillage methods and planting densities. Different letters on the graph indicate significant differences at $p < 0.05$.

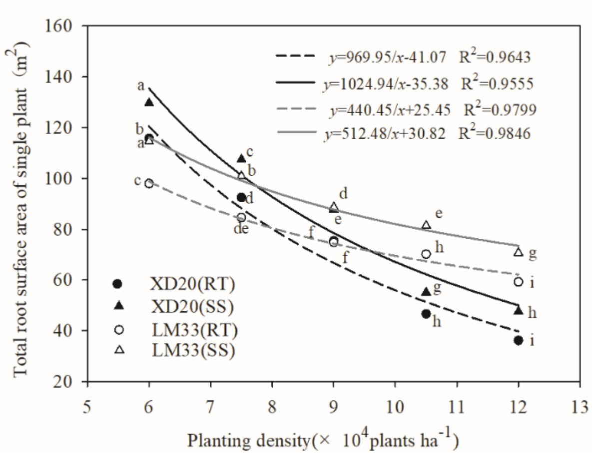

Figure 3. Root surface area of high-yielding spring maize under different tillage methods and planting densities. Different letters on the graph indicate significant differences at $p < 0.05$.

3.3. Response of Leaf Area Index (LAI) to Planting Density, Increasing Planting Density and Subsoiling

As shown in Table 3, the LAI of the XD20 improved significantly as the planting density increased during the R1 stage. During the R3 stage, LAI was highest under planting density D2, which was significantly higher than that of D1, D4, and D5. From the R1 to R3 stages, LAI at the different planting densities decreased by 24.07%, 26.67%, 33.85%, 38.97%, and 48.41%, respectively, meaning that the LAI reduction was amplified as planting density increased. Meanwhile, the LAI of the LM33 population increased significantly between the R1 and R3 stages as planting density increased, and the LAI was highest at D5. From R1 to R3, the LAI also decreased as planting density increased by 18.52%, 21.15%, 23.28%, 25.76%, and 28.57%, respectively.

Subsoiling tillage improved the LAI of high-yielding spring maize varieties at the same planting density, and the difference between subsoiling and rotary tillage was significant. During the R1 stage, subsoiling increased the LAI of XD20 by 4.72% at D1, 7.50% at D2, 10.40% at D3, 10.38% at D4, and 12.24% at D5. During the R3 stage, subsoiling increased the LAI of XD20 by 5.13%, 11.60%, 17.86%, 18.05%, and 18.52% at the different planting densities, respectively. During the R1 stage, the LAI of LM33 increased by 8.52%, 12.39%, 12.92%, 14.32%, and 16.33% at the different planting densities, respectively, and by 10.45%, 13.55%, 21.21%, 24.46%, and 26.57%, respectively, during the R3 stage.

Table 3. Leaf area index (LAI) of different high-yielding spring maize varieties under different tillage methods and planting densities.

Variety	Tillage Pattern	Density	R1 Stage	Increase of LAI by SS (%)	R3 Stage	Increase of LAI by SS (%)	Decline in LAI from R1 to R6 (%)
XD20	RT	D1	3.60 h		2.73 c		24.17
		D2	4.00 f		2.93 b		26.75
		D3	4.23 e		2.80 bc		33.81
		D4	4.53 d		2.77 c		38.85
		D5	5.23 b		2.70 c		48.37
	SS	D1	3.77 g	4.72	2.87 bc	5.13	23.87
		D2	4.30 e	7.50	3.27 a	11.60	23.95
		D3	4.67 d	10.40	3.30 a	17.86	29.34
		D4	5.00 c	10.38	3.27 a	18.05	34.60
		D5	5.87 a	12.24	3.20 a	18.52	45.49
LM33	RT	D1	2.70 g		2.20 h		18.52
		D2	3.47 e		2.73 f		21.33
		D3	3.87 d		2.97 e		23.26
		D4	4.40 c		3.27 d		25.68
		D5	4.90 b		3.50 c		28.57
	SS	D1	2.93 f	8.52	2.43 g	10.45	17.06
		D2	3.90 d	12.39	3.10 d e	13.55	20.51
		D3	4.37 c	12.92	3.60 c	21.21	17.62
		D4	5.03 b	14.32	4.07 b	24.46	19.09
		D5	5.70 a	16.33	4.43 a	26.57	22.28
Source of variance							
Variety			**		**		
Tillage pattern			**		**		
Density			**		**		
Variety × Tillage pattern			*		**		
Variety × Density			**		**		
Tillage pattern × Density pattern × Densities			**		**		
Variety × Tillage pattern × Density			ns		ns		

Different letters indicate statistically significant differences at the $p < 0.05$ level. * Significant at $p < 0.05$, ** Significant at $p < 0.01$, and ns, not significant.

From R1 to R3, subsoiling reduced the degree of decrease in the LAI of XD20 by 0.29%, 2.80%, 4.47%, 4.25%, and 2.89% at the different planting densities, respectively. For LM33, subsoiling reduced the degree of decrease in LAI by 1.45%, 0.81%, 5.64%, 6.60%, and 6.29%, respectively.

The above analysis indicates that subsoiling eased the effects of increased planting densities on the LAI of high-yielding spring maize varieties, and that the subsoiling effect was stronger in high density-tolerant varieties than low density-tolerant varieties.

An appropriate LAI can guarantee high maize yields. Therefore, a regression analysis was carried out for the LAI and yield of high-yielding spring maize during the silking stage under different tillage patterns. As shown in Figure 4, there was a significant quadratic regression relationship between LAI and yield, and the relationship could be expressed as $y = ax^2 + bx + c$. Under the condition of rotary tillage and when the yield of XD20 and LM33 reached their theoretical maximum, the appropriate LAI at the silking stage was 3.51 and 4.11, respectively. Subsoiling tillage significantly increased maize yield. In addition, when the yield of XD20 and LM33 peaked, their LAIs were 4.53 and 5.65, respectively, suggesting that subsoiling tillage can increase maize yield by increasing the LAI of high-yielding spring maize during the silking stage.

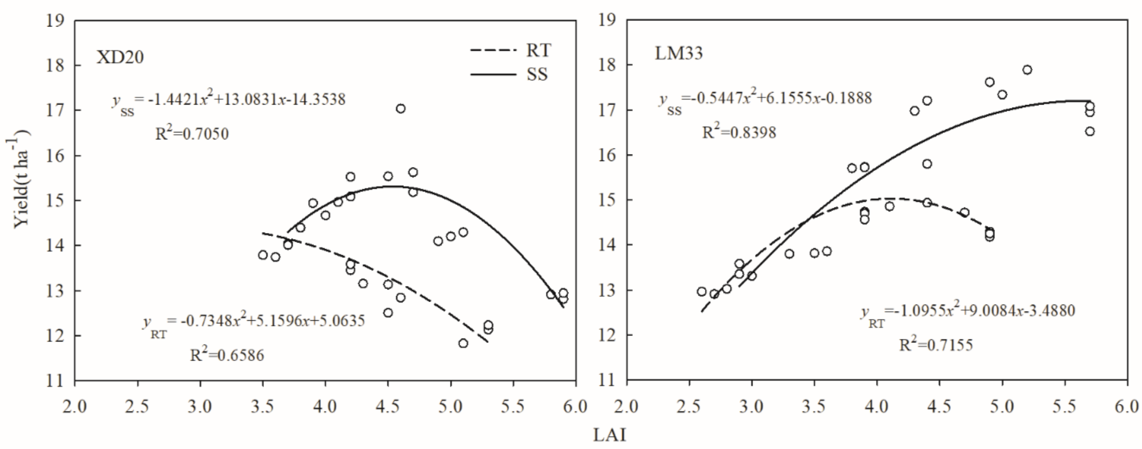

Figure 4. Regression analysis of LAI and yield for high-yielding spring maize.

3.4. Response of Canopy LTP to Planting Density, Increasing Planting Density and Subsoiling

As shown in Table 4, the LTP of the ear layer and bottom layer in high-yielding spring maize decreased significantly as planting density increased, and the degree of the reduction was dependent on density-tolerance of maize varieties. During the R1 period, the LTP of the ear layer and the bottom layer of XD20 decreased by an average of 2.21% and 1.92%, respectively, and the maximum reduction occurred between D1 and D2 and between D2 and D3, respectively. For LM33, the LTP of the ear layer and bottom layer decreased by an average of 1.22% and 0.88%, respectively, and the maximum reduction occurred between D4 and D5 and between D3 and D4, respectively. During the R3 period, the LTP of the ear layer and bottom layer of XD20 decreased by an average of 1.80% and 1.32%, respectively, and the maximum reductions both occurred between D3 and D4. For LM33, the LTP of the ear layer and bottom layer decreased by an average of 1.09% and 0.90%, respectively, and the maximum reductions emerged between D4 and D5. Overall, the reductions in LTP were smaller in the variety with high tolerance to high planting density than in the low tolerance variety. In addition, the largest LTP reduction occurred at a higher planting density interval for the high density-tolerant variety than for the low density-tolerant variety.

After subsoiling, the LTP of ear leaves and bottom leaves of the high-yield spring maize varieties increased significantly. During the R1 period, the LTP of the ear layer and bottom layer of XD20 increased by 17.53% and 37.84%, respectively, and the maximum increase occurred with planting densities D3 and D4. During this period, the LTP of the LM33 ear layer and bottom layer increased by 9.09% and 14.51%, respectively, and the maximum increase emerged at planting density D5. During the R3 period, the LTP of the ear layer and bottom layer of XD20 increased by 14.51% and 12.23%, respectively, and the maximum increase occurred at planting densities D4 and D5. During this period, the LTP of the LM33 ear layer and bottom layer increased by 12.23% and 17.40%, respectively, and the maximum increases of both occurred with planting density D5. These results indicate that subsoiling improved the LTP of high-yielding spring maize at high planting densities. In particular, subsoiling significantly raised the planting densities at which the largest LTP decline occurred. In addition, the subsoiling effect was stronger for the low density-tolerant variety than for the high density-tolerant variety.

Table 4. Ear and bottom layer leaf light transmission percentage (LTP) of high-yielding spring maize under different tillage methods and planting densities.

Variety	Tillage Pattern	Density	R1		R3	
			Ear Layer	Bottom	Ear Layer	Bottom
XD20	RT	D1	22.92 b	13.02 b	24.02 d	14.72 b
		D2	18.81 e	11.32 d	22.48 e	13.05 d
		D3	17.13 f	7.88 e	21.37 f	10.92 e
		D4	15.09 h	5.23 g	17.62 h	8.72 g
		D5	13.33 i	4.28 h	16.33 i	6.97 h
	SS	D1	24.05 a	14.22 a	26.82 a	15.60 a
		D2	21.97 c	12.99 b	25.38 b	14.83 b
		D3	20.83 d	12.32 c	24.56 c	13.81 c
		D4	18.68 e	8.16 e	22.00 e	12.80 d
		D5	17.07 g	6.55 f	19.62 g	10.33 f
LM33	RT	D1	25.37 ab	13.57 c	26.67 cd	16.28 c
		D2	23.92 c	13.19 cd	26.55 d	15.58 d
		D3	22.18 d	12.28 e	24.54 e	14.49 e
		D4	20.04 f	10.54 g	23.37 f	13.81 f
		D5	17.63 g	9.33 h	21.17 g	12.22 g
	SS	D1	25.78 a	14.93 a	29.42 a	18.73 a
		D2	24.94 b	14.23 b	28.43 b	17.78 b
		D3	23.87 c	13.53 c	27.32 c	16.73 c
		D4	22.75 d	12.87 d	26.91 cd	16.24 c
		D5	20.88 e	11.43 f	25.06 e	15.15 d
Source of variance						
Variety			**	**	**	**
Tillage pattern			**	**	**	**
Density			**	**	**	**
Variety × Tillage pattern			**	**	**	**
Variety × Density			**	**	**	**
Tillage pattern × Density			**	**	**	**
Variety × Tillage pattern × Density			**	**	**	**

The mean values of the different treatments in the 2 years are shown. Different letters indicate statistically significant differences at the $p < 0.05$ level (ANOVA and Duncan's multiple range test; $n = 3$). * Significant at $p < 0.05$, ** Significant at $p < 0.01$, and ns, not significant.

3.5. Response of Leaf SPAD Value to Planting Density, Increasing Planting Density and Subsoiling

As shown in Figure 5, after R1, the leaf SPAD value of high-yielding spring maize varieties decreased as growth progressed, but the degree of decrease was different between high and low tolerance varieties. For XD20, the leaf SPAD value between R1 and R3 declined by an average decline of 10.83% under the different planting densities. Over the same period, the leaf SPAD value of LM33 decreased by an average decrease of 6.89%.

Subsoiling increased the leaf SPAD value of high-yielding spring maize during the R1, R2, and R3 growth stages. The leaf SPAD value of XD20 increased by 2.68%, 5.38%, and 6.79%, respectively. For LM33, the leaf SPAD value increased by 2.60%, 4.48%, and 3.62%, respectively, and there were significant differences with the SPAD value of rotary tillage during the R2 and R3 stages. From R1 to R3, the SPAD values of XD20 decreased by an average of 8.51%. SPAD values of LM33 under the same conditions decreased by an average of 5.19%. These results demonstrate that subsoiling could delay the senescence of post-anthesis leaves of high-yielding spring maize. In addition, the effects of subsoiling were stronger in the low tolerance variety.

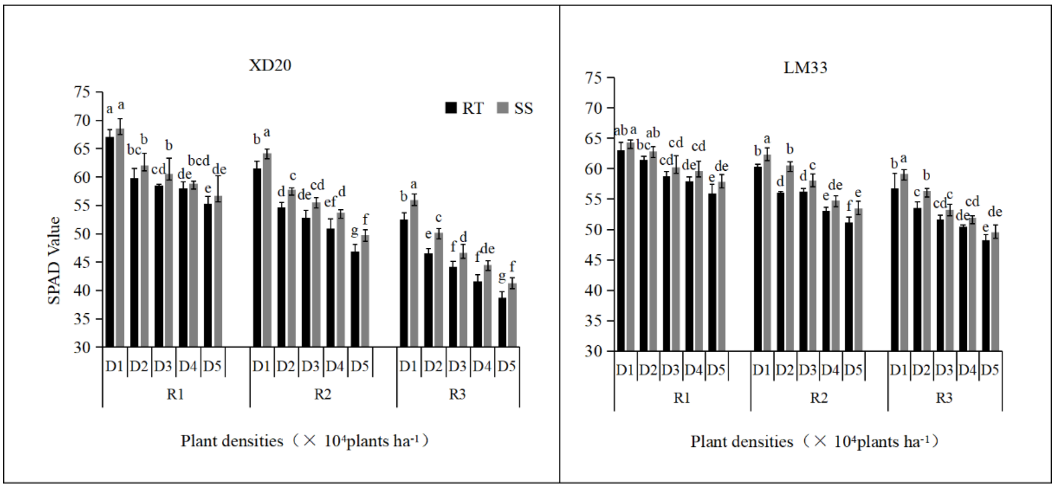

Figure 5. Relative chlorophyll content (SPAD) values of high-yielding spring maize under different tillage methods and planting densities. Different letters on the graph indicate significant differences at $p < 0.05$.

3.6. Response of Post-Anthesis Dry Matter Accumulation to Planting Density, Increasing Planting Density and Subsoiling

Dry matter accumulation in maize populations is the basis of maize grain formation. As shown in Figure 6, after the silking stage, the accumulation of dry matter in the maize population showed a parabolic relationship with planting density.

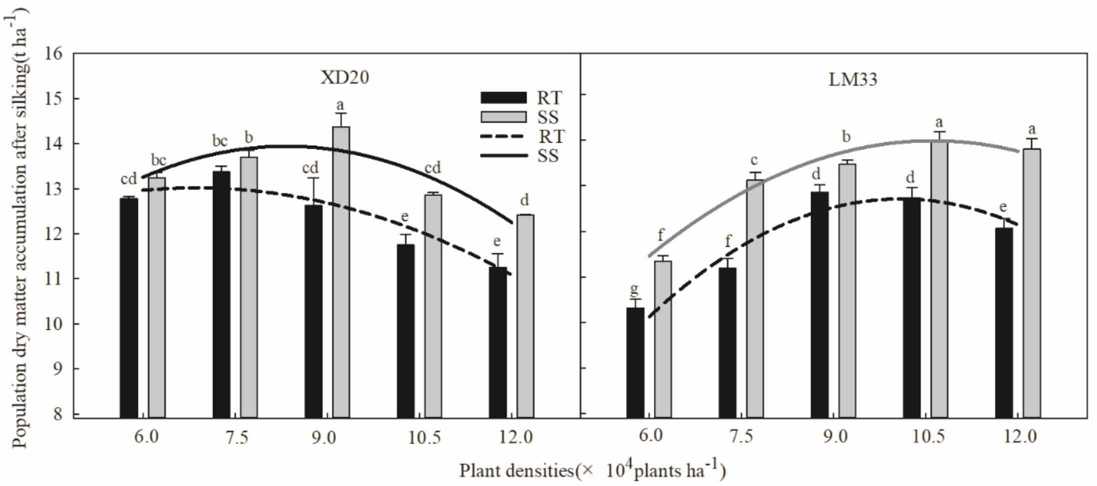

Figure 6. Accumulation of dry matter by high-yielding spring maize under different cultivation methods and planting densities. Different letters on the graph indicate significant differences at $p < 0.05$.

Under rotary tillage, the regression equations for the amount of post-anthesis dry matter accumulation with planting density were $Y_{XD20} = -0.0731x^2 + 1.0033x + 9.5750$ ($R^2 = 0.7526$) for XD20, and $Y_{LM33} = -0.1548x^2 + 3.1221x - 3.0281$ ($R^2 = 0.9067$) for LM33. After solving these equations, the optimal planting density was determined to be 68,600 plants ha^{-1} for XD20 and 100,800 plants ha^{-1} for LM33. At such planting densities, the highest accumulation of dry matter was 13.02 t ha^{-1} for XD20 and 12.71 t ha^{-1} for LM33. These results show that the high tolerance-variety maintained a higher level of post-anthesis dry matter accumulation under high planting densities than did the low tolerance variety, thus establishing a material basis for yield improvement by dense planting.

Under subsoiling conditions, the regression equation for the amount of post-silking dry matter accumulation with planting density was $Y_{XD20} = -0.1261x^2 + 2.1025x + 5.1738$ ($R^2 = 0.7236$) for XD20 and $Y_{LM33} = -0.1188x^2 + 2.5213x + 0.6121$ ($R^2 = 0.9497$) for LM33. After solving variances, the optimal planting density for XD20 determined to be 83,400 plants ha^{-1} and 106,100 plants ha^{-1} for LM33. At these planting densities, the highest post-silking dry matter accumulation was 13.94 t ha^{-1} for XD20 and 14.39 t ha^{-1} for LM33. These results show that subsoiling increased the optimal planting density of high-yielding spring maize by 14,800 plants ha^{-1} for XD20 and 5300 plants ha^{-1} for LM33, and that the amount of post-silking accumulation of dry matter increased by 7.07% and 13.18%, respectively.

3.7. Path-Coefficient Analysis Regarding the Root/Canopy Index and Yield of High-Yielding Spring Maize under Different Tillage Methods

We carried out a path-coefficient analysis, using yield as the basis, for the root/canopy index, and yield of high-yielding spring maize under rotary tillage conditions. Through stepwise regression analysis, the parameters for the mass of population dry matter, root surface area, and bottom layer LTP were included in the regression equation, $y = 2.690 + 0.805x_3 + 0.0004x_5 + 0.429x_{10}$, and reached significance. The results of the path-coefficient analysis (Table 5) indicate that the mass of dry matter and bottom layer LTP were directly and positively correlated with yield, yielding direct path coefficients 0.7383 and 1.3321, respectively. In contrast, root surface area exerted a direct negative effect on yield. However, because root surface area exerted an indirect positive effect on yield and the bottom layer LTP with an indirect path coefficient of 1.1509, and its direct negative effect was weaker than its indirect positive effect, it was still significantly and positively correlated with yield.

Table 5. Results of the path analysis of the indices and yield of high-yielding spring maize under rotary tillage.

Index	Correlation Coefficient	Direct Path Coefficient	Indirect Path Coefficient		
			Accumulation of Dry Matter	Root Surface Area	Transparency of Underlying Leaves
			X_3	X_5	X_{10}
X_3	0.6525	0.7383		−0.1746	0.0888
X_5	0.3770	−0.9148	0.1409		1.1509
X_{10}	0.5910	1.3321	0.0492	−0.7904	

Through the path-coefficient analysis of various indexes of high-yielding spring maize yields under subsoiling conditions (Table 6), the amount of dry matter, ear leaf LTP, root dry weight, 1000-grain weight, and LAI were left in the final regression equation after stepwise regression analysis. The regression equation was established as $y = -15.022 + 0.6766x_3 + 0.3460x_9 - 0.2568x_6 + 0.0420x_2 + 0.8469x_7$, which reached a significant level. The results of the path-coefficient analysis showed that post-anthesis population dry matter exerted a direct positive effect on yield, as well as a significantly indirect positive effect on yield and the root dry weight. Therefore, it was the factor most closely related to yield, with a correlation coefficient of 0.7912. Furthermore, ear leaf LTP exhibited a direct positive with yield, as well as an indirect positive with yield through the 1000-grain weight. However, the positive effect of ear layer LTP was offset by the indirect negative effect of root dry weight. Therefore, the final correlation coefficient between the ear layer LTP and yield was 0.2017. Whereas root dry weight produced a direct negative effect on yield, it also produced a larger indirect positive effect on yield and the 1000-grain weight, which offset most of the negative effect of root dry weight and resulted in a relatively small (−0.1528) correlation coefficient between root dry weight and yield. The 1000-grain weight exerted a direct positive effect on yield. Meanwhile, it exerted a relatively significant negative effect on yield and root dry weight. Therefore, the final correlation coefficient between 1000-grain weight and yield was the smallest among the measured correlations (0.1218). The LAI exerted a direct positive effect on yield, an indirect positive effect on yield and dry root weight, and an indirect negative effect on yield, ear leaf LTP, and 1000-grain weight. The correlation coefficient between the LAI and yield was 0.2527. This analysis shows that the root dry weight and 1000-grain weight had strong and direct impacts on the plant canopy index, while the plant canopy mainly affected yield, root dry weight, and 1000-grain weight.

Table 6. Results of the path analysis of the indices and yield of high-yielding spring maize under subsoiling.

Index	Correlation Coefficient	Direct Path Coefficient	Indirect Path Coefficient				
			Accumulation of Dry Matter	Transparency of the Ear Leaf	Root Dry Weight	1000-Kernel Weight	LAI
			X_3	X_9	X_6	X_2	X_7
X_3	0.7912	0.3962		−0.0657	0.3102	−0.0478	0.1983
X_9	0.2017	0.6892	−0.0378		−1.1127	1.0861	−0.4232
X_6	−0.1528	−1.2908	−0.0952	0.1390		1.1050	−0.4660
X_2	0.1218	1.1632	−0.0163	0.4750	−1.2262		−0.4424
X_7	0.2571	0.5063	0.1552	−0.5761	1.1881	−1.0164	

4. Discussion

The main function of the root system is to absorb water and nutrients from the soil, while the main function of the canopy is to synthesize carbohydrates. The matter and energy exchange between roots and canopy constitutes the overall structural and functional system that crops use for plant growth and yield formation [29,30]. In the process of maize yield formation, efficient root architecture and a reasonable canopy structure are important guarantees for ensuring high yields [31,32]. Previous studies have focused primarily on the effects of planting density on the structure and functioning of maize roots/canopy and on maize yields, but these results were not entirely consistent under high planting densities. Hutchings et al. [32], Wang et al. [33], and Antonietta et al. [34] showed that premature senescence of lower leaves in densely planted maize populations decreased the photosynthetic performance of post-anthesis ear leaves. As a result, the amount of photosynthetic products transported to the roots declined significantly, causing root performance to decline during the maturity stage, root nitrogen uptake to decrease significantly post-anthesis, the photosynthesis rate of leaves to decline, accelerated leaf senescence, and significantly decreased grain yields of single plants. Sangoi [35] reported that the decreasing performance of maize roots limited them to absorb the nitrogen, caused the photosynthetic performance of the plant canopy to decrease, and thus decreased yield. Yan et al. [36] and Li et al. [37] studied the relationship between the root/canopy and yield of different maize varieties under high planting densities. Their results showed that the canopy of spreading-leaf varieties was more sensitive to growth space than that of upright-leaf varieties and that the competition of roots to growth space was stronger than the canopy; therefore, the main factor limiting yields of spreading-leaf varieties was the storage capacity of grains. In contrast, the upright-leaf maize root was more sensitive to growth space and competition of canopy to growth space was stronger than that of roots. For upright-leaf varieties, the main factor limiting yield was the number of spikes per unit area. In this study, a path-coefficient analysis was carried out among the root, canopy, and yield index of high-yielding spring maize under rotary tillage conditions. The results show that the post-anthesis dry matter mass and the LTP of the bottom layer exerted direct positive effects on yield, and the root surface area indirectly and positively affected the yield by bottom layer LTP. These results are consistent with the findings of Yan et al. [36] and Li et al. [37].

Cai et al. [38] and XM et al. [25] showed that subsoiling reduced soil bulk density and compaction, and enhanced soil porosity, water storage, and temperature regulation improved the soil environment. As a result, subsoiling promoted root to deep grow; increased root surface area, root dry weight, LAI, and dry weight of the plant; reduced the root-shoot ratio; and increased the number of kernels per spike, 1000-kernel weight, and yield. Wang et al. [39] showed that under high planting densities, subsoiling promoted the accumulation of root dry matter during the early stages of maize growth, enlarged the root-shoot ratio, improved the ability of roots to absorb water and nutrients, promoted maize root growth, and improved maize yields. The results of this study show that as planting density increased, the biomass of high-yielding spring maize increased. A further analysis of the relationships among roots, canopy, and yield showed that maize roots played a more important role in canopy performance and maize yield under subsoiling conditions than under rotary tillage conditions. In addition, under subsoiling conditions, the mass of canopy dry matter, the LTP of the ear layer, and LAI all indirectly affected yield through the dry weight of roots (the indirect correlation coefficients reached 0.3102, −1.1127, −1.2262, and 1.1881, respectively), and their indirect effects were greater than their direct effects. These results showed that subsoiling changed the soil environment and caused the root system to become a dominant factor affecting yield. Changes in the maize root system caused subsequent changes in canopy structure and function that improved the coordination of roots and canopy, resulting in adaptation to the environment and ensuring high yields.

5. Conclusions

Under traditional rotary tillage, the yield of high-yielding spring maize was mainly affected by dry matter accumulation, the LTP of bottom layer leaves, and root surface area. These three factors had a significantly positive correlation with maize yield. As planting density increased, dry matter mass, bottom layer LTP, and root surface area all decreased. When planting density increased from 75,000 plants ha^{-1} to 90,000 plants ha^{-1}, dry matter mass, and the decreasing scope of bottom layer LTP and the root surface all reached the maximum. Yield nearly also peaked at this point, without any improvement along with density increase. Under subsoiling conditions, the main factors affecting the high-yielding spring maize yield were the dry matter mass of the population, ear leaf LTP, root dry weight, 1000-kernel weight, and LAI. Subsoiling reduced the reduction extent of root and shoot index as the increase of planting density. The optimum planting density that raised the maximum decrease of the root dry weight, ear leaf LTP, and 1000-kernel weight was increased by 15,000 plants ha^{-1}, and produced the maximum dry matter accumulation of the population increased by 5300 plants ha^{-1}–14,800 plants ha^{-1}. Therefore, utilizing subsoiling measures could further increase the planting density of high-yielding spring maize varieties by 15,000 plants ha^{-1} and improve yield to 1.08 t ha^{-1} or 1.94 t ha^{-1}. The root dry weight and 1000-kernel weight exerted the strongest direct positive effects on canopy indicators, thus directly and indirectly affecting maize yields. Therefore, under subsoiling conditions, increasing planting density reasonably could cause root and canopy to coordinate growth, improve 1000-kernel weight, and realize maize yields improvements.

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