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Effects of narrow plant spacing on root distribution and physiological nitrogen use efficiency in summer maize

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ABSTRACT

The objective of this study was to understand the effects of plant spacing on grain yield and root competition in summer maize (*Zea mays* L.). Maize cultivar Denghai 661 was planted in rectangular tanks (0.54 m × 0.27 m × 1.00 m) under 27 cm (normal) and 6 cm (narrow) plant spacing and treated with zero and 7.5 g nitrogen (N) per plant. Compared to normal plant spacing, narrow plant spacing generated less root biomass in the 0–20 cm zone under both N rates, slight reductions of dry root weight in the 20–40 cm and 40–70 cm zones at the mid-grain filling stage, and slight variation of dry root weights in the 70–100 cm zone during the whole growth period. Narrow plant spacing decreased root reductive activity in all root zones, especially at the grain-filling stage. Grain yield and above-ground biomass were 5.0% and 8.4% lower in the narrow plant spacing than with normal plant spacing, although narrow plant spacing significantly increased N harvest index and N use efficiency in both grain yield and biomass, and higher N translocation rates from vegetative organs. These results indicate that the reductive activity of maize roots in all soil layers and dry weights of shallow roots were significantly decreased under narrow plant spacing conditions, resulting in lower root biomass and yield reduction at maturity. Therefore, a moderately dense sowing is a basis for high yield in summer maize.

1. Introduction

Population structure is of great importance for maximizing yield in crops. Plant density acts as a key factor in regulating plant competition within the population and optimal plant densities are very important for efficient agronomic practice. Plant spacing varies with the growth of plants and the growing environments [1]. To date, diverse planting patterns, such as narrow spacing [2,3], wide–narrow rows [4–6], and multiple-plant hill plots [7], have been developed in maize (*Zea mays* L.) in pursuit of high grain yields under different growing conditions. Studies addressing the effects of plant spacing on yield have largely focused on improvement of above-ground canopy structure, resulting in photosynthetic rate increases via effective interception of solar radiation [3,6] or better photosynthetic performance of ear leaves [7]. These strategies often result in reduction in plant competition for light resources at high planting densities. However, individual plants always compete for nutrition, water and root space [8], and few reports are available regarding root nutrient absorption under different plant spacings.

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The fibrous root system of maize radiates outward and more than 90% of the dry root weight in soil is distributed in the top 20 cm, and 60% in the soil region within 10 cm from each plant [9]. Mineral nutrient absorption by roots results in the formation of a nutritional gradient zone around each individual. When the nutritional gradient zones of neighboring plants overlap, nutrient concentration in the overlapped area remarkably decreases because of interactions between adjacent roots, resulting in reduced root absorption efficiency [10]. It has been demonstrated that root nutrient absorption in the overlapped area varies under different plant spacing strategies.

Competing neighboring roots can deplete soil nutrient resources and thus inhibit root growth. With other things being equal, plants grow roots preferentially in areas free of other roots [11]. Plant roots do not interact solely through the depletion of soil resources but may also interact, causing profound consequences for plant growth and competition [12]. Schenk provided an excellent summary of direct interactions between roots, and distinguished between two classes of interaction [13]. First, roots may exude toxic substances that cause non-specific inhibitory effects on root development of neighboring plants. Second, genetically identical plants may use non-toxic chemical signals that specifically affect the roots of neighbors. Increasing numbers of studies have shown that plants produce more root mass when sharing rooting space with a genetically similar neighbor compared with plants growing alone [11,14]. This phenomenon has been described as a “tragedy of commons” [15]. However, Hess and Kroon hypothesized that root overproduction in the presence of other plants is consistent with the effects of available larger soil volumes on plants with competition than on those growing alone [12]. Earlier, McConnaughay and Loh showed that root mass is a function of the available rooting volume, independent of the available nutrients [16,17]. Furthermore, some of the observed root overproduction could not be immediately explained solely based on soil volume and nutrient availability [12]. The results observed with competing plants may be an overall effect of the existence of interplant root interactions within a larger space.

Therefore, a thorough understanding of the effects of overlapping roots on maize root growth and nitrogen absorption and utilization will help to explore the effects of plant spacing on maize yields. In recent years, it was proposed that increasing plant populations is a key factor for improvement of maize yields in China [7,18], but few reports are available on competition between above-ground and below-ground factors while increasing plant populations. In this study, the differences between root distribution, nutrient absorption and nitrogen utilization under different conditions of plant spacing and nitrogen availability were investigated to provide guidelines for optimizing plant densities in high yield maize production.

2. Materials and methods

2.1. Plant materials and experimental designs

The field experiment was carried out at the Experimental Farm of Shandong Agricultural University, Tai'an, China (36°18′ N, 117°13′ E) in 2007 and 2008. Only one maize hybrid, Denghai 661, was used because previous experiments confirmed increased grain yield of this cultivar at high plant densities [18].

A box-type soil column cultivation method was adopted. The soil column measuring 54 cm × 27 cm × 100 cm was made of a PVC plate with bottom sealing, and one side of the planter could be dismantled to facilitate removal of the soil and roots without damage to the study materials. The soil column was placed in an 80 cm deep square pit filled with soil both inside and outside the column and made soil compact by watering. The distance between soil columns was 11 cm, that is, the row width was 65 cm, and surrounded by the board rows (Fig. 1).

Two plants were grown in each soil column. Plants in one column were planted under normal spacing (NS, 27 cm), and the other under narrow spacing (CS, 6 cm). The columns were treated at two nitrogen levels, N0 (no N) and N1 (7.5 g N plant^{-1}), and for the N1 treatment, nitrogen fertilizer was applied by 20%, 50% and 30% at the seedling, male-tetrad and flowering stages, respectively. The experimental design included four treatments (N0 × NS, N0 × CS, N1 × NS and N1 × CS) and 30 separate soil columns were planted in each treatment.

Samples of the soil columns (top 40 cm) were mixed and screened with 20 mesh sieving. Then they were mixed with clean river sand in a ratio of 3:1 by volume of topsoil to sand.

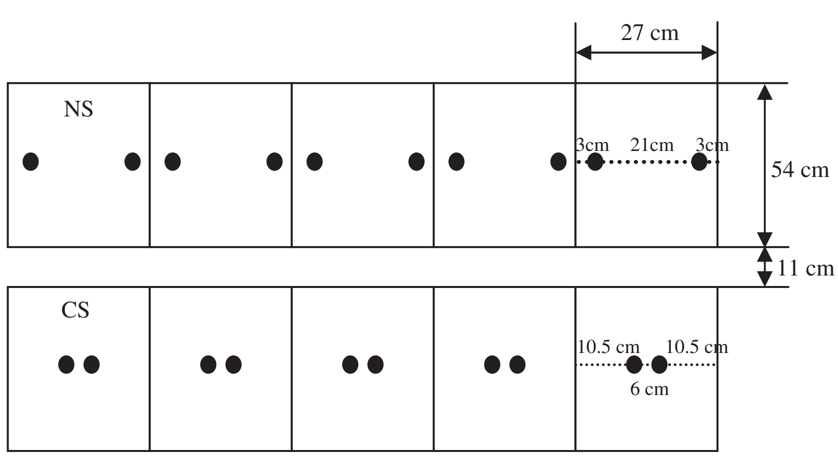

Fig. 1 – Field arrangement of different experiments.

The mixed soil nutrient contents were as follows: organic matter 7.1 g kg^{-1}, total nitrogen (N) 0.62 g kg^{-1}, mean available mineral phosphorous (P) 46 mg kg^{-1}, and exchangeable potassium (K) 59 mg kg^{-1}.

All treatments were fertilized with P and K according to nutrient demand, and each unit of experimental treatment was fertilized with 2.5 g of phosphate (P_2O_5) and 6.25 g of potash (K_2O), with both applied at the seedling stage. Required irrigation was also applied from the outlet of a pump by using plastic pipes.

2.2. *Measurements and calculation*

At the onset of pollination, three replicates of each treatment were sampled on the same day fortnightly. The above-ground plant parts were divided into leaves, grains and stems (remaining parts except for leaves and grains). Roots were separated from various layers of the soil profile, viz. 0–20, 20–40, 40–70 and >70 cm, and washed to remove all soil residues. Root layers were mixed well after removing impurities, and fine roots were selected and temporarily stored at 0 °C. 2,3,5-triphenyl tetrazolium chloride (TTC) reduction was applied to determine root reductive activity [19]; fresh root samples (0.5 g) were exposed to 0.4% TTC and 0.2 mol L^{-1} tricine-HCl buffer (pH 8.4), then placed in a darkroom at 37 °C for 6 h to induce reduction of TTC to triphenyl formazan (TTF), following the method described by Duncan and Widholm [19]. To quantify the amount of TTC reduced, we extracted the tissues with 95% ethanol at room temperature for 48 h, and then performed spectrophotometric analysis at 485 nm. The results were expressed as μg TTF g^{-1} root mass h^{-1}. At maturity, the remaining aboveground parts were completely harvested to calculate average dry matter weight per plant and weight distribution.

The remaining roots and above-ground samples were fixed at 105 °C for 30 min. Samples were subsequently baked at 75 °C until a constant weight was reached and recorded. The dried samples were smashed and steamed with H_2SO_4–H_2O_2. Nitrogen content was measured using semi-micro-kjeldahl determination [20].

Nitrogen parameters were calculated following the method of Moll et al. [21]:

Nitrogen accumulation (g $plant^{-1}$) = plant nitrogen content (%) × biomass (g $plant^{-1}$)
N use efficiency in grain (NUEg) = grain yield / total plant nitrogen accumulation
N use efficiency per plant (NUEbiomass) = biomass / total plant nitrogen accumulation
N harvest index (NHI) = grain nitrogen content / total plant nitrogen accumulation
N partial factor productivity in grain (PFP_N) = grain yield / total plant nitrogen applied
Transfer volume = plant vegetative nitrogen content at flowering–plant vegetative nitrogen content at maturity
Transfer rate = transfer volume/plant vegetative nitrogen content at flowering.

2.3. *Statistical analysis*

Data were statistically evaluated by one-way analysis of variance (ANOVA) with the program Data Processing System [22]. Duncan's multiple range test was carried out to determine if significant ($P < 0.05$) differences occurred between treatments.

3. Results

3.1. *Dry matter accumulation*

Significant effects of plant spacing and nitrogen on dry matter accumulation ($P < 0.01$) were detected in each plant part (stem and sheath-SS, leaves-L, bract leaves-BL, cob-C and grain-G). However, no significant interaction was found between plant spacing and nitrogen. Compared with NS, under CS dry matter accumulation of SS, L, BL, C and G decreased respectively by

Table 1 – Effects of plant spacing and nitrogen treatments on dry matter accumulation in above ground organs (g $plant^{-1}$).

Year	Treatment		SS	L	BL	C	G	Total
2007	N0	NS	84.6	42.6	24.2	42.9	226.8	421.1
		CS	68.1	38.9	22.0	36.0	212.0	377.0
	N1	NS	108.6	51.7	28.8	47.0	251.7	487.8
		CS	93.6	46.7	26.0	42.3	238.8	447.4
2008	N0	NS	84.2	43.8	24.7	41.3	231.5	425.5
		CS	71.0	41.5	21.9	37.4	217.3	389.1
	N1	NS	108.8	51.4	30.4	46.0	256.4	493.0
		CS	90.6	49.0	27.1	42.6	250.2	459.5
Source	*df*	SS	L	BL	C	G	Source	*df*
S	1	2472.52**	112.71**	75.46**	222.86**	1446.80**	S	1
N	1	5494.69**	637.08**	234.93**	256.47**	7495.66**	N	1
S × N	1	7.20	1.12	0.81	4.44	58.64	S × N	1
Error	36	68.13	13.72	8.83	19.88	185.13	Error	36

NS: normal spacing; CS: narrow spacing; S: spacing; N: nitrogen; SS: stem and sheath; L: leaf; BL: bract leaves; C: cob; G: grain. The sample size was 10.
** $P < 0.01$.

Table 2 – Nitrogen accumulation and utilization under different plant spacing treatments.

Year	Treatment		Grain (g plant^{-1})	Shoot (g plant^{-1})	NUEg	NHI	NUE biomass	PFP_N
2007	N1	NS	3.51 a	5.41 a	46.51 d	0.65 c	90.13 d	33.56 a
		CS	3.24 b	4.81 b	49.57 c	0.68 b	93.06 c	31.84 a
	N0	NS	2.99 c	4.35 c	52.20 b	0.69 b	96.79 b	–
		CS	2.64 d	3.62 d	58.55 a	0.73 a	104.18 a	–
2008	N1	NS	3.57 a	5.48 a	46.82 d	0.68 a	90.00 d	34.19 a
		CS	3.40 b	4.98 b	50.26 c	0.67 a	92.31 c	33.36 a
	N0	NS	3.05 c	4.42 c	52.47 b	0.69 a	96.23 b	–
		CS	2.70 d	3.73 d	58.22 a	0.72 a	104.14 a	–

Values in each column followed by a different letter are significantly different at $P = 0.05$ ($n = 5$). The sample size was 10.

16.3%, 7.1%, 10.2%, 10.7% and 5.0%, and the average decrease in aboveground dry weight was 8.4%. Further multiple comparisons among all treatments showed that with and without N application, CS did not significantly reduce grain yield, but reduced biomass by 7.5% for N0 and 9.5% for N1 (Table 1).

3.2. *Nitrogen accumulation and utilization*

Significant differences were detected for grain yield and aboveground nitrogen accumulation in vegetative organs between different nitrogen and plant spacing treatments ($P < 0.05$) (Table 2). Compared with NS, grain yield and aboveground nitrogen accumulation of CS were decreased by 8.6% and 12.8%, respectively. Nitrogen use efficiency for grain, harvest index and nitrogen production efficiency in plant dry matter were significantly higher under CS, with increases of 8.9%, 4.8% and 5.0%, respectively ($P < 0.05$). Compared with NS, the N partial factor productivity (PFP) in grain of CS decreased by 3.76%, but the difference was not significant statistically.

3.3. *Nitrogen absorption and translocation*

Compared with NS, SS nitrogen accumulation at silking and maturity were significantly lower under CS ($P < 0.05$). R nitrogen accumulation was significantly lower for N1 at the maturity stage ($P < 0.05$), and leaf nitrogen accumulation in N0 significantly decreased ($P < 0.05$) under CS. Compared to NS, the total nitrogen accumulation of R, L and SS in CS treatment were significantly lower ($P < 0.05$), with 12.8% and 20.9% decreases at the silking and maturity stages, respectively. However, the nitrogen translocation rates of R, L and SS in CS increased by 23.9% (Table 3).

3.4. *Temporal and spatial distribution of dry root weight*

Compared with NS, dry root weight of CS was lower in the 0–20 cm root layer at both nitrogen levels, and dry root weights in the 20–40 cm and 40–70 cm layers were also slightly reduced at late grain filling. However, dry root weight at 70–100 cm for the closely spaced plants remained fairly constant during the entire period. Closely spaced plants showed a significant decrease in dry root matter in the 0–20 cm layer; and the ratio of dry root weight/biomass and total dry root weight also showed obvious declines (Fig. 2).

N application resulted in a change in dry root weight from each soil layer throughout plant development (to maturity) and exhibited a single-peak curve at specific days post pollination (Fig. 2). Dry root weight in the 0–20 cm soil layer peaked at 14 d after pollination, and at 28 d for soils 20–40 cm and below. In the N0 treatment, dry root weight in the 0–20 cm layer peaked 14 d after pollination, but below 20 cm the dry root weight was reduced. Compared with N1, the N0 treatment showed a significant ($P < 0.05$) decrease in dry root weight at 0–20 cm soil depth, but there was a significant ($P < 0.05$) increase in the 70–100 cm layer. Changes in dry root weight in the 20–40 cm and 40–70 cm soil layers were not significantly different; however, the deep root ratio of N0 was significantly higher than that of N1.

3.5. *Spatial and temporal distribution of root reductive activity*

Root reductive activity is a comprehensive index that reflects root absorption function [13]. After pollination, root reductive activity in each soil layer changed as the plants matured

Table 3 – Nitrogen accumulation and translocation in roots, leaves, stems and sheaths under different plant spacing treatments.

Treatment		N accumulation (g plant^{-1})						Translocation rate		
		Silking			Maturity					
		R	L	SS	R	L	SS	R	L	SS
N1	NS	0.41 a	1.28 a	1.00 a	0.45 a	0.67 a	0.90 a	−0.09 b	0.48 a	0.09 c
	CS	0.38 a	1.27 a	0.79 b	0.34 b	0.62 a	0.70 b	0.09 a	0.51 a	0.11 c
N0	NS	0.28 b	0.91 b	0.81 b	0.25 c	0.55 b	0.54 c	0.10 a	0.39 b	0.33 b
	CS	0.24 b	0.83 b	0.58 c	0.21 c	0.49 c	0.30 d	0.13 a	0.42 b	0.48 a

Values in each column followed by a different letter are significantly different at $P = 0.05$. R: root; L: leaf; SS: stem and sheath. The data are average values from 2007 to 2008 experiments.

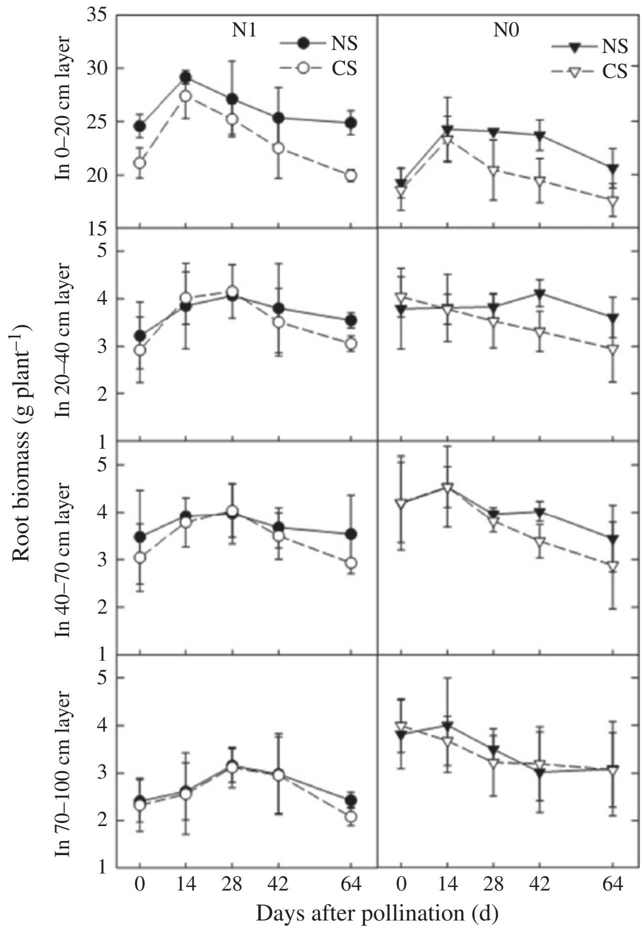

Fig. 2 – Dynamics of dry root weight in each soil layer with different plant spacing treatments.

(Fig. 3), exhibiting single-peak increases before decreasing. Under N1, root reductive activities underwent significant increases in the 0–20 cm and 20–40 cm soil layers, with peaks exhibiting prolonged durations. Root reductive activity in the 70–100 cm layer under N0 showed a steady decrease compared with N1. Under both nitrogen levels, root reductive activity decreased in each layer of closely spaced plants, and the greatest difference between treatments was observed during the grain-filling stage. At late grain filling, differences were not as evident.

4. Discussion

The effects of different plant spacing treatments on maize grain yield are influenced by interactions between aboveground and belowground resource competitions. Compared with competition for light aboveground, nutrient competition in roots includes more than 20 nutrient elements, which have substantial differences in molecular weight, soil oxidation state and mobility, and there are more significant effects of nutrient competition in roots on the growth of plant [8].

Narrow spacing is chosen most often to increase photosynthetic capacity by increasing the interception of available solar radiation, resulting in improved maize yield [6]. However, some studies have demonstrated that an increase in solar radiation does not increase but decrease maize production [23,24]. In this study, excluding interference due to aboveground competition for light, narrow spaced plants significantly decreased aboveground dry matter accumulation and grain yield by 8.4% and 5.0%, respectively.

Aboveground dry weight and grain production are closely related to nitrogen accumulation, translocation and utilization. Above-ground nitrogen accumulation in the narrow plant spacing treatment was decreased by an average 12.8%. However, compared with the normal spacing treatment, nitrogen translocation in roots, leaves and stem-sheaths significantly increased under narrow spacing following pollination, with increases in nitrogen harvest index and utilization being also observed. In other studies lower nitrogen accumulation treatment exhibited higher translocation rates and nitrogen utilization [25,26], and partially alleviated nitrogen shortage in yield.

Nitrogen uptake relies mainly on root biomass, root spatial distribution and per unit root nitrogen uptake rate [27]. In addition, nitrogen uptake by neighboring plants can limit nitrogen accumulation [8]. Narrow spacing significantly increased nutrient absorption in areas of adjacent overlapping

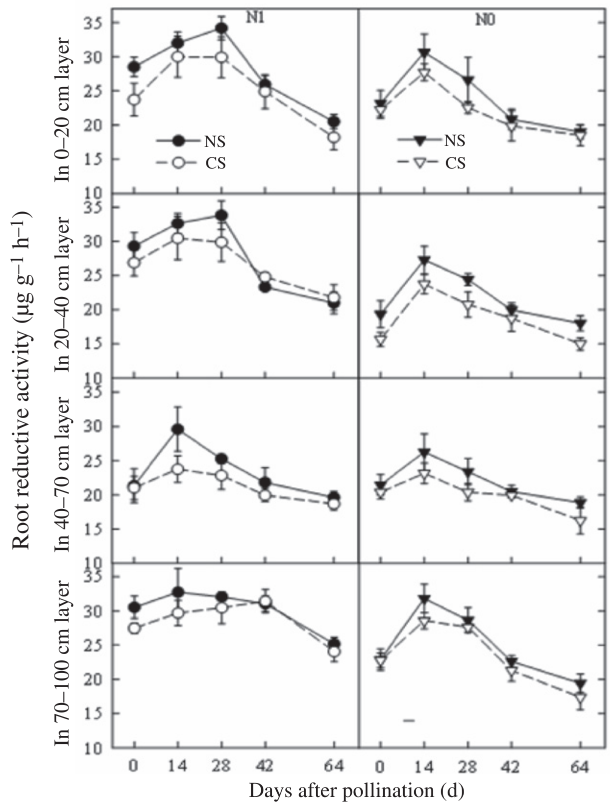

Fig. 3 – Dynamics of root reductive activity in each soil layer for different plant spacing treatments.

plants, especially when neighboring plants exhibited similar root architecture. However nutrient concentration in the overlapped areas markedly declined, decreasing nutrient uptake. Sharratt et al. and Barbieri et al. both suggested that uniform plant distributions are conducive to water and nitrogen uptake [3,28]. Because of root plasticity, lower nutrient concentrations in nutritional absorption of overlapped areas may limit the horizontal distribution of root systems [29]. In the present study, dry root weight in the 0–20 cm soil layer under narrow spacing was significantly decreased, and root reductive activity in all soil layers was clearly lower during the active grain-filling stage relative to normal spacing. Root size plays a leading role in nitrogen uptake, and roots in the upper soil layer have advantages in nutrient uptake [18]; however, reductions in root biomass, percentage of root in shallow soil layer and root reductive activity all circumvent nitrogen uptake.

5. Conclusions

Dry root weights of narrow spaced plants were significantly lower in the shallow soil layer, and root reductive activity in each soil layer was markedly reduced, along with lower root biomass and plant nitrogen uptake. Narrow spacing led to higher nitrogen use efficiency in grain, harvest index and dry matter production capacity. The nitrogen translocation rates of roots, leaves and stem-sheaths were higher during grain formation. However, these increases did not compensate for the impact of decreased nitrogen accumulation on production. Thus grain yield increases in summer maize could be achieved with modest increases in plant density.

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